


AJB REVIEW

# Get the shovel: morphological and evolutionary complexities of belowground organs in geophytes

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Manuscript received 2 June 2020; revision accepted 4 January 2021.

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**Citation:** Tribble, C. M., J. Martínez-Gómez, C. C. Howard, J. Males, V. Sosa, E. B. Sessa, N. Cellinese, and C. D. Specht. 2020. Get the shovel: morphological and evolutionary complexities of belowground organs in geophytes. *American Journal of Botany* 108(3): 1–16.

doi:10.1002/ajb2.1623

Herbaceous plants collectively known as geophytes, which regrow from belowground buds, are distributed around the globe and throughout the land plant tree of life. The geophytic habit is an evolutionarily and ecologically important growth form in plants, permitting novel life history strategies, enabling the occupation of more seasonal climates, mediating interactions between plants and their water and nutrient resources, and influencing macroevolutionary patterns by enabling differential diversification and adaptation. These taxa are excellent study systems for understanding how convergence on a similar growth habit (i.e., geophytism) can occur via different morphological and developmental mechanisms. Despite the importance of belowground organs for characterizing whole-plant morphological diversity, the morphology and evolution of these organs have been vastly understudied with most research focusing on only a few crop systems. Here, we clarify the terminology commonly used (and sometimes misused) to describe geophytes and their underground organs and highlight key evolutionary patterns of the belowground morphology of geophytic plants. Additionally, we advocate for increasing resources for geophyte research and implementing standardized ontological definitions of geophytic organs to improve our understanding of the factors controlling, promoting, and maintaining geophyte diversity.

**KEY WORDS** bulb; corm; development; evolution; geophytes; morphology; rhizome; tuber; underground storage organ.

While the evolution of major innovations in plant habit has long been of interest to plant biologists, belowground traits characterizing the geophytic habit have only recently received greater attention in ecological and phylogenetic frameworks (Pausas et al., 2018; Ott et al., 2019; Herben and Klimešová, 2020; Howard et al., 2020). Fibrous roots are increasingly the focus of physiological and molecular genetic investigation due to their undeniable importance in nutrient and water uptake (Pec et al., 2019, among others). However, far less attention has been paid to the belowground structures of geophytes (defined below), such as bulbs, corms, tubers, and tuberous roots (Raunkiaer, 1934). To advance research on these fascinating structures, we offer a concise definition of the term geophyte,

review historical and recent work on the evolution and development of the belowground organs of geophytes, and describe several avenues for future research.

The defining quality of geophytic plants is that they resprout from buds located on belowground organs, typically following the loss of ephemeral aboveground parts. The term geophyte was coined by Raunkiaer (1934) as part of his innovative work classifying plant life forms based on the location of their perennating buds relative to the soil level. He defined geophytes as terrestrial plants that have resting, or renewal, buds that arise from belowground structures, or organs, such as bulbs. In his system, geophytes, along with hydrophytes (aquatic plants) and helophytes

(marsh plants), are part of a larger group termed cryptophytes. Since the introduction of these terms, inconsistency and confusion have surrounded the definition of geophyte and which plants should be considered geophytic. For example, some authors restrict the term geophyte to plants whose renewal growth emerges from underground storage organs (USOs), as opposed to other types of underground organs. This definition excludes plants with, for example, thin rhizomes, even if they have renewal buds at or below ground level (Pate and Dixon, 1982; Rundel, 1996; Parsons and Hopper, 2003). Furthermore, diagnosing the type of underground organ on which the renewal bud sits, and whether it is a storage organ or otherwise, is not always clear cut. For example, designations of underground organs as USOs often appear to be based on the relative size of the belowground organ—despite continuous variation within and across lineages as well as ecological settings—on the assumption that size indicates storage function. Characterizing which tissue(s) have been modified for storage has been a useful and likely more reproducible tool than size in creating definitions, in the case of USOs (discussed extensively below). Excluding taxa from the geophyte definition based on organ size (in the case of USOs) or habitat preference (in the case of helo- and hydrophytes) could lead researchers to omit taxa and traits from the geophyte definition that have relevant morphologies and/or ecological roles, and whose inclusion could therefore lend power to understanding relationships between form and function in geophytic structures.

Here, we use broad-based definitions of geophytism and geophytes. We prefer describing geophytism as a plant habit based on bud location, without asserting that the organs that bear these buds have a particular physiological function (e.g., storage). We prioritize bud placement over organ type or function in our definition because bud placement is a major factor in determining plant responses to climate, disturbance, fire, etc. (Ott et al., 2019). Although our treatment includes plants that Raunkiaer (1934) would have broadly classified as cryptophytes (i.e., geophytes, hydrophytes, and helophytes), we prefer the term geophyte (“earth plant”) over cryptophyte given the connotation associated with the root term *crypto-* (hidden), because not all geophytes go dormant and become “hidden” belowground, despite having underground renewal buds (e.g., several *Crinum* spp., tropical ginger). Importantly, cryptophyte is also used to refer to the cryptomonads (a clade of algae) (e.g., Kim et al., 2017), and using cryptophyte to refer to a convergent plant habit as well as a specifically defined evolutionary group increases ambiguity in the literature. Additionally, several helo- and hydrophytes (marsh- or water-dwelling plants) have traits commonly associated with geophytism (e.g., *Isoetes* corms, *Nelumbo* rhizomes). Although these plants likely have physiological specializations to survive in wet or submerged habitats (Matthews and Seymour, 2006), the processes by which they develop underground organs are likely relevant to generating a broad understanding of belowground organ evolution. Therefore, while we recognize that some may consider this position controversial, we include these taxa in our definition.

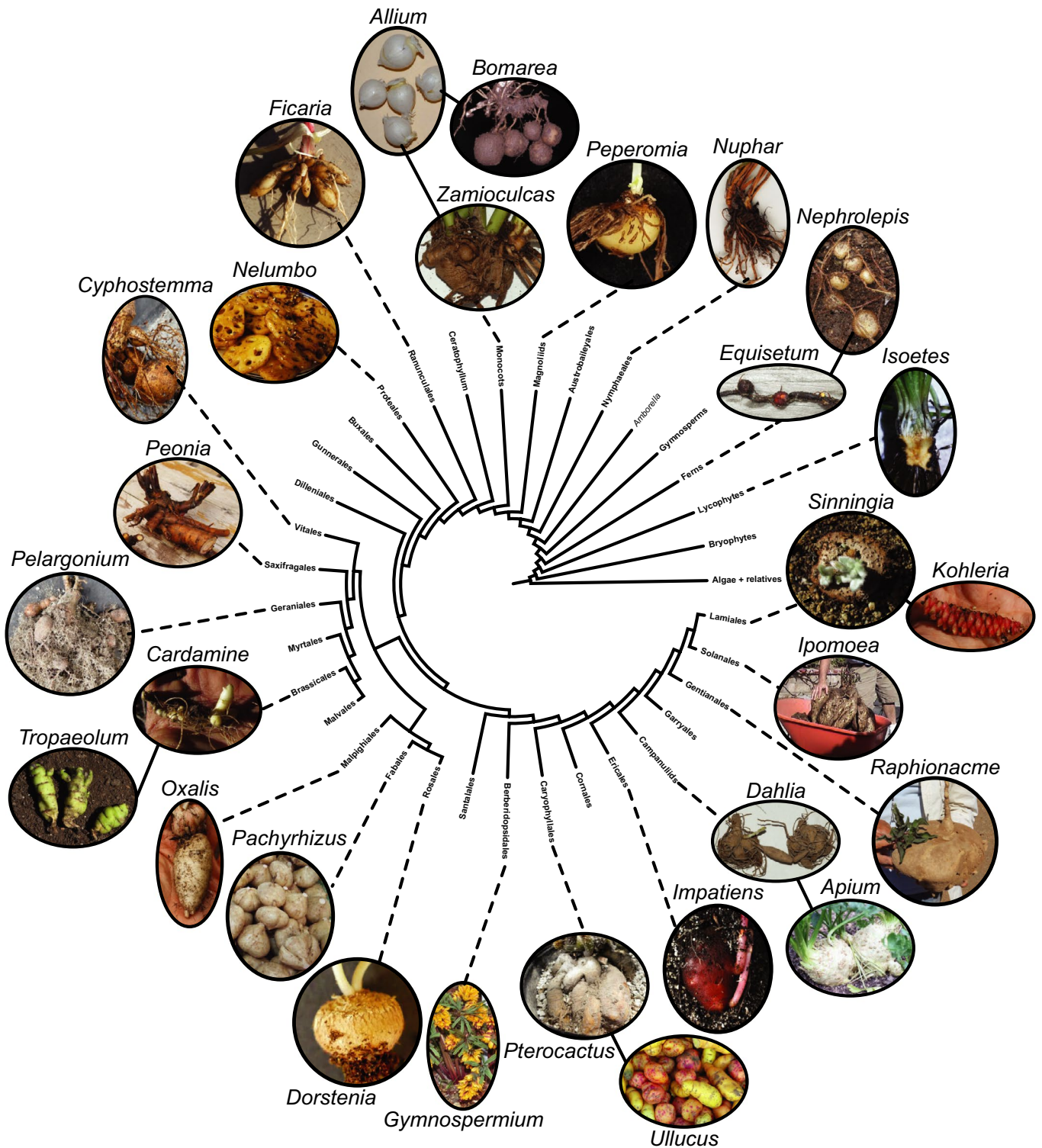
Additionally, depending on bud depth, terrestrial taxa may be classified as hemicryptophytes (buds at or near the soil line) or geophytes (buds below soil line) since many can adjust bud depth over time through renewal bud placement and/or root contraction (Galil, 1981; Pütz and Sukkau, 2002). The appropriate bud depth for distinguishing between a geophyte or hemicryptophyte has not been clearly defined, and while bud depth can have ecological

consequences (Lubbe and Henry, 2019), the potentially transient placement of some buds relative to the soil line may not be relevant for understanding the macroevolutionary patterns of geophyte morphology and development. Thus, an inclusive definition of geophyte is favored here: plants with renewal buds at or below the soil line.

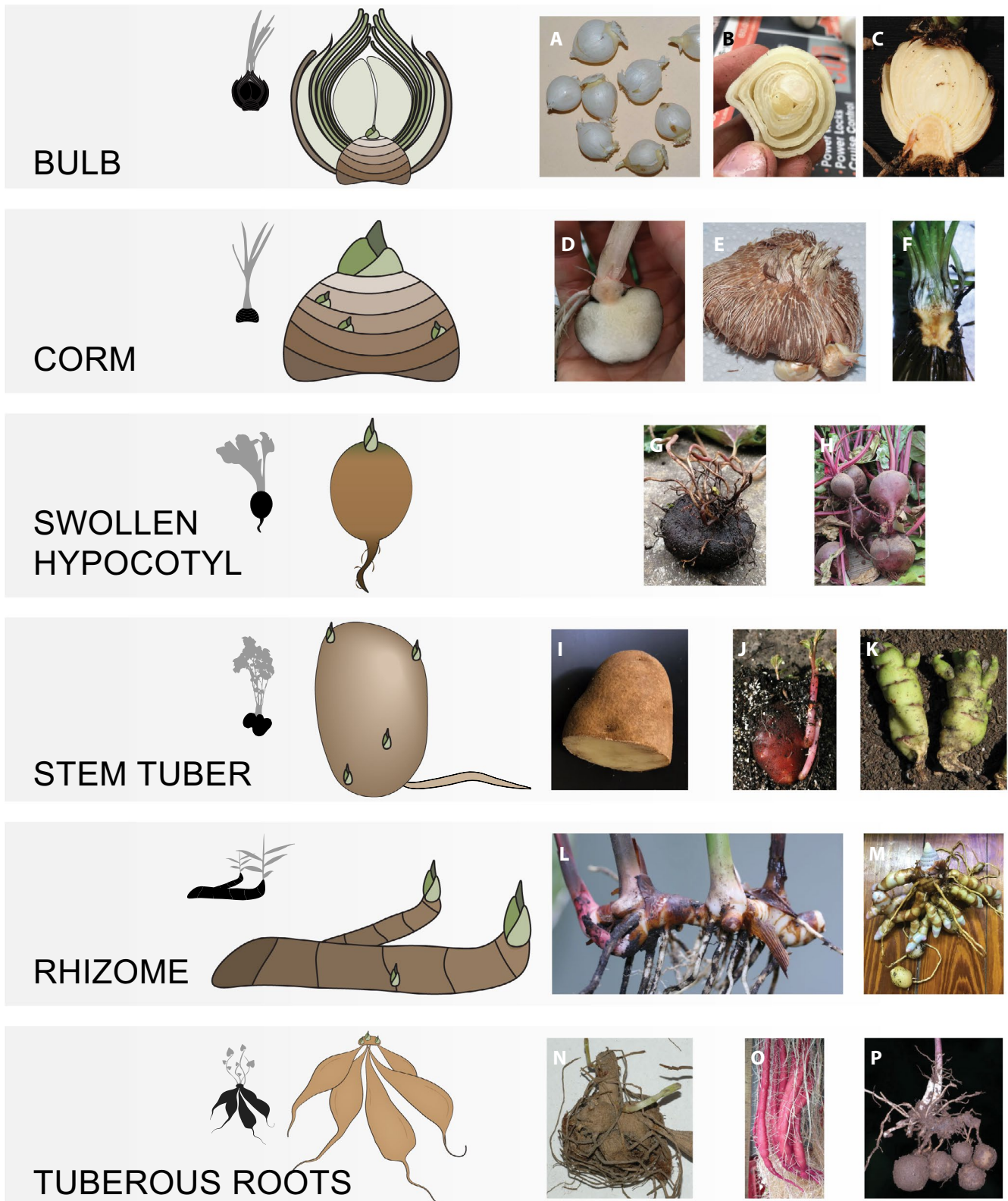
Despite their many origins in the plant tree of life (Fig. 1), geophytes are often found in similar habitats and are characteristic elements of many ecosystems. Belowground buds (often in addition to belowground allocation of carbohydrates and water in USOs) allow a plant to thrive in habitats with strongly seasonal climate patterns (e.g., wet and dry seasons) or disturbance regimes (e.g., fire) (Sosa and Loera, 2017; Pausas et al., 2018; Howard et al., 2019). Geophytes make up approximately 8% of plant species diversity in mediterranean-climate regions, a pattern that is particularly striking in South Africa, where 14.4% of plants in the Cape region are geophytic (Parsons and Hopper, 2003). Outside of mediterranean climates, geophytes are also substantial contributors to overall biodiversity, particularly in arid or seasonally dry/cold habitats. In Mexico, for example, roughly 10% of all monocots are geophytic, and most geophyte diversity occurs in dry or semi-arid habitats (Cuéllar-Martínez and Sosa, 2016). Geophytes are also common spring ephemerals in the understory of deciduous woodlands, where their ability to quickly respond to favorable environmental conditions allows them to emerge before trees have fully flushed and thus blocked the majority of sunlight from reaching the forest floor (Whigham, 2004). A better understanding of the morphological and ecological diversity of geophytes could be used to identify the consequences of organ evolution in response to these many different habitats and biomes.

The comparative framework used to study the ecology and evolution of other plant habits, such as transitions between woody and herbaceous growth forms (Carlquist, 1996; Smith and Donoghue, 2008; Tank and Olmstead, 2008), or the climbing habit (Angyalossy et al., 2012; Chery et al., 2020), can serve as a guide for future geophyte research. To study such innovations in habits and growth forms, researchers have typically taken a three-pronged approach. They have (1) generated a detailed understanding of plant anatomy through extensive descriptive work (Carlquist, 1996, among many others) and ensured corresponding terminology was used consistently throughout their collaborative efforts (IAWA, 1964), allowing the development of a comprehensive plant trait ontology (Lens et al., 2012); (2) built and maintained extensive tissue collections, even though those collections often require nonstandard preservation techniques (e.g., spirit collections and wood samples housed separately from herbarium sheets); and (3) employed up-to-date methods in comparative analyses to better understand the intersection of evolution and development in the context of phylogenies (Pace et al., 2009; Chery et al., 2020).

Much like the climbing habit and woody and herbaceous growth forms, geophytism has evolved multiple times, independently, across diverse plant lineages including ferns, lycophytes, magnoliids, eudicots, and monocots (Fig. 1). Repeated evolution of, or convergence upon, a particular life history strategy provides a powerful scheme for studying the evolution and development of such phenomena (Wake et al., 2011) and allows us to characterize the mechanisms driving these independent origins as well as the concomitant morphological, genetic, and physiological innovations. Here, we summarize the morphology, development, and evolution of geophytes and their belowground organs, beginning with definitions for the most common geophytic organs, USOs. We introduce



**FIGURE 1.** Geophytes and their underground storage organs across the plant tree of life. Taxa represented are not a comprehensive sampling of all known geophytes but exemplify the phylogenetic breadth of geophytism. Phylogenetic relationships are based on the cpDNA phylogeny of Gitzendanner et al. (2018). All images supplied by original photographer with the exception of *Pachyrhizus erosus* image from Midori (GFDL, <http://www.gnu.org/copyleft/fdl.html>), CC-BY-SA-3.0 (<http://creativecommons.org/licenses/by-sa/3.0/>) from Wikimedia Commons; *Ullucus tuberosus* image from Eric Hunt (GFDL, <http://www.gnu.org/copyleft/fdl.html>), CC-BY-SA-3.0 (<http://creativecommons.org/licenses/by-sa/3.0/>) from Wikimedia Commons; *Ficaria verna* image from Stefan Lefnaer, CC BY-SA 4.0 (<https://creativecommons.org/licenses/by-sa/4.0/>) from Wikimedia Commons; *Paeonia* × (Itoh) 'Court Jester' image from F.D. Richards, CC-BY-SA 2.0 (<https://creativecommons.org/licenses/by-sa/2.0/legalcode>) from Flickr; *Nuphar advena* image from University of Florida Herbarium specimen, FLAS 219447, Florida Museum of Natural History, by Kathy M. Davis on 04 May 2010.



**FIGURE 2.** Illustrations of belowground traits within the context of the whole plant (smaller, gray and black illustrations): bulb, corm, hypocotyl, stem tuber, rhizome, and tuberous roots. Plant images for each trait are as follows: bulb: (A) *Allium oreophyllum*, (B) *Tulipa* cultivar, (C) *Ledebouria* sp.; corm: (D) *Amorphophallus* sp., (E) *Chasmanthe* sp., (F) *Isoetes storkii*; swollen hypocotyl: (G) *Cyclamen hederifolium*, (H) *Beta vulgaris*; stem tuber: (I) *Solanum tuberosum*, (J) *Impatiens flanaganae*, (K) *Tropaeolum tuberosum*; rhizome: (L) *Hedychium* sp., (M) *Curcuma* hybrid; tuberous roots: (N) *Dahlia* sp., (O) *Ipomoea batatas*, (P) *Bomarea obovata*.

hypotheses explaining the evolution of geophytic belowground traits and discuss the implications of these hypotheses from an evo-devo perspective. Finally, we suggest avenues for future research based on the comparative framework described above, focusing on the evolution of geophytes' understudied characteristics.

## ORGAN TERMINOLOGY AND MORPHOLOGY

Varying definitions of belowground organs and their corresponding tissue types have limited attempts to conduct broad, comprehensive studies on the diversity of belowground organ morphology. Before summarizing geophyte developmental evolution, we must provide universally applicable descriptions of geophytic belowground structures and their morphologies (see also Fig. 2). While the presence and position of renewal buds are essential for determining whether a plant is a geophyte, distinguishing between the variety of organs on which these buds occur requires a more thorough understanding of these organs and how they have developed. Critically, plants with swollen belowground organs may or may not be geophytes according to our definition. However, because the majority of belowground, bud-supporting organs in geophytes are also storage organs, we focus below on broad morphological descriptions for a variety of underground storage organs and discuss how they fit into our definition of geophytic lineages.

### Bulbs

Bulbs are vertically oriented (orthotropic), compressed shoot systems. Within these shoot systems, the stems have short internodes and the apical and axillary buds are surrounded by layers of leaves that function in storage, photosynthesis and/or protection, among others (see Case study 1: Monocots for discussion on the development of these different leaf types) (Rees, 1972; McNeal and Ownbey, 1973; De Hertogh and Nard, 1993; Kamenetsky and Okubo, 2012). While most common among the monocots, bulbs are also found within the eudicot *Oxalis* (Oxalidales) (Oberlander et al., 2009). The outermost leaves of most bulbs dry and become papery before dormancy. When persistent, these dried leaves are referred to as tunics, and the bulbs are called tunicate. Bulbs lacking tunics are considered to be imbricate and are commonly found in *Lilium*, *Fritillaria*, and *Nomocharis* (Liliaceae) (Rees, 1972). Bulbs can further be differentiated by the leaf composition of the bulb at dormancy: (1) the persistent leaf base of a previously photosynthetic leaf (e.g., *Hyacinthus*, Asparagaceae), (2) scale leaves, i.e., leaves with a highly reduced lamina (e.g., *Tulipa*, Liliaceae), or (3) both (e.g., *Narcissus*, Amaryllidaceae) (Rees, 1972). The number of consecutive leaf layers and/or scale leaves contributing to the formation of a bulb can vary both within and among clades. For example, within *Iris* (Asparagales), bulbs have evolved independently multiple times, with morphological differences between bulbs from different lineages (Wilson, 2006). In *Iris*, some bulbs consist of a single scale leaf, others of multiple partially fused scale leaves, and others of unfused scale leaves resulting in a bulb with a loose appearance (Wilson, 2006). Similar patterns of scale leaf number and composition have also been found in Liliaceae (Patterson and Givnish, 2002) and Melanthiaceae (Zomlefer et al., 2006). See Case study 1: Monocots for additional discussion of bulb composition.

It is unclear why bulbous geophytes are more prevalent in monocots, but shared morphological features, such as sheathing leaf

bases, have been hypothesized to serve as precursors to the evolution of the bulb within this lineage (Holtum, 1955; Givnish et al., 2018). In addition to the bulbous groups already mentioned, others include the Scilloideae and Amaryllidaceae (Asparagales) (Rees, 1972), Chlorogaloideae (Agavoideae, Asparagaceae) (Archibald et al., 2015), and Haemodoraceae (Commelinales) (Pate and Dixon, 1982), and perhaps less well-known examples include taxa within the Cyperaceae (e.g., *Cyperus usitatus*) and Poaceae (e.g., *Poa bulbosa*) (Medwecka-Kornaś and Kornaś, 1985; Cabi et al., 2016).

### Corms

Corms, colloquially described as “solid bulbs”, are rotund, vertically oriented stems with short internodes, and the entirety of the belowground stem is uniformly swollen (unlike stem tubers) (Pate and Dixon, 1982; De Hertogh and Nard, 1993; Kamenetsky and Okubo, 2012). In a corm, stem tissue acts as the main repository for carbohydrates and water. Similar to bulbs, many corms have dried, outer coverings formed from leaf bases of previous years' growth called tunics; however, these are typically more fibrous than those associated with bulbs (Goldblatt and Manning, 1990; Erol et al., 2008). Corms are commonly replaced on an annual basis, and the new corm is produced either laterally from an axillary bud or apically from the shoot apical meristem (SAM) (Pate and Dixon, 1982; Kamenetsky and Okubo, 2012). Annual corm replacement is particularly common in Iridaceae, Colchicaceae, and Tecophilaceae (Kubitzki, 1998; Kamenetsky and Okubo, 2012). Other taxa (e.g., Zingiberales, Araceae) do not replace corms regularly; rather, the corm is maintained over time and gradually increases in length orthotropically (vertically) and in girth, rather than plagiotropically (horizontally) like a rhizome. Corms have evolved multiple times and are particularly characteristic of taxa within the Iridaceae, Colchicaceae, *Isoëtes* (Lycophyta), *Liatris* (Asteraceae), and several Cyperaceae and Poaceae (Burns, 1946; Rodrigues and Estelita, 2009).

### Swollen hypocotyls

The hypocotyl—the region of stem below the first cotyledon but above the radicle or root—can function as a storage organ at multiple stages of plant development (De Hertogh and Nard, 1993). Hypocotyls are a single stem internode; as such, they do not harbor axillary buds. The hypocotyl is distinct from the rest of the internodes of the vegetative shoot system, as demonstrated by anatomical and functional modifications specific to the hypocotylar region including those for seedling emergence (e.g., in *Phaseolus* [bean]), seedling protection (e.g., in *Rhizophora*; Gill and Tomlinson, 1969), or carbohydrate storage (e.g., in *Beta* [beet]). Perhaps the most well-known example of hypocotylar storage is the beet, *Beta vulgaris* (Amaranthaceae), in which only the hypocotyl is enlarged (Artschwager, 1926). However, in other lineages, the hypocotyl expands radially in conjunction with adjacent parts of either the stem or root system, such as the enlarged stems of kohlrabi and turnips (*Brassica* spp., Brassicaceae), or the swollen radical/root system of *Adenia* (Passifloraceae) (Selman and Kulasegaram, 1967; Hearn, 2009). Note that under our definition of geophyte, only plants that have belowground perennating buds are classified as geophytes. As hypocotyls alone do not produce buds, technically geophytes only includes plants in which the hypocotyl serves as a storage organ in combination with belowground buds. Moreover, due to difficulties

in determining the exact position of radial growth, the contribution of swollen hypocotyl tissue to the form and function of corms, rhizomes, and stem tubers has likely been overlooked in the study of geophytes. For example, the belowground organs of *Dioscorea* (Dioscoreaceae) contain a swollen hypocotyl (Martin and Ortiz, 1963; Sharma, 1976). In rhizomatous *Dioscorea*, the swollen hypocotyl persists and contributes to the entire stem-based storage system, referred to in the literature inconsistently as either tuber or rhizome (Martin and Ortiz, 1963; Sharma, 1976). Due to the potential for misclassification of belowground morphology across *Dioscorea* (and other geophytic taxa), the contribution of the swollen hypocotyl, either alone or in combination with its surrounding tissues, is not well understood.

### Stem tubers

Stem tubers are localized expansions of belowground stems. In angiosperms, stem tubers are composed of internodes, nodes, and axillary renewal buds along their length (Adrianse and Brison, 1939; Kamenetsky and Okubo, 2012). Because the term tuber is widely used as a catch-all to identify any stem-derived swelling (Pate and Dixon, 1982), it can be difficult to distinguish between stem tubers, corms, rhizomes, and swollen hypocotyls. A major defining feature of stem tubers is that radial growth is often non-uniform (i.e., localized) across the entirety of the belowground stem (Fig. 2), which is illustrated in the potato (Solanaceae), where thin belowground stems connect to swollen stem tubers (Pate and Dixon, 1982). Two distinct types of stem tubers have been classified based on tuberization along the stem axis: (1) those where radial growth occurs in various locations (the internodes or nodes, depending on taxon) along the length of the belowground stem (e.g., some *Poa* spp. and *Geodorum* spp.; Pate and Dixon, 1982), and (2) those comprising lateral branches with terminal radial growth (Pate and Dixon, 1982). In this latter type, the main stem remains unswollen, and only the ends of lateral branches expand radially, encompassing multiple internodes. Stem tubers are more common in herbaceous eudicots relative to woody eudicots or monocots (Gregory, 1965) and have also been described in ferns, such as *Nephrolepis* and *Equisetum* (Sahni, 1916; Bir, 1978; Zhang et al., 2007).

### Rhizomes

Rhizomes are horizontally spreading shoot systems that are more or less uniform in width along their length (vs. unequal swelling in stem tubers). Rhizomes are associated with a variety of growth habits, including epiphytes, trees, and geophytes (Holm, 1929; Bell and Tomlinson, 1980; Verdagner, 2020) and vary greatly in their size, branching patterns, and anatomical features (Bell and Tomlinson, 1980; Klimešová, 2018). According to Link (1824), the term rhizome was first applied to the horizontal stem of *Polypodium*, a fern (Ehrhart, 1788). However, since the early 19th century, the term has been applied both prolifically and inconsistently (Holm, 1929; Bell and Tomlinson, 1980). The exact definition of rhizome has been debated and modified using criteria based on function (i.e., storage, dormancy) and morphology (i.e., thickness, position above vs. below ground, presence of lateral buds) (Bell and Tomlinson, 1980; Pate and Dixon, 1982; Rees, 1989). In ferns, rhizome refers to the stem from which fronds and roots emerge; only in some cases is the rhizome subterranean or horizontal (Lellinger, 2002). In

angiosperms, the rhizome is characterized by uniform radial expansion along the stem and plagiotropic (horizontal) growth.

When considering the definition of a rhizome within the context of the geophytic habit, rhizomes produce lateral or axillary buds situated at or below the soil level. Some authors require the rhizome to be thickened for the taxon to be considered a rhizomatous geophyte (Hoffman 1933; Procheş et al., 2006; Parsons, 2000). For example, Raunkiaer (1934) considered several *Juncus* and *Scirpus* (Cyperaceae) geophytic, but many such taxa were later excluded as geophytes due to their slender rhizomes and lack of annual dormancy (Pate and Dixon, 1982; Rundel, 1996). Here, we consider bud placement relative to soil level as qualifying such taxa as geophytes regardless of rhizome girth.

### Tuberous roots

In contrast to the shoot-based structures described above, tuberous roots are modifications of the root system in which roots or entire root systems function in storage and are wider than fibrous roots of the same plant. The gross morphology of tuberous roots and the specific root tissue utilized for nutrient storage vary greatly across taxa. For example, most *Alstroemeria* (Alstroemeriaceae) have tuberous roots that are swollen along the length of the root, resulting in a cylindrical tuber with a large diameter compared to their nontuberous roots (Sanso, 2001). In contrast, the tuberous roots of many species in the sister lineage *Bomarea* exhibit a distally swollen root apex, forming a rounded structure at the tip of an otherwise fibrous root (Sanso, 2001). Tuberous roots also differ in whether they originate from other roots or from shoot systems, in their uniformity and the location of thickening along the root, and in the seasonality of tuberous root growth (Pate and Dixon, 1982).

Importantly, tuberous roots are different from the shoot-based structures described above in that they may not be the primary source of perennating buds; instead, nutrients stored within tuberous roots are drawn upon to fuel bud growth elsewhere in the plant. Therefore, a plant with tuberous roots that does not bear belowground buds should not be considered a geophyte (e.g., in cassava, *Manihot esculenta*, Euphorbiaceae, buds are found on the aboveground stem) (Chaweewan and Taylor, 2015). Interestingly, root-borne shoots have been reported in a number of geophytes (e.g., sweet potato, *Ipomoea batatas*) (Wilson and Lowe, 1973). Alternatively, many rhizomatous plants, where the rhizomes serve as the sources of perennating buds, also bear tuberous roots (e.g., *Bomarea*; Sanso, 2001). Plants such as tuberous-rooted, rhizomatous geophytes suggest that modifications to the root and shoot may provide complementary functions for these particular geophytes.

Tuberous roots are common across monocots, such as *Alstroemeria* and *Bomarea* as well as *Curcuma* and other Zingiberales. Tuberous roots are also found in the gymnospermous cycads (*Macrozamia*) and within a diversity of non-monocot angiosperms, including Fabaceae, Vitaceae, Malvaceae, and many others (Pate and Dixon, 1982; Meve and Liede, 2004). Quantitative and qualitative observations of root morphology associated with a variety of taxa in different habitats will facilitate more objective ways to distinguish different root variations and their presumed associated functions.

### “Rhizophores”

Here we discuss the term rhizophore as it appears in geophyte literature. Since the original introduction of the term rhizophore

to describe the leafless, root-bearing shoots unique to modern *Selaginella* (Lycophytes) (Nägeli et al., 1858), subsequent authors have applied this term to swollen, belowground stem structures in several angiosperm lineages (Goebel, 1905; de Menezes et al., 1979; Rocha and de Menezes, 1997; Andreatta and de Menezes, 1999; Hayashi and Appezzato-da-Glória, 2005) and to the stilt roots of certain mangrove species (e.g., *Rhizophora*; de Menezes, 2006). In both cases, the use of the term rhizophore was justified based on a positively geotropic habit and the possession of intermediate

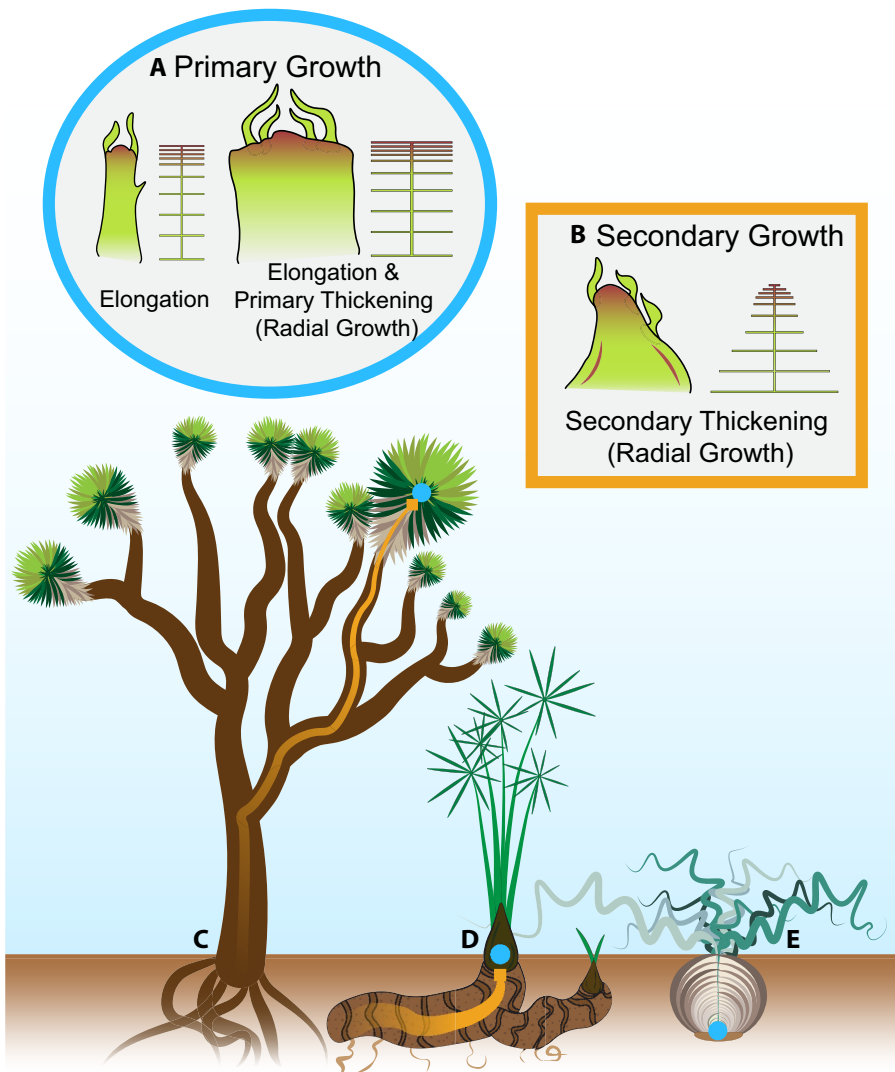
characteristics between a stem and root. However, these angiosperm “rhizophores” have independent morphological origins. For example, the “rhizophore” is a cotyledonary bud or plumular axis in *Smilax* (Andreatta and de Menezes, 1999; Martins et al., 2011), a stem in *Dioscorea* (Rocha and de Menezes, 1997), and a hypocotyl in *Rhizophora* (de Menezes, 2006). While angiosperm “rhizophores” imply a geophytic habit (except in *Rhizophora*), differences in developmental origins and lack of uniform anatomical or morphological features indicate that angiosperm “rhizophores” are not homologous to one another nor to the true rhizophore of *Selaginella*. We recommend that researchers use terminology indicative of the developmental origins and features of the structures under study and that rhizophore be reserved for the root-bearing shoots of *Selaginella*.

### EVOLUTION OF THE DEVELOPMENTAL PATTERNS OF GEOPHYTIC BELOWGROUND ORGANS

Across geophytes, developmental studies are necessary to identify homologous organs and to tease apart confounding patterns of convergent evolution. Many developmental processes contribute to the diversity of belowground organs. Radial growth in roots, stems, and leaves drives the unique morphologies that distinguish the various geophytic organs described above. There are two different types of stem thickening: primary thickening growth (PTG), occurring at the shoot apex *in tandem* with internodal elongation in stems (Fig. 3A), and secondary thickening growth (STG), which occurs in regions where elongation has already taken place (Fig. 3B) (Kaplan and Specht, 2021; Troll, 1937; Tomlinson, 1961). The meristematic origin and anatomical locus of stem and root thickening vary across lineages. Leaf thickening is less-well described but seems to occur primarily through cellular expansion. Based on the mechanisms of radial growth in these structures, we can begin to untangle how specific developmental processes give rise to belowground morphological diversity. Below, we review the developmental morphology of geophytic structures in three distinct plant lineages.

#### Case study 1: Monocots

In monocot stems, distinct primary and secondary thickening meristems have been proposed to underlie the separate processes of PTG and STG for many species (DeMason, 1983; Rudall, 1991;



**FIGURE 3.** Illustrations of stem growth mechanisms in the context of the plant body. (A, B) Representations of shoot apex longitudinal sections next to diagrammatic representations of internode length; distance between bars indicates distance between nodes, width corresponds to thickening growth and colors indicate active meristematic regions found near the apex or the vascular cambium (B: vertical lines). (A) Primary growth (blue circle) includes elongation of the shoot (left), and primary thickening (right), which occurs in tandem with internode elongation. (B) Secondary thickening growth (orange square) occurs after internodal elongation and may occur via the vascular cambium (vertical lines). The location(s) of primary (blue dots) and secondary (orange line) growth (A, B) are mapped onto three representative plant growth habits (not drawn to scale): arborescent (C, as in *Yucca brevifolia*; Simpson, 1975), rhizomatous (D, as in *Cyperus papyrus*; Rodrigues and Estelita, 2002) and bulbous (E, as in *Allium cepa*; DeMason, 1979).

but see de Menezes et al., 2005, 2012 for a different interpretation). The primary thickening meristem (PTM) is thought to contribute to thickening growth in a diverse array of monocot structures including the rhizomatous stems of *Iris*, *Cyperus*, *Musa*, and *Zingiber* (Fig. 3D) (Skutch, 1932; Rudall, 1989; Rodrigues and Estelita, 2002; Liu et al., 2020) and the short stem found in the *Allium* bulb (DeMason, 1979). Secondary thickening growth in monocots occurs via the secondary thickening meristem (STM; i.e., the monocot cambium), which has only been characterized in some members of Asparagales (Rudall, 1995). In Asparagales, STM activity is typically associated with arborescence (Rudall, 1984; Conran, 1999). However, STM activity has also been reported in rhizomes and corms of some Asparagalean geophytes (Rudall, 1984, 1995; Solano et al., 2013). Radial growth in these geophytic structures can occur via both a primary and a secondary thickening meristem, each producing vascular systems and parenchyma derivatives (Rudall, 1991). The below-ground storage systems of several *Dioscorea* (Dioscoreales) also expand radially through both primary and secondary thickening growth (Martin and Ortiz, 1963; Sharma, 1976, 1980). In these taxa, rhizomes and stem tubers develop from a swollen hypocotyl that expands first via PTG and subsequently on an annual basis via STG. While the primary thickening meristem has been described as being responsible for both primary and secondary thickening in *Dioscorea* (Sharma, 1975), the activity of the meristem during secondary thickening growth is more consistent with activity of a separate secondary thickening meristem as found in Asparagales (Sharma, 1980; Diggle and DeMason, 1983; Cattai and de Menezes, 2010). As such, the role of the primary thickening meristem in *Dioscorea* should be revisited.

While many monocots produce tuberous roots, lack of developmental research on these taxa makes it difficult to distinguish between contributions from primary vs. secondary radial growth, which limits our ability to understand whether the key developmental and growth patterns that characterize shoot-based organs can also be applied to roots. However, some anatomical work indicates that the position of expansion (i.e., tissue type) differs between taxa. In tuberous roots of *Roscoea cautleyoides* (Zingiberaceae), *Triglochin procerum* (Juncaginaceae), and *Alstroemeria* (Alstroemeriaceae), the cortex is expanded relative to the remaining root tissues. In contrast, tuberous roots of *Hemerocallis* (Asphodelaceae), *Asphodelus* (Asphodelaceae), *Dioscorea* (Dioscoreaceae), and *Bomarea* (Alstroemeriaceae) show expansion in both the cortex and pith regions (Arber, 1925; Lawton and Lawton, 1969; Hofreiter and Rodríguez, 2006). Expansion of the cortex, while described in aboveground stems of some succulent eudicots (e.g., *Sempervivum*, *Echinopsis*; Troll and Rauh, 1950), is not observed in monocotyledonous stem-derived geophytic structures. Therefore, within the monocotyledons, cortical thickening may be unique to tuberous roots.

Leaves and especially leaf bases are an important component in all shoot-derived storage structures, particularly in bulbs. Leaves consist of a lower leaf zone (in monocots, typically a sheathing base that wraps around the SAM) and an upper leaf zone (Conklin et al., 2019). In bulbs, these two regions serve various functions including storage, protection against desiccation, or prevention of active respiration, which reduces carbohydrate stores during dormancy (Kamerbeek, 1962). In all cases, the sheathing leaf base is the locus of both storage and protective functions. In bulbs, these functions have evolved in various ways. In some cases, the leaf has evolved to serve a specific function (either protection or storage), and its

structure is modified early in development. In other cases, an otherwise photosynthetic leaf is modified during development to serve a secondary or tertiary function.

Currently, classification of leaf type is confusing due to terminology that is taxon-specific and based on observed function rather than developmental origins. For example, the term *storage leaf* may be applied to a swollen scale leaf in garlic or to a swollen base of a previously photosynthetic leaf in onion. Rees (1972) addressed this by applying the term *scale leaf* to those leaves where the upper leaf zone does not usually develop into a lamina and reserved the term *true photosynthetic leaf* for all others. While we reject the notion that scale leaves are not true leaf homologs, the morphological term *scale leaf* is useful in this context. The addition of a qualifier (e.g., *swollen scale leaf*, *protective scale leaf*, and *sheathing scale leaf*) helps discriminate between form and function. For bulb leaves with a photosynthetic function, we prefer *foliage-leaf-derived swollen leaf base* and *foliage-leaf-derived protective leaf base* because these incorporate the developmental trajectory and are amenable to ontologization (Howard et al., 2021, in this issue). Bulb leaf diversity can occur both between and within taxa; for example, *Allium* species exhibit different mechanisms for how their foliage-leaf-derived protective leaf bases develop, including which cellular layer (abaxial v. adaxial epidermis) becomes sclerified (i.e., hardened) (Mann, 1960). In this way, many of the definitions may require some degree of taxon specificity; below, we provide an example of how a universal terminology can be adapted and applied to monocot bulb leaf development.

Scale leaves, sometimes referred to as cataphylls (Rees, 1972; McNeal and Ownbey, 1973), are an important bulb leaf type that can serve either a primarily storage (e.g., swollen scale leaf in *Allium sativum*) or protective (e.g., protective scale leaf in *Allium neapolitanum*) function (Mann, 1952, 1960). In both cases, the lower leaf zone takes on the respective function (i.e., storage or protection), while the upper leaf zone remains small and membranous (but see Reese [1972] for an exception that we would not consider a scale leaf). In some species, a foliage leaf can take on a second function. Initially, the upper leaf zone is photosynthetic but eventually senesces, while the lower sheathing leaf base is persistent and takes on a secondary role, either storage (e.g., *Lilium*; also called radical leaves) or protection (e.g., *Allium acuminatum*; also called a resistant layer) (Rees, 1972; McNeal and Ownbey, 1973).

The protective leaves, which collectively comprise the bulb tunic, can arise from two independent developmental pathways. In bulbs consisting only of scale leaves, a swollen scale leaf (primary role) can later dry up and serve a protective function (secondary role) (Rees, 1972). On the other hand, in *Allium cepa* (onion), a photosynthetic leaf (primary role) loses its upper leaf zone, while the leaf base is persistent and becomes a storage leaf base (secondary role) which can then further desiccate to become a protective leaf base (tertiary role; Hoffman, 1933). The presence of these leaf types in a bulb are not mutually exclusive. For example, garlic has two types of protective leaves that coexist in the bulb: (1) a protective scale leaf surrounds each storage scale leaf, which together form the clove, and (2) multiple cloves are surrounded by foliage-leaf-derived protective leaf bases (Mann, 1952; Rees, 1972).

A final modification to the leaf base can be found in the so-called sheath leaves (called sprout leaves in garlic), which resemble the leaf bases of photosynthetic leaves (e.g., in some *Allium* and *Iris*). These develop before the photosynthetic foliage leaves and are likely involved in protection of the young foliage leaf primordia and as such are best classified as a type of scale leaf (Rees, 1972; McNeal and

Ownbey, 1973). In contrast to garlic, the sheath leaf of *Allium acuminatum* completely envelops the following year's growth and is subsequently torn through by photosynthetic leaves at the start of the growing season. Likely due to their ephemeral nature, sheath leaves are not typically treated in discussions of leaf types (Rees et al., 1972).

The developmental mechanisms involved in thickening of storage leaves and the formation of sclerified layers in protective leaves are not well understood. In some succulent leaves (e.g., Bromeliaceae), developmental thickening occurs through a combination of increased division of mesophyll cells, leading to a higher total number of cell files and volumetric expansion of mesophyll cells (Males, 2017). Similarly, cellular expansion leads to thickening in the storage leaves of onion (*Allium cepa*), although it occurs via the loss of cortical microtubules rather than increased cellular division (Hoffman, 1933; Heath, 1945; Mita and Shibaoka, 1983). The storage leaves of garlic (*A. sativum*) are composed of uniformly packed parenchyma mesophyll, but the mechanism of expansion is unknown (Mann, 1952). In the protective leaf of a garlic clove, the outer epidermis becomes sclerified at maturity and persists along with the vascular tissue, while the mesophyll desiccates and disappears; a similar pattern occurs in the foliage-leaf-derived protective leaf bases of garlic (Mann, 1952). In *Allium acuminatum*, it is the adaxial epidermal layer of the leaf base of a previously photosynthetic leaf that becomes sclerified (McNeal and Ownbey, 1973). In *Allium* section *Molium*, two leaves fuse postgenitally (i.e., primordia form independently and fuse later during development) along their adjacent epidermal layers (i.e., abaxial surface of older leaf and adaxial surface of younger leaf). Sclerification of this structure, collectively referred to as the protective layer, occurs on the adaxial epidermal layer of the younger leaf (Mann, 1960). The variation in morphology and development of bulb leaves within *Allium* alone, arguably the most well-studied bulbous lineage, suggests that developmental processes are likely vastly under-characterized in other bulbous lineages (Blodgett, 1910; Rees, 1968, 1972).

### Case study 2: Eudicots

Unlike in monocots, radial growth via primary thickening in eudicots is overshadowed by secondary thickening growth, which can occur in stem, hypocotyl, and root tissues. However, PTG still plays a role, albeit reduced, in the formation of many eudicot belowground structures. A thoroughly described case is the stem tuber of potato (*Solanum tuberosum*, Solanaceae), which has minimal thickening growth at the apex. However, thickening growth after elongation of the apical tip (i.e., STG) is responsible for the majority of the radial growth, resulting in a round tuber with a narrower apex (fig. 62 of Troll and Rauh, 1950). Two types of secondary thickening occur in *S. tuberosum* immediately after internodal elongation stops (Xu et al., 1998). First, cellular division and expansion contribute to the slight expansion of the pith and cortex, which are derived from the ground meristem. Second, cellular division of the procambium in the perimedullary zone produces storage parenchyma (Reeve et al., 1969). Cellular expansion of this storage parenchyma contributes to most of the potato diameter. Secondary thickening also occurs in stem tubers of Jerusalem artichoke (*Helianthus tuberosus*, Asteraceae) (Reed, 1910). Non-uniform cellular expansion can generate other unique morphological patterns, such as the moniliform (i.e., resembling a string of beads) stem tubers found in *Stachys affinis* (Lamiaceae), in which cells at the nodes are not expanded relative to cells at the internodes (Troll and Rauh, 1950).

The hypocotyl of the beet (*Beta vulgaris*, Amaranthaceae) originates through a unique form of STG (Artschwager, 1926). The beet contains multiple cambia termed "successive" cambia (also called annular rings). The first successive cambium arises from the pericycle and primary cambium, while the second successive cambium is derived from primary phloem parenchyma produced by the first successive cambium. All subsequent cambia are derived from the second successive cambium. Cells in the second successive cambium divide, and the inner daughter cells give rise to another successive cambium, while the outer daughter cells give rise to tissue termed the annular zone. This zone is composed of a thin cell layer of vascular tissue and a thicker cell layer of storage parenchyma, which contributes to most of the stem diameter upon expansion.

The storage roots of *Adenia* and many other eudicot taxa also expand through STG. In *Adenia*, pith parenchyma cells divide and expand, eventually rupturing the primary vasculature and extending into the secondary xylem. However, most girth comes from secondary xylem produced by the vascular cambium (Hearn, 2009). Secondary thickening via a single vascular cambium is also responsible for thickening of tuberous roots in some *Mandevilla* spp. (Apocynaceae) (Appezato-Da-Glória and Estelita, 2000) and cassava (Euphorbiaceae) (Chaweewan and Taylor, 2015). In these cases, the vascular cambium produces storage parenchyma. In sweet potato (*Ipomoea batatas*, Convolvulaceae), tuberous roots are initiated via the activity of the vascular cambium, which produces secondary vasculature. However, thickening growth occurs largely through the activity of anomalous cambia that form around the protophloem and metaxylem. These cambia give rise to storage parenchyma and occasionally secondary and tertiary cambia (Artschwager, 1924; Wilson and Lowe, 1973). This form of STG is also present in other Convolvulaceae (Wilson and Lowe, 1973; Eserman et al., 2018) and Fabaceae (*Pachyrhizus erosus* (Dabydeen and Sirju-Charran, 1990). In another example of irregular STG, the tuberous roots of *Perideridia kelloggii* (Apiaceae) are multistelic. They contain four to five primary xylem bundles alternating with secondary vasculature and surrounding the pith storage parenchyma but without an anomalous cambium (Chuang, 1970). Together, these examples demonstrate that, while the development of eudicot tuberous roots occurs via secondary thickening growth, there is remarkable variation in exactly how cambia contribute to girth. More descriptive research could indicate how pervasive these processes are across the breadth of taxa with tuberous roots.

Corms and bulbs can also be found within the eudicots but are significantly less common than in the monocots. Secondary thickening growth via an anomalous lateral meristem has been reported in the perennial corms of *Liatris* (Werner, 1978). Leaf "tubers" have been reported in *Dicentra* (Papaveraceae), in which, similar to storage leaves in monocot bulbs, the leaf base is enlarged and serves a storage function (Walton and Hufford, 1994). Similar storage leaves can also be found in the asexual propogules (also called brood leaves) of *Erythranthe gemmiparus* (Phrymaceae; Moody et al., 1999). In neither case has the mechanism of thickening been identified, and it remains to be seen whether similar processes underlie leaf modification in monocots and eudicots.

### Case study 3: Pteridophytes

In addition to rhizomes, which are characteristic of most ferns, some pteridophytes have belowground organs that share gross morphological features with those found in seed plants but differ in

their generative developmental processes. The lycophyte *Isoetes* is classically known for its perennial corm, although the term rhizomorph is also used (Gómez, 1980). The lycophyte *Phylloglossum drummondii* and some fern taxa in *Equisetum* and *Nephrolepis* produce stem tubers (Bower, 1885; du Sablon, 1892; Sahni, 1916; Paolillo, 1982). The *Isoetes* corm develops through STG via two bifacial and continuous meristems, termed the lateral meristem and the basal meristem (Paolillo, 1963, 1982). Both meristems contribute to the radial growth of the corm; however, cortex accumulation via the lateral meristem contributes more to the overall girth (DeMason, 1979). *Phylloglossum drummondii* is the only other extant lycophyte known to form perennial belowground structures. Tuberization occurs below the apical meristem resulting in a widened stem base, a feature characteristic of STG (Fig. 3B). Within the tuber, an endodermis-like layer (also called peripheral layer) surrounds a parenchymatous pith and could be responsible for tuberization (Bower, 1885; Wernham, 1910; Sampson, 1916).

Taxa in two fern lineages, *Equisetum* and *Nephrolepis*, produce stem tubers that enlarge in similar ways. Stem tubers of *Nephrolepis* are located terminally on belowground shoots (rhizomes) (similar to potato; see Case study 2), and occasionally produce roots (Sahni, 1916). Stem tubers of extinct and extant *Equisetum* are located in various positions on the rhizome and exhibit wide variety in morphology. They can encompass multiple internodes (similar to *Stachys*; see Case study 2) or either emerge singly or in a rosette around a single node (Barratt, 1920; Sun et al., 2013). Despite morphological differences, tubers in both *Equisetum* and *Nephrolepis* have shared anatomical characteristics (du Sablon, 1892; Sahni, 1916; Barratt, 1920; Bir, 1978). The pith is largely expanded in the center of the tuber and tapered on each end, a pattern indicative of secondary thickening growth (Kaplan and Specht, 2021). No meristematic region has been implicated in this thickening growth; however, expansion of pith via primary thickening growth has been described in *Polypodium* rhizomes (Wetter and Wetter, 1954). Further comparative studies detailing morphological, anatomical, and structural features of these organs in both pteridophytes and angiosperms would help to ascertain the developmental mechanisms by which distantly related plants have converged on similar traits and/or habits despite millions of years of evolutionary divergence.

### Summary

The case studies above summarize the developmental and morphological characteristics associated with radial growth of geophytic organs in monocots, eudicots, and pteridophytes. Ontogenetic studies of the groups described would help to define homologies and characterize cases of convergent and parallel (i.e., convergence via homologous mechanisms) evolution (Wake et al., 2011). For example, tuberous roots in eudicots expand via secondary thickening growth, but through distinct developmental mechanisms, either by formation of anomalous cambia as seen in Convolvulaceae or by a single vascular cambium as observed in *Manihot* (Euphorbiaceae) (Wilson and Lowe, 1973; Chaweevan and Taylor, 2015; Eserman et al., 2018). In both cases, the cambium gives rise to storage parenchyma; therefore, despite differing growth patterns, there may be deep homology at the cellular level across these two tuberous root types. In contrast, PTG via the same mechanism, the primary thickening meristem, is involved in radial growth of stem tissue in rhizomes, corms, and bulbs of many monocots. These structures may otherwise be considered nonhomologous given their

diverse morphology, yet a primary thickening meristem involved in the radial growth of all these structures indicates a potentially homologous process. Similarly, differential cellular elongation at nodes and internodes produces the moniliform tubers of evolutionarily distant *Stachys* and *Equisetum*, among others (Barratt, 1920; Pate and Dixon, 1982). These examples demonstrate, at three different macroevolutionary scales (within eudicots, all monocots, between eudicots and ferns), how evolution has resulted in both similarity and variation in form and function. Additional morphological and developmental studies of diverse taxa and the variety of organs they produce are necessary to understand how these often overlooked belowground structures evolve.

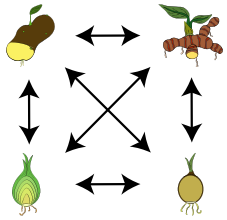
### EVOLUTIONARY HISTORY OF GEOPHYTIC MORPHOLOGY AND ECOLOGY

Ontogenetic studies can reveal the mechanisms by which diverse morphological structures form and thus can provide evidence of homology across evolutionary lineages (Rieppel, 2015). However, hypotheses of homology require a phylogenetic framework to explicitly account for evolutionary history. To date, few comparative studies of geophytic development and/or morphology have been placed within a phylogenetic context, but those few studies have provided novel insights into the evolution of geophytic structures within specific lineages (Box 1). For example, the bulbs of all *Iris* spp. had previously been considered homologous and derived from a common rhizomatous ancestor (Rodionenko, 1987). However, a phylogenetic analysis clearly demonstrated independent origins of the three different bulb types (Wilson, 2006). The ancestor of *Dioscorea* was also hypothesized to be rhizomatous (Burkill, 1960), which was supported by a recent phylogenetic study (Howard et al., 2019). In *Adenia* (Passifloraceae), phylogenetic analyses have shown multiple, rapid transitions between water storage in stems and water storage in tuberous roots (Hearn, 2006). It was hypothesized that the evolution of STG-derived vascular strands and storage parenchyma in liana-like ancestors allowed for the rapid co-option of similar sets of gene regulatory networks in different organs, which may have given rise to succulent stems and succulent, tuberous roots in this group via parallel evolution and allowed for rapid transitions between these forms of succulence (e.g., Box 1B) (Hearn, 2006, 2009). Further studies showed that aboveground and belowground succulence (characterized as having a subterranean root and stem tuber or hypocotyl) are phylogenetically correlated in the eudicots, providing additional evidence for a conserved developmental mechanism for thickening and storage (Hearn et al., 2013).

Comprehensive studies that include phylogenetic data can examine broad-scale macroevolutionary patterns. For example, Howard et al. (2020) found overall higher transition rates from rhizomes to bulbs compared to the reverse, across monocots, demonstrating potential developmental canalization (e.g., Box 1B). A phylogenetic framework can also provide information on the temporal order of trait acquisition. For example, root succulence, which is associated with geophytism in *Adenia*, may precede the evolution of stem succulence indicating that a trait, once evolved, may be deployed at different temporal and spatial scales during development (Hearn et al., 2013). Many of the evolutionary trends discussed thus far indicate that some belowground organs likely develop via modifications of preexisting gene networks and developmental processes that originally evolved outside of the geophytic context and that evolutionary

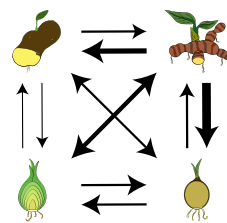
**Box 1** The consolidation of available work on the evolution and development of belowground morphologies suggests several hypotheses for how such structures have evolved in plants. Here, we present three hypotheses for general patterns of belowground shoot modifications that should be tested within a phylogenetic framework in clades across the plant tree of life. These hypotheses not only differentiate distinct modes of trait evolution, but also can provide insights into the potential for shared mechanisms of developmental and anatomical similarity.

**A. All transitions equally likely**



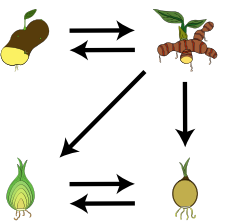
There may be no detectable pattern of ordered evolution between belowground shoot morphologies. This pattern would suggest that it is as probable for a bulbous plant to evolve from a cormous plant as from a rhizomatous or tuberous plant; however, current evidence suggests that such a pattern is likely not the case (Patterson and Givnish, 2002; Wilson, 2006; Howard et al., 2019, 2020; Herben and Klimešová, 2020). Support for this hypothesis in particular clades could indicate either the complete lack of significant barriers for evolutionary transitions between different morphologies or the presence of identical barriers for all transitions. These potential barriers could include the extent to which developmental processes such as genetic pathways for starch production and storage, thickening growth in belowground tissues, etc., are shared between distinct underground morphologies.

**B. Unequal transitions between states**



Transitions between some underground shoot morphologies may be more common than others, evidenced by faster transitions (meaning that transitions are more common across the phylogeny). For example, transition between rhizomes and bulbs appears to be faster than between non-geophytes and bulbs (Howard et al., 2019, 2020). This pattern might suggest that some of the developmental mechanisms between these morphologies are shared between some but not all morphologies, leading to more transitions between some traits once certain mechanisms have arisen in a particular ancestor.

**C. Ordered evolution**



As demonstrated by recent work, some underground traits may only evolve via an intermediary morphology, corresponding to ordered evolutionary transitions between morphologies. For example, the rhizomatous habit may have a precursory role in the evolution of other belowground, bud-bearing organs; bulbs and corms may only evolve from a rhizomatous ancestor (Patterson and Givnish, 2002; Wilson, 2006; Howard et al., 2019, 2020). Some support for this hypothesis can be found in “transitory” *Allium* that has rhizomatous bulbs (McNeal and Ownbey, 1973; Kamenetsky, 1996) and rhizomes of *Musa* (Musaceae) that forms corms at the soil surface (Huber et al., 2013). This hypothesis may only be pertinent to the monocots, but recent work hints at the possibility that ordered transitions could be occurring in the eudicots as well (i.e., tuberous *Claytonia*; Stoughton et al., 2018), though more work is needed in non-monocots.

transitions between certain morphologies are more likely than others. These transitions could be due to a conserved underlying mechanism(s), whether that be common anatomies or developmental programs (i.e., deep homology), that allow for the modification of or transition between different structures and growth types (Box 1A and/or 1B). In contrast, ordered evolution of characters, where only transitions between certain character states occur, demonstrates that not all taxa have access to the same underlying anatomical or developmental processes (Box 1C). Thus, reconstructing patterns through evolutionary time will greatly increase our ability to uncover the molecular and anatomical developmental processes that have led to the many forms of geophytism across taxa.

The ecological role that geophytes play is important and has been elaborated on elsewhere (see Pausas et al., 2018; Klimešová et al., 2018; Ott et al., 2019). Several other studies have found parallels between the ecological function and morphological evolution of many geophytes that are relevant for our discussion; there are repeated transitions not only between traits but also ecological

settings. In Liliales, *Allium*, and *Iris*, it has been repeatedly noted that rhizomatous taxa inhabit forested, mesic environments (the hypothesized ancestral trait and habitat), while bulbous relatives are found in sunnier, more xeric habitats (Kamenetsky, 1996; Rundel, 1996; Patterson and Givnish, 2002). The transition from rhizomatous to bulbous morphology is thought to have occurred in response to historical changes in seasonality: bulbous plants are found in regions with shorter growing seasons, whereas rhizomatous plants occur in areas with longer growing seasons (Rundel, 1996; Patterson and Givnish, 2002). In epiphytic orchids, many of which have swollen storage structures, an evolutionary shift from an epiphytic to a geophytic habit was associated with occurrence in more seasonal climates (Sosa et al., 2016). The swollen structures of both orchidaceous epiphytes and geophytes are important, but it is the protection afforded to them by having belowground buds that likely allowed this habitat transition to occur. Corms and bulbs inhabit similar climates overall (Howard et al., 2019), but we see few transitions between these

traits. Most transitions to a bulbous or cormous state appear to come from a rhizomatous ancestor (Howard et al., 2020), so bulbs and corms may have evolved in response to similar stimuli and could represent alternative morphological paths to convergent functions. Teasing apart complex ecological influences on geophyte developmental and morphological evolution could provide a more nuanced picture of the drivers behind underground morphological diversity.

The studies discussed above illustrate what can be gained by viewing belowground morphology through a comparative framework, but they also draw attention to the relative paucity of such work. To our knowledge, few studies have explicitly addressed the evolution of the geophytic habit within a robust, lineage-specific, phylogenetic context (Evans et al., 2014; Sosa et al., 2016), while others have investigated the evolution of belowground structures at larger phylogenetic scales (Howard et al., 2019, 2020; Herben and Klimešová, 2020). These comparative studies rely heavily on adequate and comparable coding of characters and character states, but terminological confusion has subjected large-scale comparative work on belowground morphology to reduced data sets and has increased concern for accuracy in character coding.

## FILLING IN THE HOLES OF GEOPHYTIC RESEARCH

### Ontologies

Since Raunkiaer's (1934) classification of geophytes, researchers have used diverse terminology to describe belowground structures, often ambiguously and inconsistently. These ambiguities are complicated by the inherent complexities of geophyte morphology. A major step in advancing our evolutionary understanding of geophytes is increased research on morphology and development paired with terminological standardization using controlled vocabularies and ontologies (see Howard et al., 2021, in this issue). An ontology describes a specific trait as an unambiguous phenotypic feature, characteristic, or quality, whether in a developing or mature organ/individual. Ontological databases provide a repository of controlled vocabularies arranged into a format that allows computers to “understand” how terms are related to one other. Ontologies can be used to capture nuances of

trait diversity as well as taxon-specific qualities. By linking together ontologies from different disciplines (e.g., morphology and physiology) through shared terminology, researchers can use these resources to investigate complex questions at different levels of biological organization (Howard et al., 2021, in this issue). Ontologies can encapsulate morphology, anatomy, and developmental processes, which can then be used to test homology between convergent morphological structures (Stevenson and Zumajo-Cardona, 2018; Walls et al., 2019). Although ontologies are powerful, they can be narrow, and they inherently rely on information that only detailed morphological and developmental research can provide. For example, the current formulation for “bulb” in Planteome ([www.planteome.org](http://www.planteome.org)) does not cover the morphological variation found in bulbs from diverse taxa. In Planteome, a “tuberous root” is enlarged in relation to other roots but not as enlarged as a “tuberous root tuber”, and the amount of enlargement required to be considered one or the other is unknown. The lack of ontologies for many plant traits suggests a need for generating new controlled vocabularies and ontological terms and reviewing and updating available ontologies based on detailed studies and thorough input from domain experts. Such investment into ontologies will improve our power to test hypotheses related to the evolution of geophytic belowground organs (Box 1) at multiple scales across lineages.

### Collections

Biological collections harbor an enormous wealth of data and are actively being used to investigate ecological and evolutionary processes (Soltis, 2017; Howard and Cellinese, 2020). Unfortunately, many geophytic belowground organs lack representation in herbaria (Table 1). This lack limits our ability to use collections to understand morphological variation within and among geophytes at any scale, a problem explicitly stated in a study on geophytic Piperaceae (Samain et al., 2011). Furthermore, during the preservation process, USOs easily lose characteristics such as shape, size, and color. This loss requires the use of techniques that preserve these data, such as photographs or spirit collections. One exciting and largely unexplored preservation option for geophytes is microcomputed tomography (micro-CT), which can digitally preserve the internal and external three-dimensional structure of a

**TABLE 1.** Belowground organ specimen representation across a diversity of plant taxa with different geophytic structures demonstrating the current difficulties in using collections for characterizing belowground organs. Taxa listed as “Genus spp.” include all vouchers for a given genus; however, some were filtered based on locality. See Appendix S1 for further details on methodology and the corresponding GBIF information.

Taxon	Belowground organ	Number of vouchers examined	Percentage of vouchers with organ present
<i>Bomarea</i> spp. (monocot)	tuberous roots and/or rhizomes	335	0
<i>Cyclamen hederifolium</i> (eudicot)	swollen hypocotyl	514	45
<i>Dichelostemma</i> spp. (monocot)	corm	148	28
<i>Gloriosa</i> spp. (monocot)	stem tuber	45	16
<i>Haemodorum</i> spp. (monocot)	bulb (tunicate)	101	25
<i>Hyacinthus</i> spp. (monocot)	bulb (tunicate)	241	54
<i>Iris foetidissima</i> (monocot)	rhizome	273	23
<i>Iris xiphium</i> (monocot)	bulb (tunicate)	185	51
<i>Isoetes nuttallii</i> (lycophyte)	corm	76	93
<i>Lachenalia</i> spp. (monocot)	bulb (tunicate)	335	55
<i>Lilium canadense</i> (monocot)	bulb (imbricate)	118	30
<i>Nephrolepis cordifolia</i> (fern)	tuberous roots	57	2
<i>Stachys floridana</i> (eudicot)	stem tuber	208	9
<b>TOTAL</b>		<b>2636</b>	<b>33</b>

geophytic structure. These data could then be linked to herbarium specimens. Lastly, botanical gardens remain underutilized despite housing a diversity of living specimens. Geophytes in these settings would be amenable to techniques such as micro-CT but would also be available for detailed developmental observations. It is critical we think “outside of the box” when it comes to preserving and studying geophytes’ unique belowground structures, whose lack of accurate representation in collections and textbooks has had a profound impact on how belowground structures are interpreted and perceived (Klimešová et al., 2020).

### Phylogenies

Current hypotheses addressing geophyte evolution were largely formulated through the study of groups such as Iridaceae (Wilson, 2006) and Liliales (Patterson and Givnish, 2002; Zomlefer et al., 2006). However, these studies can be improved through more detailed character assignment and the use of robust analytical methods. Numerous geophytic lineages also have yet to be studied within a phylogenetic framework. Groups in the Poales (e.g., Poaceae, Cyperaceae, Juncaceae), *Oxalis*, and Apiaceae as well as pteridophytes like *Isöetes* and *Equisetum* provide a broad sample for generating hypotheses about the evolution of geophytism in its many forms (e.g., bulb, corm, swollen hypocotyl). Nevertheless, we still lack sufficient taxonomic and morphological sampling to ask many outstanding questions about geophyte evolution and development. For example, what role does rhizome morphology play in the evolution of different belowground structures, if any? How does the evolutionary trajectory of corms found in Iridaceae (monocots) compare with that of Asteraceae (eudicots)? These, plus many other questions, placed within the broader evolutionary context of non-geophytes, would facilitate even greater insights into the ecological consequences associated with geophytism and the morphological relationships between different growth habits (Box 1).

### CONCLUSIONS

The integration of developmental, morphological, and phylogenetic studies can be messy, but studying geophytes requires getting our hands dirty from time to time. In this review, we have consolidated recent and not-so-recent work on the morphology, development, and evolution of geophytes. Since underground storage organs are often mischaracterized in the literature, we have provided guidance on the appropriate definitions of these sometimes-confusing morphological terms. To better understand how this morphological diversity is generated, we presented primary and secondary thickening growth as a partial framework for categorizing the developmental mechanisms that underlie belowground organ formation in roots and shoots, and pteridophytes and angiosperms. If developmental morphology is considered in a phylogenetic framework, then hypotheses for how, when, and why these diverse belowground structures have evolved can be proposed.

As a more detailed picture of geophyte morphology emerges, incorporating findings from morphological, genomic, and ecological studies into an ontological structure will prove to be a worthwhile endeavor. Such practices will bring confidence in comparability and data reusability across studies, and ontologies will improve our ability to holistically examine geophyte evolution by allowing interdisciplinary data integration. These efforts rely on the continuation of

detailed morphological study, a renewed commitment to building biological collections of diverse morphologies, and the adoption of novel analytical methods and phylogenetic studies of diverse taxa. Through these practices, we will be able to examine the hidden and complex aspects of geophytes’ morphology more thoroughly, bringing to light the belowground contributions to overall plant form and function. Below our feet awaits a buried trove of discovery; grab a shovel and start digging.

### ACKNOWLEDGMENTS

The authors thank Robbin Moran, Nhu Nguyen, Tim Harvey, Karen Zimmerman, Ryan Folk, William Baker, Zach Siders, and Arthur Villordan for images used in Figs. 1 and 2, University of Florida undergraduate researchers Halle Marchese and Kevin Truong for examining herbarium specimens to obtain the data found in Table 1, and Thomas Givnish, Pamela Diggle, an anonymous reviewer for *AJB* and three anonymous reviewers in prior submissions for their extensive feedback on earlier versions of this manuscript.

### AUTHOR CONTRIBUTIONS

C.M.T., J.M.-G. and C.C.H. proposed and developed the ideas underlying the manuscript and contributed equally; E.B.S., N.C., and C.D.S. guided concept development; all authors contributed to the writing of the manuscript.

### SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

**Appendix S1.** GBIF records used in calculating the information found in Table 1.

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