

PALEOALLIUM BILLGENSEL GEN. ET SP. NOV.: FOSSIL MONOCOT REMAINS FROM THE LATEST EARLY EOCENE REPUBLIC FLORA, NORTHEASTERN WASHINGTON STATE, USA

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Premise of research. Fossil inflorescences (scapes) producing both pedicellate flowers and sessile bulbils, both covered partially by a persistent spathe, are described from the latest early Eocene Republic flora of north-central Washington. They are associated with an individual specimen of a single bulb with attached roots, and two small flower buds that appear to represent the same plant. The morphology of these fossils closely resembles that of certain bulb-forming monocots, such as some species of the onion genus *Allium* and other members of Amaryllidaceae.

Methodology. Compression-impression fossils preserved in a lacustrine shale were uncovered from the rock matrix to reveal morphological details and were photographed with LM. Specimens were compared morphologically with extant material of related plants, and resulting images were processed minimally with Adobe Photoshop.

Pivotal results. Specimens demonstrate an organography that is quite similar to that of modern onions and related forms. To our knowledge, this is the first description of plants showing a combination of bulbils and florets (representing asexual and sexual reproduction) among Paleogene plants. It also represents one of few reports among the fossil record of monocot plants similar to members of Amaryllidaceae.

Conclusions. Scapes bearing flowers and bulbils within a spathe similar to those of some modern Amaryllidaceae, associated flower buds, and a root-producing bulb indicate the presence of a distinctive monocot plant in the Republic flora of the latest early Eocene Okanogan Highlands, northeastern Washington. Along with other Republic plants with distinctive morphological features indicative of temperate floras (leaf dimorphism, possible hybridization), these fossils suggest that bulbil- and flower-bearing monocots with a combined asexual and sexual reproductive strategy were already well established among plants of Paleogene.

Keywords: Amaryllidaceae, asexual reproduction, bulb, bulbil, fluvial-lacustrine shale, monocot fossil record, Okanogan Highlands.

Introduction

Many plants reproduce asexually, and one means is by the production of small plantlets, or bulbils that can develop adventitiously on leaf or stem tissue or within an inflorescence. Bulbils afford the opportunity for a plant to establish propagules without depending on the sexual phase of the life cycle and to extend the distribution of clonal plants with a well-adapted genome. This capability is shared across the land plants—from the gemmae of mosses, liverworts, and lycopsids (Bower 1889–1891) to ferns with corm-borne (Boston fern *Nephrolepis* Schott) or leaf-borne plantlets (spleenwort *Asplenium bulbiferum* G. Forst., A.

daucifolium Lam.; Green Pages 2017)—and are known even in plants of the lower Devonian Rhynie chert (Kearney et al. 2016).

Among angiosperms, notable examples of plantlets are produced by such dicot families as Crassulaceae (*Kalanchoë* Adans.; Garcès et al. 2007), Gesneriaceae (*Titanotrichum oldhamii* (Hemsl.) Solereder; Wang and Cronk 2003; Wang et al. 2004), Polygonaceae (*Polygonum viviparum* L. [now *Persicaria vivipara* (L.) Ronse Decr.]; Diggle et al. 1998), and Saxifragaceae (Strawberry Begonia, *Saxifraga stolonifera* Curtis; *Tolmiea menziesii* (Pursh) Torr. & A. Gray; Yarbough 1936). In monocots, plantlets occur in Agavaceae (*Agave* L.; Arizaga and Ezcurra 1995), Bromeliaceae, Araceae (duckweed, *Lemna* L.; Grace 1993), Poaceae (Youngner 1960; Steiner et al. 2012), and the bulb-producing families Liliaceae (spider plant *Clorophytum* Ker Gael, *Lilium* L., *Gagea* Salisb.; Arber 1925; Schnittler et al. 2009) and Amaryllidaceae (*Amaryllis* L., onions and garlic, *Allium* L.; Ceplitis 2001).

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Whereas many of these plantlets are essentially miniature versions of the mature plants, other asexual propagules are formed from small, less defined structures called bulbils. The most notable of these occur in the families Poaceae (Youngner 1960; Steiner et al. 2012), Liliaceae (*Gagea*; Arber 1925; Schnittler et al. 2009), Dioscoraceae (Walick et al. 2010), and Amaryllidaceae, including members of the genus *Allium* L. such as *Allium sativum* L. (garlic), *Allium ampeloprasum* L. (Leek), *Allium canadense* L., *Allium geyeri* var. *tenerum* M. E. Jones, *Allium vineale* L., and *Allium cepa* var. *proliferum* (Moench) Schrad. ex Willd. (Egyptian walking onion, or tree onion; Arber 1925; Bengtsson and Ceplitis 2000; Ceplitis 2001; Wheeler 2011; Wheeler et al. 2013). In these plants, the inflorescence may be made up of completely flowers, only bulbils, or (in some cases) both. Flowers may contain viable pollen, seeds, and/or both or, on occasion, are completely sterile. Documentation of bulbil- and flower-producing plants has, to our knowledge, not been recorded among flowering plants in the fossil record.

In addition to the significance of bulbils and flowers denoting a complex reproductive strategy is the presence of an associated bulb covered with monocot-like leaf bases with parallel veins and producing several roots, which we suggest belongs to the same plant. Whereas bulbs are commonly known to us because of their association with economically important food plants (e.g., onions) and horticultural varieties (e.g., lilies), they are quite limited in their taxonomic distribution to only a small number of monocot groups (Dahlgren and Clifford 1982). Whereas stems are modified commonly for storage as corms and underground rhizomes, the modification of leaves as part of an underground shoot system (i.e., a bulb) appears to be limited to a much smaller group of monocots.

In this study, we describe *Paleoallium billgenseli* gen. et sp. nov. from the latest early Eocene of Republic (Ferry Co.), Washington. On the basis of its morphological features, *Paleoallium* conforms to the structure of a monocot flower- and bulbil-forming plants. Within the same matrix we found one specimen of a bulb bearing roots and remnants of leaf bases and several small floral buds that we suggest may belong to the same plant. This study increases our knowledge of bulbil-/flower-forming monocots in the fossil record and demonstrates that both asexual/sexual reproductive strategies and their bulb-like storage organs were already well established among these plants by the latest early Eocene.

Material and Methods

Fossil were collected from exposures at Boot Hill, Republic (Ferry Co.), Washington. Boot Hill occurs within the town of Republic and is the site where public collecting of fossils is mediated by the Stonerose Interpretive Center and Eocene Fossil Site (Pigg et al. 2011; Stonerose Interpretive Center 2017; stonerosefossil.org, accessed January 2017). This locality and several other nearby sites occur within the Republic Basin and are positioned stratigraphically in the Tom Thumb Member of the Klondike Mountain Formation. The site was dated latest early Eocene at 49.42 ± 0.54 Ma by ^{40}Ar - ^{39}Ar dating by Wolfe et al. (2003) in an abstract (Greenwood et al. 2016). The Republic Basin, along with the Curlew and Toroda Creek Basins to the north, are interpreted as a series of lacustrine deposits (Green-

wood et al. 2016). Exquisitely preserved plant and insect remains as well as occasional bird, crayfish, and gastropods are known (Pigg et al. 2011). Rarely are plant remains found rooted or in situ: much of the delicate material, including that of this study, is fragmentary and probably floated out on the surfaces of lakes before deposition (M. L. DeVore, personal observation, 2016). One specimen from Republic in this study (fig. 1E) was illustrated in our guidebook under “Additional Flowers” (Pigg et al. 2011, p. 59). Initially perplexed by this material, we presented two abstracts at an early stage of our study (Bryan et al. 2011, 2013).

The Republic flora occurs at the southeasternmost part of a broader floristic region extending north and westward into British Columbia known as the Okanogan Highlands (Greenwood et al. 2016). Fossils similar to those of this study are known at two localities in British Columbia. One specimen collected from Thomas Ranch (near the town of Princeton, British Columbia) was illustrated by Dillhoff et al. (2013, pl. 3, fig. 9) as “unknown structure.” Similar specimens observed from the McAbee, British Columbia, flora (Greenwood et al. 2016) are not considered here.

Specimens were uncovered from the matrix with fine needles, cleaned gently with compressed air, and photographed under a Nikon SMZ-1500 stereomicroscope with an attached Nikon D90 digital camera with a macrolens using CameraPro digital software. Additional photos were taken with a Galaxy smart phone alone or through the phototube of an Olympus stereomicroscope or Olympus compound microscope. Digital images were processed minimally with Adobe Photoshop software.

Comparative extant fruit, seed, and vegetative material was studied from the Arizona State University Vascular Plant Herbarium and live specimens of *Allium cepa* var. *proliferum*, the Egyptian onion, from the garden of Janet C. Hartford (Republic, WA) and several additional members of Amaryllidaceae from the garden at Phoenix College and Recycled City (Phoenix, AZ). Specimens with SR numbers are housed in the collections of the Stonerose Interpretive Center, Republic; those with UWBM or PB numbers are from the Burke Museum of Natural History and Culture, University of Washington, Seattle.

Systematics

Order—Asparagales Link

Family—Amaryllidaceae J.St.-Hil. *nom. cons.*

Genus—*Paleoallium* Pigg, Bryan & DeVore *gen. nov.*

Type—*Paleoallium billgenseli* Pigg, Bryan & DeVore *sp. nov.*

Species—*Paleoallium billgenseli* Pigg, Bryan & DeVore *sp. nov.*

Generic diagnosis. Scapes bearing apically small sessile bulbils and pedicellate, campanulate flowers, both partially covered by broad spathes.

Holotype. SR 10-35-06; figures 1A, 3F; finder: Daisy Valadez.

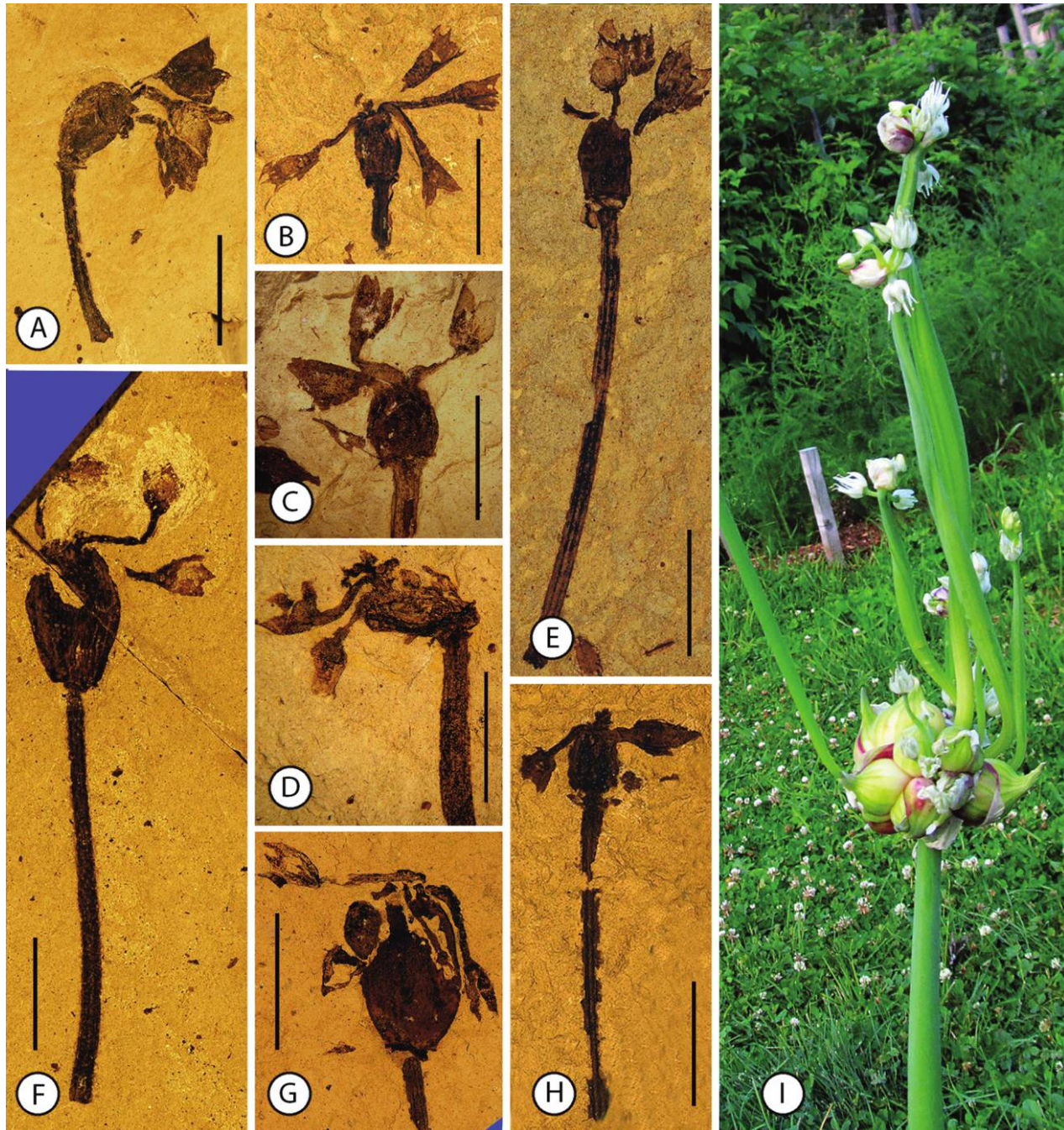


Fig. 1 A–H, *Paleoallium billgenseli*. I, Extant *Allium cepa* var. *proliferum*. Variation in general overview of fossil specimens using extant Egyptian walking onion as a model. A, Holotype showing scape, spathe, small bulbils at apex, and several flowers; SR10-35-06. B, SR 10-07-06. Note somewhat flattened flowers; photograph inverted horizontally. C, SR 13-004-012. D, SR 11-31-07. E, SR 08-36-03. F, SR 08-41-43. G, SR 11-01-02A; inverted horizontally. H, SR 08-40-10; inverted horizontally. I, *Allium cepa* var. *proliferum*. Habit shot in garden. Scale bars = 1 cm.

Species diagnosis. Spathes 5–12 mm long \times 3–8 mm wide, grown out from the scape 18–40 mm long \times 0.8–1.2 mm wide, elliptical-ovate to obovate, striate with parallel veins; bulbils sessile, 1 mm long \times 0.2 mm wide produced apically; flowers campanulate, pedicellate, pedicels 2–8 mm long \times 0.5–1.0 mm wide, corolla lobed with 3–4 lobes obvious, 4–8 mm long \times 3–6 mm wide.

Type locality. Boot Hill, Republic (Ferry Co.), Washington.
Age. Latest early Eocene or 49.42 ± 0.54 Ma by ^{40}Ar – ^{39}Ar dating (Wolfe et al. 2003; see Greenwood et al. 2016).

Stratigraphy. Tom Thumb Member, Klondike Mountain Formation.

Paratypes. Finders' names follow. Figured specimens: SR 00-05-23 AB, figures 2A, 2B, 3B, Brian P. Ochs; SR 08-36-03,

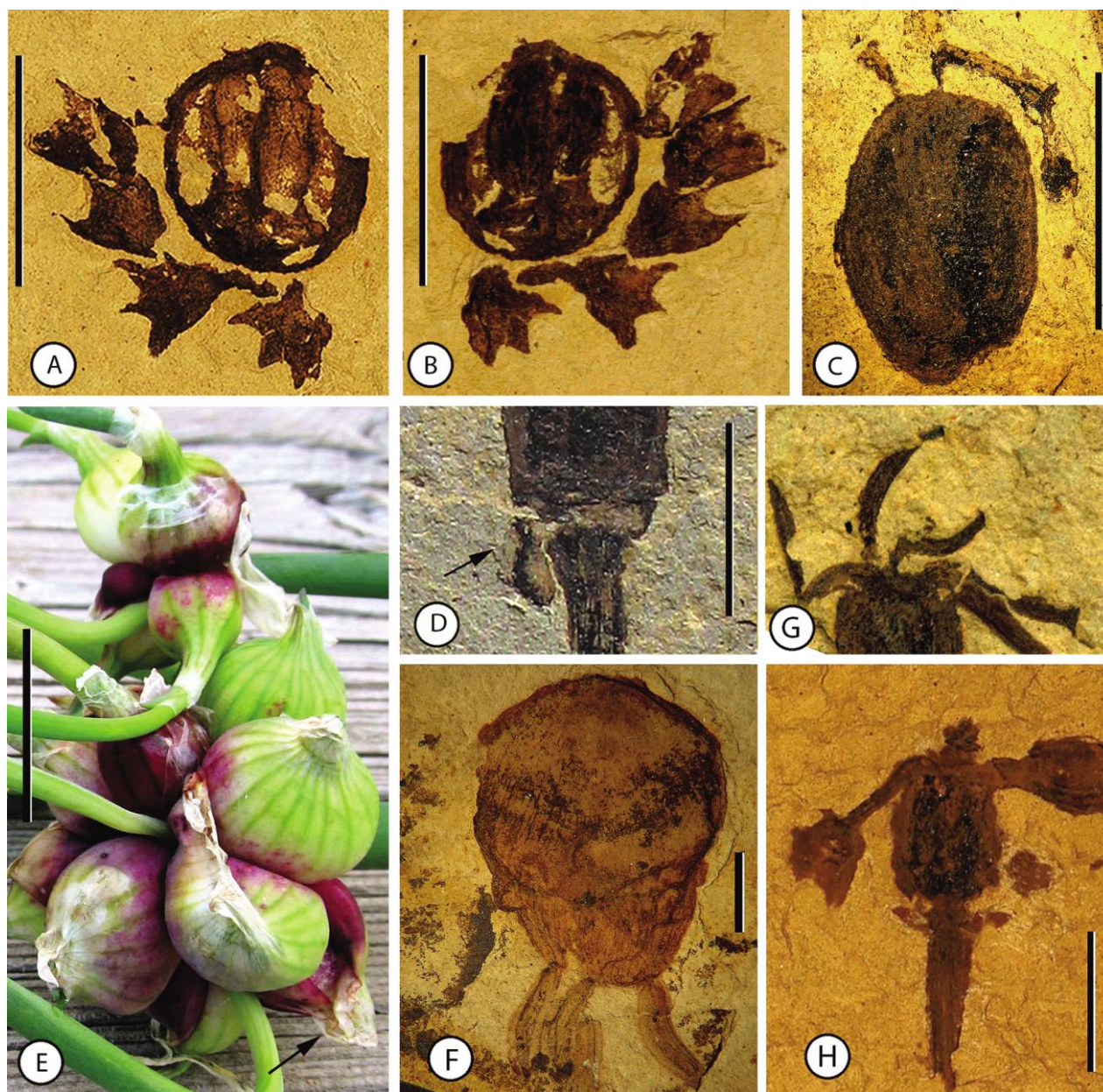


Fig. 2 A–D, *Paleoallium billgenseli*. E, *Allium cepa* var. *proliferum*. A, B, Part-counterpart specimen of a larger bulbil, surrounded by four flowers; SR 00-05-23 AB. C, Spathe with two flowers; SR 11-31-06 A. D, Base of spathe showing shred of onion skin (= protective leaf sensu Mann 1960; arrow); SR 08-36-03. E, Extant *Allium cepa* var. *proliferum* showing cluster of bulb and foliage leaves. F, Bulb with attached leaf bases and four attached roots; SR 13-004-010 A. G, Six flower pedicels bearing young or abortive flowers; 11-25-04. H, Spathe with subtending bracts; SR 08-04-10. Scale bars = 1 cm (A–C, F), 0.5 cm (D, G).

figures 1E, 2D, Stonerose Staff 1999; SR 08-40-10, figure 1H, Jr. Trejo; SR 08-41-43, figure 1F Spencer Burris; SR 10-07-06, figures 1B, 3E, 4A, 4B, Staff 2010; SR 11-01-02 AB, figure 1G, Shannon Miller; SR 11-25-04, figure 2G, Kadin Reimers; SR 11-31-06 AB, figure 2C, Thomas Dillhoff; SR 11-31-07, figures 1D, 3D, 4D, 4E, Matthew Davidson; SR 12-002-031, figure 3G, Aspen Covert; SR 13-004-012, figures 1C, 2G, 3C, 4C, Emily Batchelder. Nonfigured specimens: SR 08-38-01, Molly and Dylan Miyamoto; SR 10-51-01, Staff 2006; SR 10-51-02 AB, Staff 1997; SR 10-51-03 AB, Scott Herrick.

Etymology. The generic name, *Paleoallium*, refers to the remarkable similarity of the fossils to the modern onion/garlic genus *Allium*. The species epithet, *billgenseli*, honors the late botanist and horticulturalist William H. Gensel (Durham, NC) for his contributions to the plant sciences and for recognizing the similarities of the fossils to modern *Allium* and other bulb-forming monocots.

Previous illustration. Pigg et al. 2011, SR 08-36-03, page 51, “Additional flowers,” and Dillhoff et al. 2013, plate 3, figure 9, “Unknown structure”; UWUM locality B3263, UWBM 54633.

Results

Paleoallium billgenseli gen. et sp. nov. is based on 16 specimens, five of which are made up of part/counterparts and 11 of which are individuals (figs. 1A–1H, 2C, 2D, 2G, 2H, 3B–3G, 4A–4E). In their general organography, they consist of

an elongate inflorescence axis or scape with a distally attached elliptical-obovoid spathe surrounding 2–6 pedicillate flowers and around three small ovoid bulbils (fig. 1A). In some specimens, the spathe is subtended by a pair of bracts (fig. 2H).

In 13 of the 16 specimens where the scape was well enough preserved to measure, the range was 18–40 mm long \times 0.8–1.2 mm

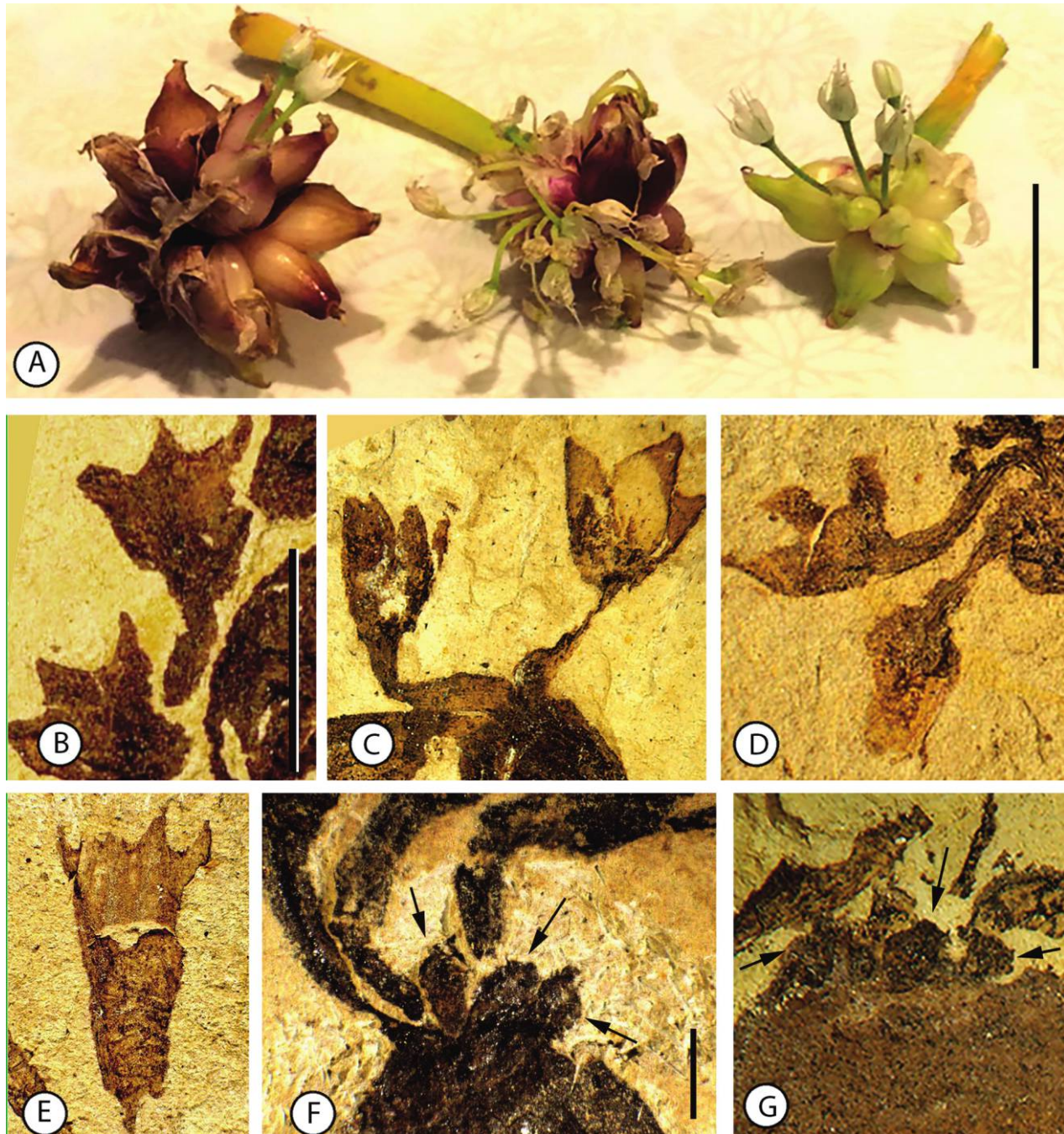


Fig. 3 A, *Allium cepa* var. *proliferum*. B–G, *Paleoallium billgenseli*. A, Three extant onion scapes showing different combinations of flowers and bulbils. One specimen has numerous bulbils (left), and two have a combination of bulbils and flower buds (center, right). Note difference in flowers and bulbils (right). B, Detail of flower; SR 00-05-23 AB. C, Detail of two flowers beside spathe; SR 13-004-012. D, Detail of two flowers; SR 11-31-07. E, Detail of individual flower; SR 10-07-06. F, Specimen showing both attached flowers and bulbils (arrows); SR 10-35-06. G, Specimen showing three attached bulbils; SR 12-002-031. Scale bars = 2 cm (A), 5 mm (B–E), 1 mm (G).

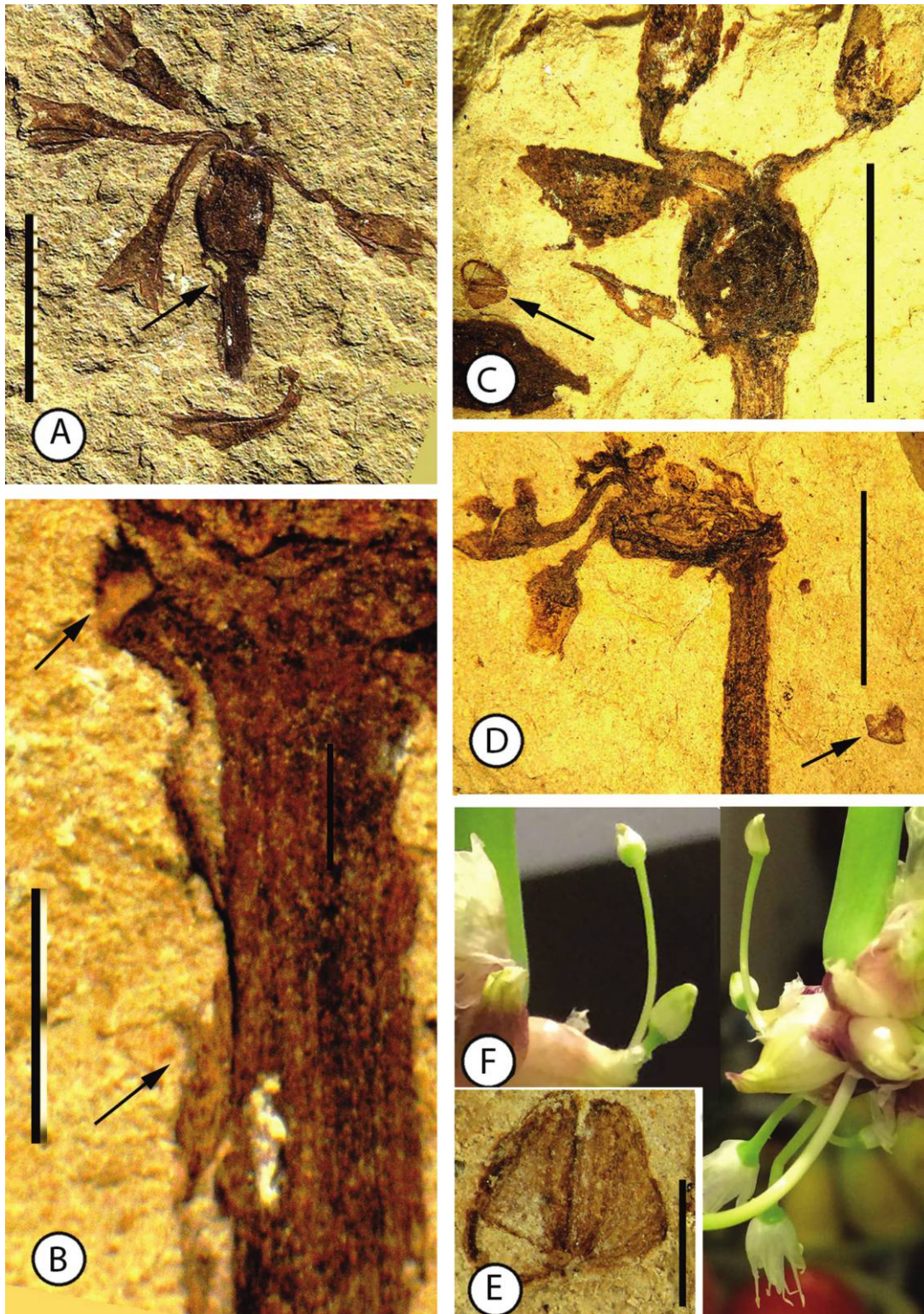


Fig. 4 A–E, *Paleoallium billgenseli*. F, *Allium cepa* var. *proliferum*. A, Specimen producing four flowers apically and two small flowers produced alongside scape (arrow); SR 10-07-06. B, Higher magnification of A; SR 10-07-06. C, Specimen showing position of associated floral bud (arrow); SR 13-004-012. D, Specimen showing position of associated floral bud (arrow); SR 11-31-07. E, Detail of C, showing associated floral bud; SR 13-004-012. F, Extant *Allium cepa* var. *proliferum*, showing morphology of attached floral buds. Scale bars = 1 cm (A, C, D), 1 mm (E), 2 mm (B).

wide (fig. 1A–1H). The scapes are torn or irregular at their basalmost areas, with no indication of an attachment to a stem or rooting structure. Surfaces of the scapes have longitudinal striations (fig. 1A, 1B, 1F), as is typical in those of some extant onions (fig. 2E). Vascular strands that dichotomize several times can be traced across the scape's surface (2F). Small wisps of irregular shreds of thin leafy tissue often subtend the spathe; these are interpreted as remnants of the outmost onion skin or protective leaf sensu Mann (1960), typical of onions (fig. 2D, 2E).

Atop the scape is a spathe 5–12 mm long \times 3–8 mm wide. Of the 12 specimens with preservation good enough to measure, six of the spathes are elliptical (length:width ratio of 1.25–1.3; fig. 1A, 1E, 1H), four are elliptical-elongate (length:width ratio of 2:1), and two are slightly obovate (fig. 1F, 1G). Three specimens are slightly asymmetric (fig. 2C), and two are tilted at right angles with respect to their subtending scape (fig. 1A, 1D).

The scapes bear two different types of structures toward their apex: longitudinally elongate bulbils of varying size (fig. 3F, 3G) and more conspicuous pedicellate flowers (figs. 1A–1H, 2C, 2H, 3B–3E, 4A, 4C, 4D). Bulbils are 1 mm long \times 0.2 mm wide and are produced as sessile structures (fig. 3F, 3G). Up to three have been distinguished within a single specimen: in some cases, additional bulbils may have been partly exposed and damaged during preparation, while others may be hidden deeper within the rock matrix. One larger, rounded structure is interpreted as a larger bulbil that has been separated from its scape (fig. 2A, 2B).

In contrast to the sessile bulbils, flowers are pedicellate with two to six borne helically near the apex of the scape. Flowers have pedicels up to 2–8 mm long \times 0.5–1.0 mm wide, with a campanulate corolla 4–8 mm long \times 3–6 mm wide with 3–4 lobes (fig. 3B–3E). Several specimens produce flowers with shorter, presumably unexpended pedicels (fig. 1G), and some specimens have elongate pedicels but either very small flower buds or perhaps aborted flowers (figs. 1G, 2G). Whereas most of the specimens produce bulbils and flowers from the apical region, one specimen has two very small flowers borne along the main leaf and presumably attached at a more proximal region (fig. 4A, 4B).

Two additional types of structures are associated with the scapes. Along with two specimens, two small structures with a triangular apex that resemble small buds of modern onions are found (fig. 4C–4F). They are 1.6 mm high \times 1.6 mm across at the greatest width. The second type of structure is a single specimen of a bulb (fig. 2F). It is obovate, 9 mm high, 5 mm across at the base, and 7 mm at the apex (SR 13-004-010 AB; Karl Volkman, finder). The surface of the bulb is covered by overlapping leaf bases, each with up to five parallel veins. Several roots are attached to the base of the bulb. They are thin and elongate, up to 4 mm long \times 0.5 mm across.

Discussion

Establishment of New Taxon

Paleoallium billgenseli is established as a new taxon on the basis of a suite of morphological characters that greatly resemble those of extant onions and other bulb-forming monocots.

Like modern onions, *Paleoallium* produces a scape that produces sessile bulbils and pedicellate, flowers with a campanulate corolla that are protected by a spathe. The general morphology of these structures is quite similar to those of several modern species of *Allium* that produce both bulbils and flowers (e.g., *Allium sativum*, *Allium canadense*, *Allium ampeloprasum*, *Allium geyeri* var. *tenerum*, *Allium vineale* L., among others). For our model, we illustrate *Allium cepa* var. *proliferum*, known as the Egyptian walking onion (figs. 1I, 2E, 3A, 4F); however, we do not imply a direct relationship to this or another particular modern species.

Despite our efforts to uncover internal floral parts, we found no clear evidence of anthers, pollen, fruits, or seeds. It is unclear whether this is a result of limited preservation or if the florets were sterile. Female sterility has been documented as a component of breeding systems within Amaryllidaceae; therefore, the presence of sterile florets would not be surprising (Morales et al. 2013).

Associated with these specimens are two small structures that we interpret as flower buds. Although they are not in organic connection to scapes, their close proximity and distinct morphology are highly convincing. The one bulb specimen we have found is likewise very similar to modern bulbs, with the presence of overlapping, leaf bases with parallel veins, the obovate structure, and the mode of attachment of the roots. We include these structures in the description above but—because of the lack of organic connections to scape—exclude them from the formal diagnosis.

The original relationship of the organs in specimens of *Paleoallium* to one another is not always clear. We recognize this is the case because of their depositional setting. Because partially preserved fragments that were possibly deposited into a lacustrine environment where they became floating fragments, their original position is distorted, in contrast to whole leaves and other organs deposited in still waters. They are not rooted nor found in situ. Nevertheless, their morphology is consistent with that of a bulb-forming monocot.

Fossil Record of Monocots

The Paleogene and Neogene monocot fossil records have been reviewed by several authors (Daghlian 1974; Stockey 2006; Pole 2007; Smith 2013; Iles et al. 2015; Kellogg 2015; see also Conran et al. 2009, 2014; Pigg and DeVore 2016). Basal monocots, particularly of the orders Arales and Alismatales, are among the best represented, probably in part because of their frequently aquatic habitat (Stockey 2006; Smith 2013). Poales—including grasses, sedges, and rushes—are also known from both megafossils, pollen and phytoliths (Kellogg 2015), and palms from their anatomically preserved stems (Daghlian 1974; Stockey 2006).

In contrast, members of Asparagales and Liliales are less common. A permineralized stem, *Soledera* Erwin and Stockey, is known from the middle Eocene Princeton chert, British Columbia (Erwin and Stockey 1991; Pigg and DeVore 2016). Permineralized stems of *Protoyucca* Tidwell and Parker have been described from the Miocene of Nevada (Tidwell and Parker 1990), and leaves of *Smilax* L. are known from the middle Miocene Emerald Creek and Clarkia sites of Idaho (Rember 2007). Other occurrences have been reported from the Miocene of New Zealand (Pole 2007), including Orchidaceae (Conran et al.

2009) and Alstroemeriaceae (Conran et al. 2014). To our knowledge, this is the first report of *Allium*-like plants in the fossil record and one of the few reports explicitly describing vegetative reproduction (see Pfefferkorn 1973; Kearney et al. 2016).

Functional Significance of Mixed Bulbil and Floret Production in Paleoallium

The Okanogan Highlands floras, including Republic, are significant to the diversification of families that are important members of the Northern Hemisphere temperate flora today (Wolfe and Wehr 1987; Wehr and Hopkins 1994). Families such as Rosaceae (e.g., DeVore et al. 2004; DeVore and Pigg 2007; Benedict et al. 2011), Betulaceae (Crane and Stockey 1986; Pigg et al. 2003), Fagaceae (Manchester and Dillhoff 2004), Ulmaceae (Denk and Dillhoff 2005), and temperate Sapindaceae (e.g., *Acer*: Wolfe and Tanai 1987; *Dipteronia*: McClain and Manchester 2001) have their earliest radiation in the fossil record of these floras. It is not surprising to find *Allium*-like plants at Republic because they are well distributed in many types of habitats throughout the Northern Hemisphere (Wheeler 2011; Wheeler et al. 2013).

In addition to an intriguing floristic composition that foreshadows the development of Northern Hemisphere deciduous forests, we have noted distinctive morphological aspects of certain Republic plants that appear to be indicative of various evolutionary mechanisms of temperate plants today. We have suggested the potential evolutionary value of these adaptations to plants diversifying in the upland latest early Eocene. For example, we documented heterophyllous leaf and long-shoot, short-shoot patterns similar to those related to dormancy mechanisms in extant *Cercidiphyllum* and in fossil forms known as *Zizyphoides* (DeVore and Pigg 2013). Additionally, we have shown evidence for possible hybridization within several families, including Rosaceae and Anacardiaceae, on the basis of distinctive leaf characters unique to hybrid leaves today (DeVore and Pigg 2016). Clearly, the life histories and evolutionary mechanisms we see in today's floras had to have ancestors with the preadaptations (if not the actual adaptations) needed for their ancestors to find niches within a deciduous forest.

In this same vein, we can consider the functional significance of bulb-like monocot plants that produce both bulbils and florets at Republic. There are two parts to this: first, the development of bulbs as specialized storage organs; and second, the value of producing both asexual, sessile bulbils in combination with, presumably, sexual florets.

Why Make a Bulb?

Although bulbs are well known to us from economically important plants such as the onions and ornamental flowering plants, they are surprisingly rare in their systematic distribution. Dahlgren and Clifford (1982) list bulbs as occurring only occasionally within the monocot orders Asparagales and Liliales, rarely in Hydrocharitales, and possibly in Zosteriales. One exception to the lack of dicot bulbs or pseudobulbs is the presence of such structures in Oxalidaceae (Oberlander et al. 2009).

Unlike typical dicot organography where stems would be the dominant structure, in bulb-forming plants it is the small apical stem meristem surrounded by modified storage and protective

leaves that functions vegetatively. These varied modified leaves—including the outermost protective leaves; the thick, modified storage leaves; and vegetative buds—make up the major vegetative structures of the plant. Axillary buds producing an additional order of vegetative structures reproductive axes (scapes) develop from within *Allium* bulbs (Mann 1960).

Holttum (1955) suggested the functioning of bulbs in part as a modification of a monocot's primarily sympodial growth system in stems that had lost the capability to produce a vascular cambium (Rees 1972). Each bulb contains a persistent meristem that is surrounded by modified leaves not only selected for storage of water and nutrients but also functioning to protect the meristem itself. Furthermore, the position of a storage organ within the soil could have placed the plant at a depth where fluctuations of temperatures could be buffered.

Why Produce a Combination of Bulbils and Flowers?

Recent research has implicated the relationship of bulbil formation to dormancy mechanisms and flux in hormonal concentration and with the KNOX gene family (Okubo 2000; Abraham-Juárez et al. 2010). This complex set of interactions includes integration of both the signals and the development of bulbils, bulbils, and floral development to become a mixed system. A stable mixed reproductive system would be an adaptation to an unpredictable, temporal variation in some suite of environmental factors, which sometimes favored sexual reproduction and at other times favored asexual reproduction (Ceplitis 2001).

It is certainly plausible that this type of variation would have been present at Republic and in the Okanogan Highlands as a whole during the latest early Eocene, especially given the amount of periodic disturbance by repeated episodes of volcanism, uplift, and rapid, associated earth surface processes occurring at the time (Greenwood et al. 2016). In particular, the relatively higher elevation of the Okanogan Highlands sites would provide an environment whereby plants adapted to lower elevations that were expanding into higher altitudes would contend with several difficulties, including suppression of insect pollinator activity by virtue of low temperature and possibly insufficient pollinator reward (Berry and Calvo 1989).

In addition to these challenges of growing at higher elevation, plants of the Republic flora also would be subject to environments of high flooding and transport. In this case, with some monocots, there has been a switch to more asexual reproduction at flooded sites. This situation occurs today among the graminoid species *Arundinella* Raddi. (Bo et al. 2006). Under those conditions, genotypes able to flourish and reproduce asexually would be constantly recruited to the less occupied higher-elevation sites (Bengtsson and Ceplitis 2000; Barsoum 2002). If *P. billgenseli* was pseudoviviparous in the sense that bulbils could obtain physiological support from the parent plant while establishing, this could ease the transition into a more restrictive set of ecological niches.

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