5-24-2012

Phylogeny and Evolution of Phemeranthus (Montiaceae) in North American Xeric Habitats

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Recommended Citation

Price, Taina, "Phylogeny and Evolution of Phemeranthus (Montiaceae) in North American Xeric Habitats" (2012). *All Theses and Dissertations (ETDs)*. 724.
https://openscholarship.wustl.edu/etd/724

WASHINGTON UNIVERSITY IN ST. LOUIS

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Phylogeny and Evolution of *Phemeranthus* (Montiaceae) in North American Xeric Habitats

by

Taina Matheson Price

A dissertation presented to the
Graduate School of Arts and Sciences
of Washington University in
partial fulfillment of the
requirements for the degree
of Doctor of Philosophy

May 2012

Saint Louis, Missouri

Abstract— The genus *Phemeranthus* (Montiaceae; fameflowers, rockpinks, sunbrights) comprises ca. 25 species of succulent, terete-leaved herbaceous perennials, mostly found in xeric rock outcrops and sand barrens. *Phemeranthus*’ center of diversity is in northern Mexico and the southwestern United States, but several species occur in glade and flat-rock ecosystems in the midwestern and southeastern United States. DNA sequences of chloroplast and low-copy nuclear regions were used to infer the phylogenetic relationships of *Phemeranthus* species. *Phemeranthus* (excluding *P. aurantiacus*) is monophyletic and likely sister to the remainder of Montiaceae. The genus contains two geographically structured and morphologically distinguishable clades: a southern clade centered in Mexico and a northern clade distributed primarily in the United States. Dramatic range disjunctions within each clade suggest broad-scale movements early in the genus’ diversification, while the current distribution indicates an origin in the southwestern United States and northern Mexico followed by northward and eastward expansion. Discordance between the chloroplast phylogeny and morphological species boundaries and between chloroplast and nuclear gene trees was further explored using multi-locus species-tree reconstruction methods. The results indicate that hybridization has played an important role in the evolution of this xerophytic genus. Finally, in a greenhouse-based experiment, seeds of the widespread species *P. parviflorus* collected from natural populations along a latitudinal gradient were chilled for varying periods prior to germination. The differential responses of seed germination to chilling duration for the sampled populations suggest the presence of local adaptation or at least of adaptive phenotypic plasticity, an important consideration for the use of this species in ecological restoration and green-roof projects.

***Keywords*—**chloroplast DNA, biogeography, disjunction, latitudinal cline, local adaptation, *matK–trnK*, maternal effects, Mexico, nuclear DNA, *ndhF*, *PepC*, *PhyB*, *PhyC*, phylogeny, Portulacineae, seed germination, southwestern United States, *Talinum*.

Acknowledgements**—**I thank my advisor, Barbara Schaal, and co-advisor, Peter Raven, for their support, encouragement, and enthusiasm for my research. I am deeply grateful for the generosity and mentorship of Paul Manos, my lab host and advisor during three years as a visiting student at Duke University. Additional support from W. Goldman enabled me to complete data collection at Duke. Many of my ideas and questions about *Phemeranthus* originated with D.J. Ferguson of Albuquerque, NM, who freely shared his expertise and unpublished manuscripts. The preliminary taxonomic treatment presented here is largely based on his work. I thank the numerous federal, state, and local land managers and private owners who permitted me to collect *Phemeranthus* on their lands. P. Price, D. Price, and I. Matheson helped with fieldwork, while W. Applequist, S. Brack, D. Burge, D.J. Ferguson, G. Ocampo, M. Ogburn, A. Weakley, and F. Zuloaga generously supplied DNA, seeds, and/or tissue samples. Special thanks are due to the greenhouse and sequencing center staffs at Washington University and Duke University, notably Mike Dyer, Michael Barnes, and Lisa Bukovnik. I also thank the administrative staff at Washington University's Division of Biology and Biomedical Sciences and Department of Biology, especially Melissa Torres and Anastasia Zylka, and at Duke University, especially Jo Bernhardt. Thanks to J. Reece and E. Green for help with analytical methods, M. Heaton for statistical advice, Y.-C. Chiang for help with primer design, J. E. Meireles for figure preparation, and D. Swofford for providing a test version of PAUP* 4.0. J. Beck, L. Johnson, R. Kiger, K. Krakos, B. Oberle, G. Ocampo, and other colleagues provided stimulating discussions and helpful comments on various manuscript drafts. Graduate research awards from Sigma Xi and the American Society of Plant Taxonomists helped to fund this study.

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CHAPTER I. BACKGROUND AND CONTEXT

Abstract— The genus *Phemeranthus* (Montiaceae; fameflowers, rockpinks, sunbrights) provides a case study in the diversification and distributional history of narrowly restricted species and their more widespread congeners in xeric habitats of North America. Fameflower species exhibit wide variation in geographic range size and habitat specificity. Some are widespread in North America, while others are endemic to one or a few localities. All species are restricted to shallow or sandy soils, often on rock outcrops; but some appear to be edaphic specialists, while others occur on a relatively wide range of soil types. Previously considered part of the genus *Talinum*, *Phemeranthus* species are now recognized as a distinct genus belonging to the family Montiaceae, which has been segregated from the traditional Portulacaceae. The taxonomic history of the group is summarized, and its phylogenetic context within the order Caryophyllales, suborder Portulacineae, and family Montiaceae are discussed. The morphology, natural history, physiology, and cytology of *Phemeranthus* species are reviewed, with a particular focus on the relatively well-studied species of the midwestern and southeastern United States. The biogeographical context of the genus' diversification is also discussed, emphasizing the nature and development of micro-desert habitats in the midwestern and eastern United States. Finally, emerging questions and hypotheses are presented to frame the subsequent chapters.

Introduction: Rarity and Endemism in Evolutionary Biology—Plant species exhibit a broad spectrum of geographic distributions. While some are nearly cosmopolitan, others are confined to only one or a few localities in a highly specific habitat type. Species with restricted geographic distributions are of great interest to evolutionary biology, as they may provide insight into the conditions promoting the origin, geographic spread, and persistence or extinction of taxa through time (Gaston 2008).

Systematic and population genetic research on rare species also carries strong conservation implications. The “hollow curve” distribution of species’ range sizes indicates that species with relatively restricted geographic distributions account for the majority of biodiversity (Brown et al. 1996; Gaston 1996, 1998; Gaston and He 2002). As the global human population continues to grow and its impact on natural processes and ecosystems continues to increase, these rare and endemic species may be especially sensitive to population decline and habitat loss.

Furthermore, while a few invasive species may benefit from human activity, habitat disruption and global climate change are likely to drive many more species toward rarity. Unless species are able to undergo wholesale geographic and habitat shifts in response to changing climate and habitat availability, they will be forced either to rapidly evolve new tolerances or to go extinct (Iverson and Prasad 1998; Davis and Shaw 2001; Reusch and Wood 2007; Hoffmann and Sgrò 2011). It is therefore imperative to understand the factors that contribute to the origin and maintenance of range restrictions and to predict how these may be affected by ongoing climate change (Sexton et al. 2009).

Stebbins (1942) proposed that rare species contain little genetic variation either because they have not yet developed much or because their genetic diversity has been depleted. However, some narrow endemics possess high genetic diversity. Recent reviews have found that while most rare species are less genetically diverse than their common relatives, some have equal or even greater diversity (Hamrick and Godt 1989; Gitzendanner and Soltis 2000). Stebbins (1980) later argued that rarity results from the interaction of genetic architecture, population structure, and localized ecological factors.

Species with highly restricted ranges or habitat preferences have originated in a variety of phylogenetic and environmental contexts. Historical factors may play a role: endemic species occur more frequently in some clades than in others. However, there are numerous examples of closely related species that differ in range size and habitat specificity (e.g., Coates et al. 2003; Moyle 2006). Therefore, phylogenetic methods are a critical component in reconstructing the past and predicting the future of any rare species or group of species that includes such taxa. Molecular phylogenetic data provide historical insight and help to reconcile competing hypotheses of vicariance and dispersal for the origins of species (Schaal et al. 1998).

Phylogenetic studies in an explicit geographic context can assess the relative roles of history and landscape in the evolution of endemic species. Such analyses can help to distinguish between alternative hypotheses concerning the origin and relationships of particular species. For example, plant geographers Engler and Willis proposed that narrow endemics were either youthful species that had not yet expanded their ranges or senescent species that had suffered range contraction (see Kruckeberg and Rabinowitz 1985). These alternatives would lead to different predictions concerning the phylogenetic position of endemics within a broader clade. Understanding the phylogenetic position of a given taxon (for example, whether a narrow endemic is closely related to a more widespread congener or whether it represents a highly divergent lineage) is important in establishing conservation priorities and planning effective management activities.

The genus *Phemeranthus* Rafinesque (Montiaceae; fameflowers, rockpinks, sunbrights) provides a case study in the diversification and distributional history of narrowly restricted species and their more widespread congeners in a North Temperate arid zone. *Phemeranthus* comprises approximately 25 species of succulent, herbaceous perennials with terete leaves and fleshy roots, most of which grow in patchy, xeric habitats such as rock outcrops and sand barrens (Figs. 1.1, 1.2; Table 1.1). Over a century ago, Harshberger (1897) claimed that, among American Portulacaceae, “there is no more interesting genus from an ecologic standpoint than the genus *Talinum*”. He referred specifically to “that group of the genus with round leaves, as distinguished from those species which have leaves more or less flattened” – that is, to the group now recognized as *Phemeranthus*. These species, he noted, were impressively adapted to withstand the long periods of drought, high temperatures, and intense sunlight characteristic of their bare, rocky habitats.

FIGURE 1.1 (FOLLOWING PAGE). Photographs of *Phemeranthus* species. A) *P. brevifolius*, UT; B) *P. confertiflorus*, AZ; C) *P. mengesii*, AL; D) *P. parvulus*, AZ; E) *P. punae*, Jujuy, Argentina (photo courtesy F. Zuloaga); F) *P. longipes*, NM; G) *P. calycinus*, AR; H) *P. sediformis*, WA; I) *P. thompsonii*, UT.

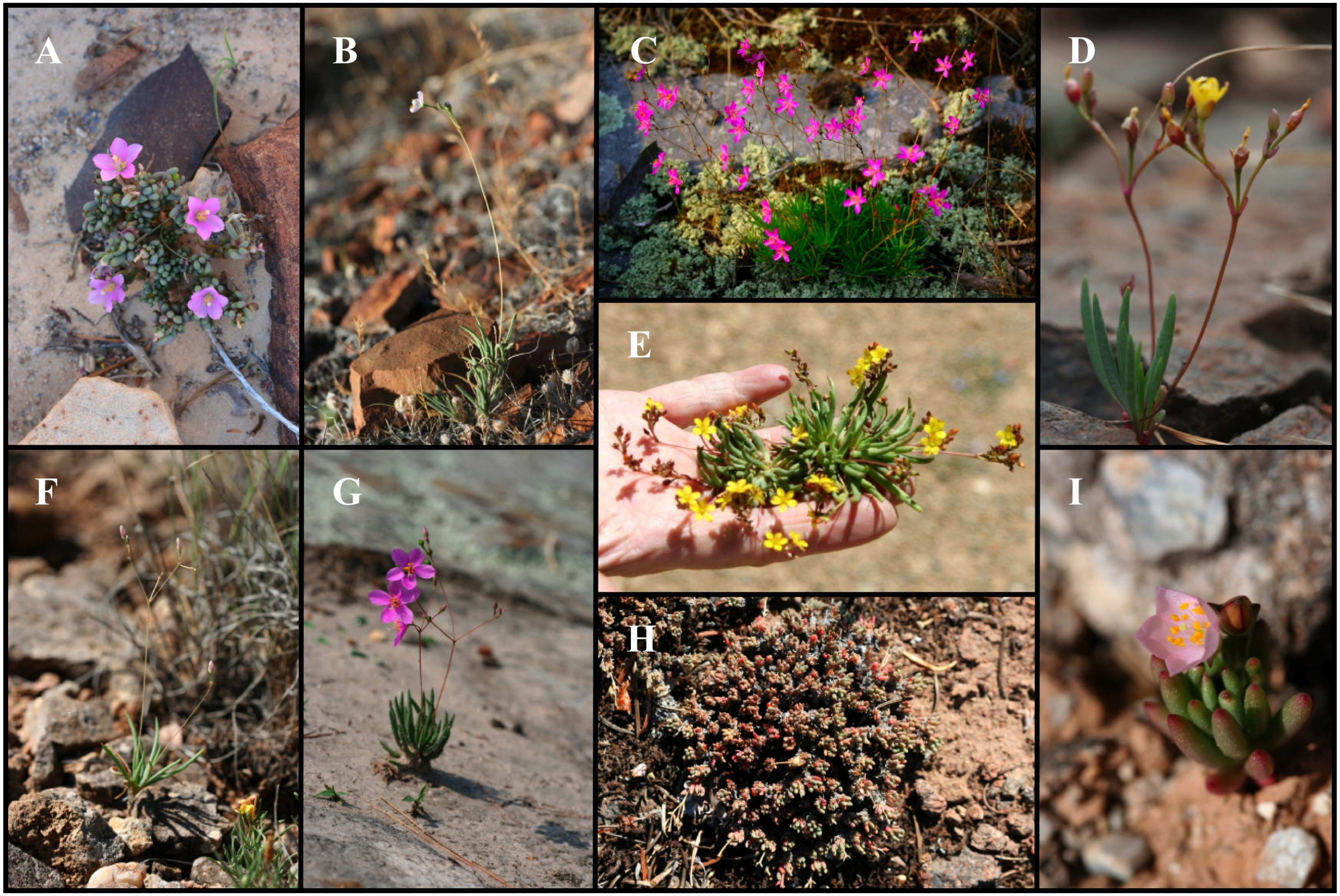
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TABLE 1.1. Distribution and substrate affinity of *Phemeranthus* species

Taxon	Approximate Distribution	Substrates
P. brevicaulis	Trans-Pecos NM & TX, n. Coahuila & Chihuahua, Mexico	Calcareous
P. brevifolius	Colorado Plateau, AZ, UT, & NM	Sandstone
P. calcaricus	Central Basin of TN, n. AL	Limestone
P. calycinus	Ozark and Ouachita highlands, AR and MO; Great plains, NE and CO south to cent. TX	Sandy prairie & sandstone outcrops; various, usually non-calcareous rock outcroppings
P. humilis	sw. NM, s. AZ, to cent. Chihuahua, Mexico	
P. longipes	n. cent. NM to n. Coahuila & Chihuahua, Mexico	Calcareous
P. mengesii	Southern Appalachia, AL, GA, & TN	Various, non-calcareous rock outcroppings
P. mexicanus	San Luis Potosi to Oaxaca, Mexico	
P. multiflorus	Durango, Mexico	
P. napiformis	Madrean region, Durango, San Luis Potosi, south to Mexico City, Mexico	Shallow soil over surfacing rock
P. oligospermus	n. cent. Mexico	
P. parviflorus	Southern Rocky Mts., Colorado Plateau, & northern Madrean region, UT, AZ, NM, w. cent. Chihuahua, & ne. Sonora, Mexico; e. Great Plains & Interior Highlands, ND south to TX & KS east to IL; cent. AL	Non-calcareous rock outcroppings and sandy prairie
P. parvulus	s. AZ & n. Mexico	Various
P. punae	Puna region, s. Andes, Bolivia & Argentina	Scree
P. piedmontanus	Piedmont, n. NC & s. VA	Mafic and ultramafic outcrops
P. rugospermus	Sandhill prairies in MN, WI, IL, IN; NE; KS; OK; e. TX & w. LA	Eolian sand, sandstone
P. sediformis	Okanagan highlands, n. WA & s. BC	Metamorphic
P. spinescens	Columbia Plateau, e.-cent. WA to n. OR	Basalt
P. teretifolius	Piedmont & Appalachia, PA to GA	Various, usually non-calcareous rock outcroppings; shale, serpentine
P. thompsonii	Cedar Mt., cent. UT	Siliceous conglomerate
P. validulus	s. UT to n. AZ	Shallow clay soils; various

Fameflower species exhibit wide variation in geographic range size and habitat specificity. Some are widespread in North America, while others are endemic to one or a few localities (Table 1.1). For example, *P. thompsonii* (N.D. Atwood & S.L. Welsh) Kiger is known from a single location in east-central Utah; *P. brevifolius* (Torr.) Hershkovitz is widespread throughout a single geographic region, the Colorado Plateau (Fig. 1.2B); and *P. parviflorus* (Nutt.) Kiger ranges from the Texas Gulf Coast to the Dakotas and from the Rocky Mountains to the southern Appalachians. All species are restricted to shallow or sandy soils, often on rock outcrops; but some appear to be edaphic specialists, while others occur on a relatively wide range of soil types (Reinhard and Ware 1989; Ware and Pinion 1990). For example, *P. calcaricus* (S. Ware) Kiger is found only on limestone cedar glades in central Tennessee (Fig. 1.2G), while *P. parviflorus* is found on sand dunes, on exposed outcrops of a variety of non-calcareous rocks (Fig. 1.2C), and in open shallow-soil grasslands. This variation in distribution, range size, and habitat specificity makes the genus an ideal study system for research on the patterns and processes involved in the evolution of species' distributions.

This thesis focuses on the phylogenetic relationships and geographical patterns of *Phemeranthus*. The results of these analyses clarify the relationships of several rare and threatened taxa that have been rather poorly known and provide insight into their biogeographic histories. Additionally, the possibility of clinal adaptation in a widespread, selfing member of the genus is examined by testing seed germination responses to chilling duration. This research has potential implications for conservation planning and for the increasing horticultural use of fameflowers in water-conservative gardening and green-roof plantings (e.g., Getter et al. 2009; Dvorak 2010).

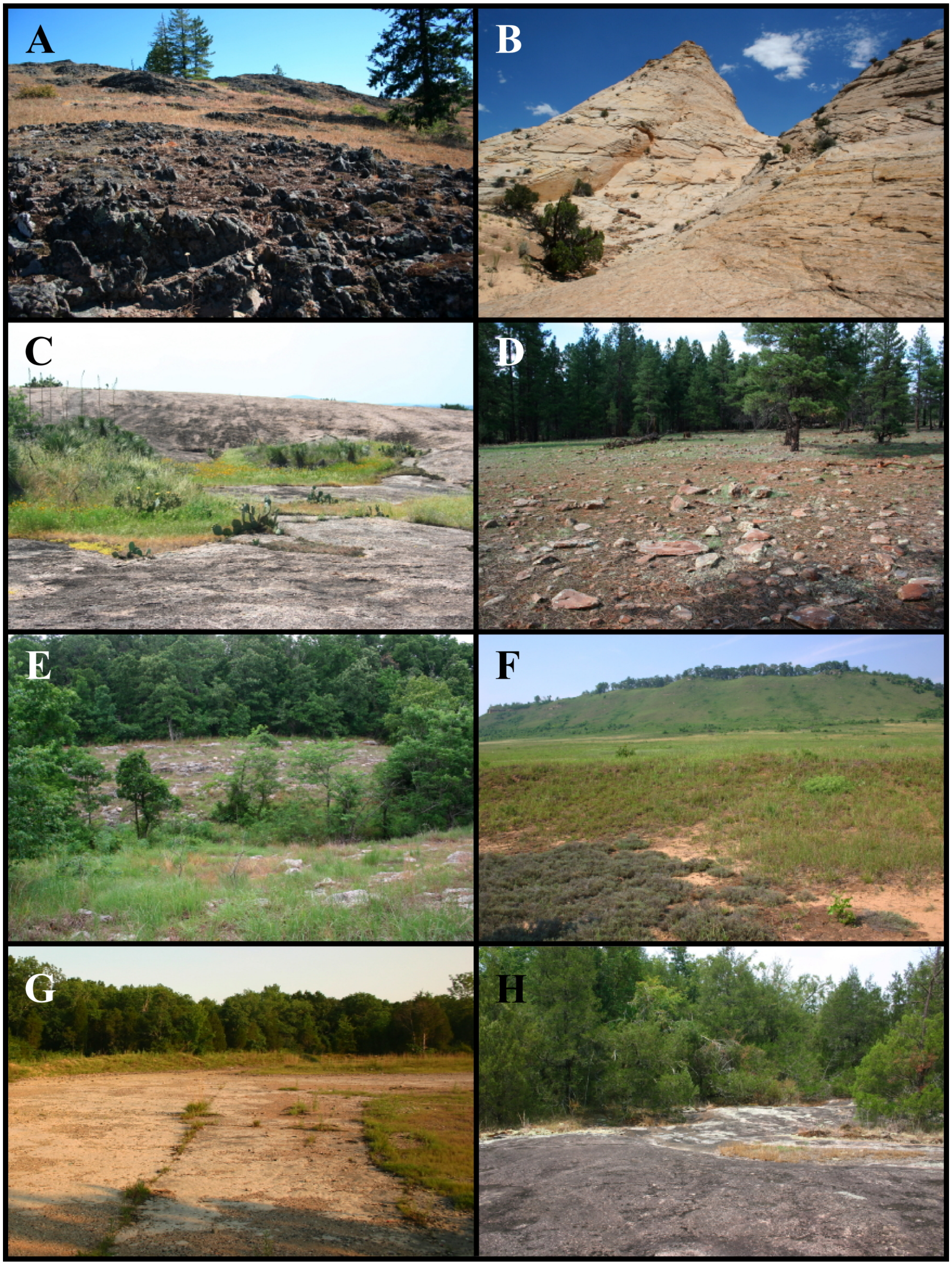

FIGURE 1.2. *Phemeranthus* habitats. A) Mountain bald, WA, *P. sediformis*; B) Sandstone, UT, *P. brevifolius* and *P. confertiflorus*; C) Granite, TX, *P. parviflorus*; D) Opening in Ponderosa pine, AZ, *P. validulus* and *P. confertiflorus*; E) Ozark glade, MO, *P. calycinus*; F) Sand blow, WI, *P. rugospermus*; G) Limestone cedar glade, TN, *P. calcaricus*; H) Granite flatrock, AL, *P. mengesii*.

***Taxonomic History of* Phemeranthus—**

Phemeranthus has a somewhat convoluted taxonomic history. The type species, which is native to Appalachia and the Piedmont region of the eastern United States, was first validly described by Frederick Pursh in 1814 as *Talinum teretifolium* Pursh. Constantine Rafinesque had published the name *Phemeranthus teretifolius* in 1808, but the name was invalid (nomen nudum) because no type was specified.

Other known species of *Talinum* Adanson had flattened leaves. Believing the new terete-leaved species to be sufficiently distinct from *Talinum* as to merit its own genus, Rafinesque validated the generic name *Phemeranthus* when he published the combination *P. teretifolius* (Pursh) Raf. in 1814. Augustin Pyramus de Candolle described a second terete-leaved species in 1828, this one from Mexico (*Talinum napiforme* DC.), and assigned it and *T. teretifolium* to *Talinum* sect. *Phemeranthus*. Rafinesque thought that *T. napiforme* also warranted its own genus; he published the combination *Eutmon napiforme* (DC.) Raf. in 1833. Numerous additional terete-leaved species have been described since 1828; notably, J. N. Rose and Paul C. Standley (Rose and Standley 1911) and Edward L. Greene (Greene 1912) described multiple species from the southwestern United States and northern Mexico. The most recently published taxon is *Phemeranthus piedmontanus* S. Ware (2011).

Like much of Rafinesque's work, the generic names *Phemeranthus* and *Eutmon* were generally ignored by subsequent workers, who almost universally followed de Candolle in treating the terete-leaved species as *Talinum* sect. *Phemeranthus*. However, in the most recent monograph of the group, von Poellnitz (1934) did not recognize any basis for maintaining the sectional divisions in *Talinum*. He recognized 47 species of

Talinum, mostly in the southwestern United States and Mexico. All members of *Talinum* sens. lat., both flat- and terete-leaved, are primarily succulent, herbaceous to suffrutescent perennials with fleshy taproots. They possess cymose inflorescences, and each pedicellate flower has two sepaloid bracts and usually five petals (tepals). Their unilocular, three-valved capsules dehisce longitudinally and often circumscissilely at the base. The seeds are reniform with coiled embryos and are borne on free-central placentae. However, these resemblances between *Talinum* and *Phemeranthus* may be symplesiomorphies (i.e., characteristics inherited from the common ancestor of Portulacineae) (Applequist and Wallace 2001). In fact, species of *Talinum* sect. *Phemeranthus* are clearly distinguished from those of *Talinum* sect. *Talinum*. Careful morphological (Carolin 1987; Hershkovitz 1993) and molecular (Hershkovitz and Zimmer 1997, 2000; Applequist and Wallace 2001; Nyffeler and Eggli 2010) studies revealed the need for taxonomic revision, demonstrating that *Phemeranthus* is only distantly related to *Talinum*.

Several morphological traits differentiate the two groups. *Phemeranthus* species possess pantocolpate pollen, while *Talinum* pollen is panporate (Carolin 1987). *Phemeranthus* capsules are held erect or nearly so (rarely pendent) and dehisce basipetally. In contrast, *Talinum* capsules are pendent to horizontal on curved pedicels and dehisce acropetally. The *Phemeranthus* fruit pericarp is undifferentiated; in *Talinum*, the exocarp and endocarp are differentiated and sometimes separate at maturity. *Phemeranthus* seeds are covered by a chartaceous membrane of funicular origin (“pellicle”). *Talinum* seeds are strophiolate but lack an investing pellicle (Carolin 1987; Hershkovitz 1993).

In addition, the basic difference in leaf morphology extends to the internal anatomy of the leaf. In *Phemeranthus*, the palisade mesophyll extends all the way around the leaf (see Ocampo and Columbus 2010, Fig. 5H), and the midvein is not externally visible. The leaves are sometimes slightly dorso-ventrally compressed, and young leaves that have been appressed in winter buds may be nearly planar adaxially with angular edges (D-shaped in cross-section) (pers. obs.). However, there is no defined lateral margin. *Talinum* species possess flattened leaves with palisade mesophyll only on the adaxial side (Ocampo and Columbus 2010). Although the margins may be revolute, particularly under drought conditions, at least the midvein is prominently visible.

Molecular phylogenetic data also indicate that the two groups are not closely related. *Talinum* sens. str. is more closely related to *Portulaca* L. and Cactaceae than to *Phemeranthus*, whose close relatives are western North American genera including *Calandrinia* Kunth, *Cistanthe* Spach, *Claytonia* L., *Lewisia* Pursh, and *Montia* L. (Hershkovitz and Zimmer 1997, 2000; Applequist and Wallace 2001; Applequist et al. 2006; Nyffeler and Eggli 2010). As a result, *Phemeranthus* has gained recognition as a separate genus. Most terete-leaved *Talinum* species distributed in the United States have been transferred to *Phemeranthus* (Hershkovitz and Zimmer 1997; Kiger 2001) and are treated as such in the *Flora of North America* (Kiger 2003). Three Mexican species have also been transferred previously (Ocampo 2002, 2003), along with a disjunct species found in northern Argentina (Nyffeler and Eggli 2010).

In addition to the terete-leaved species, Kiger (2001, 2003) placed within *Phemeranthus* the linear-leaved species *Talinum aurantiacum* Engelm. [including *T. angustissimum* (Engelm.) Wooton & Standl. and *T. whitei* I.M. Johnst., which he treated as synonyms of *T. aurantiacum*], although other workers (Applequist, pers. comm.; Ferguson, pers. comm.; Ocampo, pers. comm.; Ogburn, pers. comm.) consider these taxa to belong to *Talinum* sens. str. Molecular phylogenetic data are needed to establish whether *Phemeranthus* is monophyletic as treated by Kiger (2001, 2003) or whether the inclusion of *P. aurantiacus* (Engelm.) Kiger renders *Phemeranthus* polyphyletic.

Phylogenetic Context—

Phemeranthus belongs to the family Montiaceae, part of the traditionally recognized Portulacaceae sens. lat. The various families segregated from Portulacaceae, together with Cactaceae and other closely allied families, make up the suborder Portulacineae (Nyffeler and Eggli 2010), also known as Cactineae (Ocampo and Columbus 2010). This group is part of the order Caryophyllales (APG 2009). Below, the phylogeny and characteristics of these higher-level groups are summarized to provide a context for studies of *Phemeranthus*.

The order Caryophyllales largely corresponds to the long-recognized Centrospermae, a cohesive group distinguished by its free-central or basal placentation and a suite of embryological traits (Cronquist 1988). The discovery that most members of this group possessed betalain rather than anthocyanin pigments led to an expanded circumscription, as the betalain-containing Cactaceae and Didiereaceae were added. Caryophyllales are also distinguished by a unique type of sieve-tube plastid containing a ring of protein filament bundles (Cronquist 1988). Based on these and other morphological, ultrastructural, and chemical traits, Dahlgren (1975), Thorne (1976), Takhtajan (1980), and Cronquist (1981, 1988) all recognized Caryophyllales as including

Phytolaccaceae, Achatocarpaceae, Nyctaginaceae, Aizoaceae, Didiereaceae, Cactaceae, Chenopodiaceae, Amaranthaceae, Portulacaceae, Basellaceae, Molluginaceae, and Caryophyllaceae. They also recognized a close relationship between Caryophyllales and the families Polygonaceae and Plumbaginaceae; Cronquist (1988) assigned the latter families to Polygonales and Plumbaginales, respectively, and placed both orders together with Caryophyllales in a subclass Caryophyllidae.

Subsequently, molecular phylogenetic analyses have clarified the circumscription of the order, demonstrating that Polygonaceae and Plumbaginaceae; Droseraceae, Nepenthaceae, and Drosophyllaceae (the carnivorous clade); Ancistrocladaceae, Dioncophyllaceae, Frankeniaceae, and Tamaricaceae also belong to Caryophyllales sens. lat. (The Angiosperm Phylogeny Group 2009). This latter large clade is well supported (Soltis et al. 2011) and has sometimes been recognized as a separate order, Polygonales (Judd et al. 1999).

Many members of Caryophyllales feature unusual ecological and/or physiological traits, including carnivory, highly modified growth habits, and tolerance of saline or highly arid conditions (Stevens 2001 onwards). Anomalous secondary growth is common in the group (Cronquist 1988; Carlquist 2010). C_4 and CAM (crassulacean acid metabolism) photosynthesis and succulent growth are also widespread in Caryophyllales, suggesting adaptation to high temperatures and arid climates (Cronquist 1988). The fact that contemporary Caryophyllales often inhabit marginal, xeric habitats suggests that ancestral Caryophyllids evolved in similarly warm, arid habitats with mineral soils (Ehrendorfer 1976). Cronquist (1988) interpreted the common ancestor of Caryophyllidae as an herbaceous plant with separate carpels, superior ovaries, and lacking petals.

The order has a sparse and relatively short fossil record, dating back only to about 70–80 million years ago (Cronquist 1988; Wikstrom et al. 2001). Calibrated molecular phylogenies using a variety of genes and dating methods have recovered dates ranging from 104 to 116 million years ago for stem-group Caryophyllales and from 83 to 102 million years ago for the crown group (Wikstrom et al. 2001; Anderson et al. 2005; Magallón and Castillo 2009). An origin around 104–111 million years ago (Wikstrom et al. 2001) would predate the major diversification of insect pollinators, consistent with the hypothesis that ancestral Caryophyllids were wind pollinated (Ehrendorfer 1976).

Molecular data have produced many successive refinements of the relationships within Caryophyllales (Rettig et al. 1992; Downie and Palmer 1994; Downie et al. 1997; Cuenoud et al. 2002; Brockington et al. 2009). Using nine plastid genes, two nuclear genes, and the plastid inverted repeat, Brockington et al. (2009) studied the higher-level phylogeny of Caryophyllales sens. lat. and tested hypotheses related to pollination biology and perianth differentiation. They evaluated the classical hypothesis that the ancestral caryophyllid flower had an undifferentiated perianth and was wind-pollinated because these plants evolved in dry, marginal environments where pollinators were scarce. They found little support for wind pollination as the ancestral condition, although their analysis did suggest that an undifferentiated perianth was the ancestral condition. Subsequently, a differentiated perianth evolved at least nine independent times (Brockington et al. 2009).

Within core Caryophyllales, Portulacaceae sens. lat. is part of a well-supported group along with Basellaceae, Cactaceae, Didiereaceae, and Halophytaceae (Fig. 1.3). This group was first recognized by Thorne (Thorne 1968, 1976) and is united by the presence of a floral involucre, succulence, mucilage, and Crassulacean acid metabolism (Thorne 1976; Stevens 2001 onwards; Cuenoud et al. 2002) and by certain pollen exine characters (Nowicke 1996). The monophyly of this group of families was supported by early molecular phylogenetic studies of Caryophyllales (Rettig et al. 1992; Downie and Palmer 1994; Downie et al. 1997); its probable sister group is Molluginaceae (Cuenoud et al. 2002; Brockington et al. 2009). The group has been informally known as the "portulacaceous cohort" (Applequist and Wallace 2001; Cuenoud et al. 2002; Brockington et al. 2009) or "portulacaceous alliance" (Hershkovitz 1993; Hershkovitz and Zimmer 1997) and formally as the suborder Portulacineae (Takhtajan 1997; Nyffeler et al. 2008; Nyffeler and Eggli 2010) or Cactineae (Thorne 2000; Ocampo and Columbus 2010). Here, I use the name Portulacineae.

Members of Portulacineae are found in Mediterranean, desert, alpine, and boreal habitats on four of the six continents. The group is poorly represented in Eurasia and in Africa north of the equator (Hershkovitz and Zimmer 2000), and its members are predominantly distributed in the New World (Applequist et al. 2006). Molecular data (e.g., Applequist and Wallace 2001) support the hypothesis that Portulacineae originated in South America or southern North America.

Portulacineae is especially interesting in that about 90% of its ~2200 species are succulent to some degree in leaf, stem, and/or root, including representatives of all three major types of succulent life forms: stem succulents, leaf succulents, and caudiciform and pachycaul succulents (Nyffeler et al. 2008). This diversity appears to reflect parallel evolution of distinct succulent life-forms from similar ancestral conditions. Most Portulacineae inhabit warm, arid environments, and possibly all members of the group have at least some ability to recycle respired CO_2 under drought conditions via facultative CAM-cycling.

This large clade represents one of the many origins of a differentiated perianth within Caryophyllales. In Portulacineae, preceding bracts have been recruited to form perianth parts. This involucre consists of two leafy sepaloid bracts below the petaloid perianth parts. The phyllomes or bracts enclose the developing floral meristem, thus playing the role of a calyx. The petaloid parts, meanwhile, are derived from bracts (or sepals) rather than from stamens. The ancestral condition of the clade is a uniseriate pentamerous flower (Brockington et al. 2009). Portulacaceae sens. lat. have diverse pollen, varying from tricolpate to pantocolpate, polypantocolpate, pantoporate, or polyporate, with echinate to almost glabrous surface ornamentation (Nyananyo and Mensah 2004). Basic chromosome numbers range from two to twelve (Nyananyo and Mensah 2004). Like most Caryophyllales, portulacaceous plants contain betalains rather than anthocyanins in their floral and vegetative tissues (Nyananyo and Mensah 2004).

As traditionally circumscribed, Portulacaceae included several more or less cosmopolitan genera along with genera endemic to Africa, Madagascar, Oceania, Eurasia, North America and South America, suggesting a pre-Tertiary origin (Hershkovitz and Zimmer 1997). The family was hypothesized to have originated in Gondwanaland (Applequist and Wallace 2001) and to have spread by long-distance dispersal following its breakup (Nyananyo and Mensah 2004). Portulacaceae sens. lat. was thought to have originated relatively recently, in the late Miocene (UCMB 1994-2007), in part because the habitats occupied by most contemporary Portulacaceae and allied families formed during the Miocene or later. However, the fossil record of the group is almost non-existent. Possible *Montia*-like pollen has been reported from the Cenomanian of Iowa (Ravn 1987), but this interpretation of the fossil is suspect (Hershkovitz and Zimmer 2000). Polyrugate Portulacaceae-like pollen has also been reported from the upper Miocene and Pliocene of Alaska (Muller 1981). Despite their often distinctive pollen and durable cuticles, spines, and glochids, Cactaceae have not left a fossil record. Arid-adapted portulacaceous lineages likely originated during the late Cretaceous or early Tertiary after the breakup of Gondwana and later spread with the widespread aridification in the late Tertiary (Raven and Axelrod 1974). Hershkovitz & Zimmer (2000) suggested a late Eocene to Miocene origin for Cactaceae. They attributed the present-day distributions of portulacaceous taxa to late Tertiary–early Quaternary climate trends that caused the development of arid habitats in temperate regions of western North and South America, thus opening new niches and promoting speciation (Raven 1963; Raven and Axelrod 1974, 1978; Axelrod 1979, 1983). The many 5000–15000-km disjunctions within Portulacineae show low ITS divergences, suggesting relatively recent long-distance dispersal. Morphological evidence also suggests that disjunctions in *Talinum*, *Phemeranthus*, other western North American genera, and Cactaceae are due to recent long-distance dispersal (Hershkovitz and Zimmer 2000).

Portulacineae comprises four major lineages (Fig. 1.3): Basellaceae (small-flowered vines with fleshy rhizomes or tubers from Africa and Central and South America); Didiereaceae (large woody trees or shrubs, some cactus-like, from eastern and southern Africa and Madagascar); Montiaceae (herbaceous plants, often rosette-forming, with clasping, non-constricted leaf bases, mostly from North and South America and Australia); and the large, diverse "ACPT clade", which includes Anacampserotaceae, Cactaceae, *Portulaca* (Portulacaceae sens. str.), and *Talinum* (Talinaceae) (Stevens 2001 onwards; Nyffeler et al. 2008; Nyffeler and Eggli 2010). Although relationships within Portulacineae, especially within the ACPT clade, remain somewhat problematic, the ACPT clade as a whole is consistently well supported (Hershkovitz and Zimmer 1997; Applequist and Wallace 2001; Nyffeler 2007; Brockington et al. 2009; Nyffeler and Eggli 2010). Thus, Portulacaceae sens. lat. is paraphyletic with respect to Cactaceae, necessitating either the lumping of Cactaceae into Portulacaceae—an unattractive prospect—or the recognition of several small segregate families (Hershkovitz and Zimmer 2000), leaving only *Portulaca* in Portulacaceae sens. str. (APG 2009; Nyffeler and Eggli 2010).

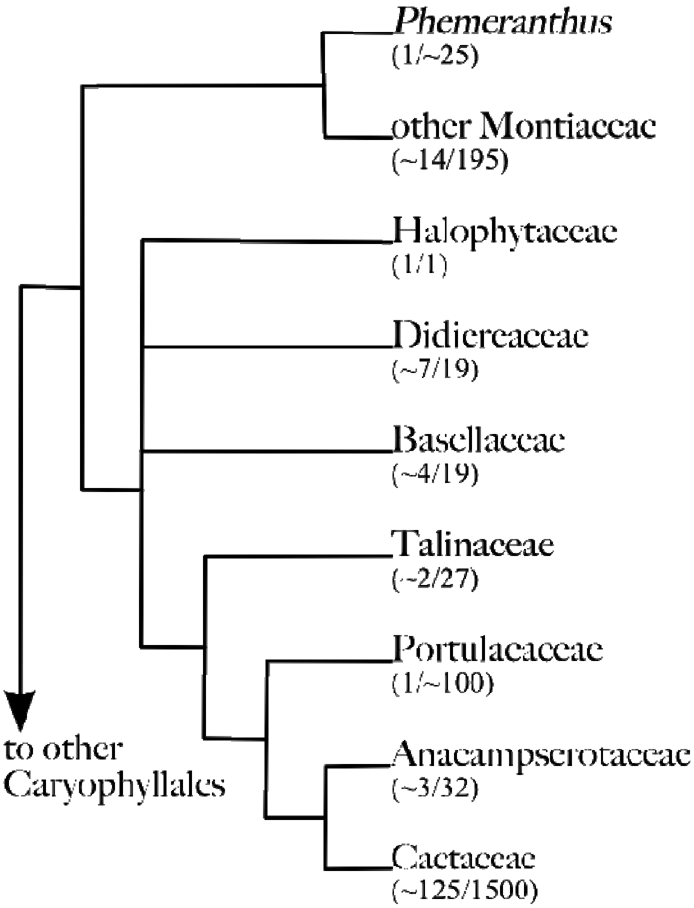

FIGURE 1.3. Schematic cladogram showing relationships in Portulacineae. Approximate numbers of genera and species are given for each family. Tree based on Nyffeler & Eggli (2010), Fig. 1; genera and species numbers from Nyffeler & Eggli (2010) and Stevens (2001 onwards).

This breakdown of the traditional Portulacaceae and that of *Talinum* within it were hinted at by early morphological cladistic studies of the group. In a 1987 review, Roger Carolin performed a cladistic analysis of Portulacaceae at the generic and sectional level using 40 morphological characters. Accepting the classical view that Cactaceae and Aizoaceae were close relatives, he used those families as the outgroup to Portulacaceae + [Basellaceae + Didiereaceae]. This rooting resulted in a rather chaotic tree, with most tribes and several genera appearing polyphyletic. *Talinum* sect. *Phemeranthus* never formed a clade with *Talinum* sect. *Talinum*. Carolin noted that the investing aril of sect. *Phemeranthus* was an important difference from sect. *Talinum*, but its homology was difficult to interpret, and *Talinum* needed further study. He did not propose to divide the genus, and his analyses recovered sect. *Phemeranthus* as sister to a large clade including portions of various genera that are now assigned to Talinaceae, Montiaceae, Portulacaceae, and Anacampserotaceae. The genera now assigned to Montiaceae were divided among several clades (Carolin 1987).

Subsequently, Hershkovitz (1993) used 46 morphological characters in a cladistic analysis focusing on the relationships of *Calandrinia*. Like Carolin (1987), Hershkovitz found support for a fundamental division of Portulacaceae and their relatives between predominantly eastern American and African taxa (which were paraphyletic with respect to Basellaceae, Cactaceae, and Didiereaceae) vs. western North and South American and Australian taxa. He recovered *Talinum* sect. *Phemeranthus* in a basal position within the former group, although it did not form a clade with *Talinum* sect. *Talinum*. Hershkovitz (1993) suggested that additional phylogenetic analyses would support segregating "most or all of the western American taxa into a distinct family, expanding the existing circumscriptions of Cactaceae, Basellaceae, and Didiereaceae to include their portulacaceous sister taxa, and retaining Portulacaceae only for their monophyletic residue."

In a phylogenetic study directed at understanding the evolutionary relationships and antiquity of Cactacaeae, Hershkovitz and Zimmer (1997) regarded *Phemeranthus* as distinct from *Talinum* and published nomenclatural combinations for the three *Phemeranthus* species in their ITS data set [*P. brevifolius* (Torr.) Hershkovitz, *P. confertiflorus* (Greene) Hershkovitz, and *P. spinescens* (Torr.) Hershkovitz]. In contrast to the earlier morphological analyses, they recovered *Phemeranthus* in the western American and Australian clade of Portulacaceae, rather than the eastern American and African clade. The six *Talinum* and *Talinella* Baill. exemplars did not form a clade, but their positions lacked support. The three *Phemeranthus* exemplars formed a strongly supported clade that was sister to a group consisting of an Australian *Calandrinia*, two *Cistanthe* species, and a *Montia*. The authors referred to this large clade as the PAW clade (for *Phemeranthus*, Australia, Western America) (Hershkovitz and Zimmer 1997, 2000). It in turn was sister to the ACPT clade, though with poor support.

Applequist and Wallace (2001) applied sequence data from the chloroplast gene *ndhF* to further elucidate relationships among the major lineages of Portulacaceae, Basellaceae, Cactaceae, and Didiereaceae. They found two large clades within this group: the ACPT clade and the remainder of Portulacaceae (including the terete-leaved *Talinum mengesii*) plus Basellaceae and Didiereaceae. Thus, their chloroplast sequence data reinforced the earlier morphological and molecular evidence that *Talinum* sens. lat. was polyphyletic, with terete-leaved *Phemeranthus* being unrelated to true *Talinum*. The polyphyly of *Talinum* may have contributed to the failure of previous infrafamilial classifications to correspond to monophyletic groups (Applequist and Wallace 2001).

Subsequently, Applequist and colleagues (Applequist et al. 2006) added the enigmatic New Zealand cushion-forming plant *Hectorella caespitosa* Hook. f. to the *ndhF* dataset, also incorporating *matK* and *rbcL* sequences for many taxa. The familial placement of *Hectorella* had been controversial; variously associated with Portulacaceae and Caryophyllaceae, it had commonly been accepted as a separate family within Caryophyllales, Hectorellaceae. The molecular data showed that not only did *Hectorella* belong within Portulacaceae, but it was nested within the PAW clade.

As support for the monophyly of the PAW clade accumulated (Hershkovitz and Zimmer 1997, 2000; Applequist and Wallace 2001; Applequist et al. 2006; Nyffeler 2007), it was recognized at the family level as Montiaceae (APG 2009; Nyffeler and Eggli 2010). After the hyper-diverse Cactaceae, Montiaceae is the most diverse clade within Portulacineae, with about 200 species in 15 genera (Table 1.2) (Hershkovitz and Zimmer 1997; Nyffeler and Eggli 2010). All are low-growing herbaceous plants. The species in this group are divided approximately equally between North and South America, with concentrations in California and northern Chile (Hershkovitz 2006) and members in Australia and New Zealand. Using a rough calibration based on published divergence rates for the ribosomal DNA internal transcribed spacer region (ITS), Hershkovitz and Zimmer (2000) estimated that this group originated during or later than the mid-Miocene.

Montiaceae are notable for their pattern of closely related species in temperate North and South America (Hershkovitz 1993; Hershkovitz and Zimmer 2000; Hershkovitz 2006), a pattern recognized in several plant groups (Raven 1963). *Phemeranthus* is one example, with a single species found in the southern Andes and the remainder north of the Isthmus of Tehuantepec in Mexico. Raven & Axelrod (1978) argued that the North American taxa in this group were derived from South American ancestors. Hershkovitz and Zimmer (2000) focused on the relationships and biogeography of western American Portulacaceae using ITS data. Their analysis strongly supported the monophyly of the PAW clade (i.e., Montiaceae) and indicated multiple intercontinental disjunctions, with 8–13 dispersal and colonization events across distances exceeding 2000 km. However, the choice of outgroup would affect the ancestral area inferred for *Phemeranthus*. If the chosen outgroup were distributed predominantly in South America, the optimal ancestral area for *Phemeranthus* would be South America, even though only one species occurs there. *Phemeranthus* seemed more likely to have originated in North America (Hershkovitz and Zimmer 2000).

Nuclear ITS data do not provide strong support for relationships among the genera of Montiaceae. In a maximum-parsimony analysis, *Phemeranthus* was sister to all other members of Montiaceae; in a maximum-likelihood tree, *Phemeranthus* was sister to a clade consisting of *Calyptridium*, part of *Cistanthe* and other segregates of *Calandrinia* (Hershkovitz and Zimmer 2000). Chloroplast *ndhF* and *matK* data supported *Phemeranthus* as sister to the remainder of Montiaceae (Applequist and Wallace 2001; Nyffeler and Eggli 2010) (Fig. 1.3). The pattern of well-supported major lineages separated by relatively long branch lengths but with short internal branch lengths and poor internal resolution might reflect rapid origin and diversification of the lineages in association with the late Tertiary–early Quaternary geological and climatological events that produced the diverse topography and vegetative communities of western North America and temperate South America. The low interspecific divergence and conflict between the relationships inferred from nuclear DNA, chloroplast DNA, and morphology could also be explained by widespread hybridization (Hershkovitz 2006).

TABLE 1.2. Genera of Montiaceae

Genus	**# of spp.**	**Distribution**
Calandrinia Kunth	~14	Western North, Central, and South America
Calyptridium Torr. & A. Gray	~14	California
Cistanthe Spach	~20	Western North and South America
Claytonia L.	~27	North and Central America, Siberia
Hectorella Hook. f.	1	New Zealand
Lenzia Phil.	1	Chile
Lewisia L.	~16	Western North America
Lewisiopsis Govaerts	1	Western North America
Lyallia Hook. f.	1	Kerguelen Islands (southern Indian Ocean)
Montia L.	~12	Western North America, Siberia, circumboreal, Colombia, Australia
Montiopsis Kuntze	~40	Western South America
Parakeelya Hershk. (Australian *Calandrinia*)	~40	Australia
Phemeranthus Raf.	~25	North America and Argentinean Andes
Philippiamra Kuntze	~8	Western South America
Schreiteria Carolin	1	Argentinean Andes

Sources: Nyffeler (2010); Hershkovitz & Zimmer (2000); www.tropicos.org

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All *Phemeranthus* species are succulent perennials with stout rhizomes, fleshy taproots, or tuberous roots (Fig. 1.1). The herbaceous stems are usually short, with contracted internodes, so that the leaves are more or less rosette-forming. In most species, the aboveground growth dies back each winter, and the plants regenerate in the spring from resting buds on a usually underground caudex. In some species, vegetative propagules form as thickened winter buds clad in appressed scale leaves that break off from the main stem as the aboveground portion of the plant dies back in the fall (Harshberger 1897; Ware 1972). Some *Phemeranthus* possess perennial, branched, woody above-ground stems (e.g., the mat-forming *P. spinescens* and *P. sediformis* of the inland Northwest and some Mexican species). This herbaceous or slightly woody, rosulate growth form is widespread in Montiaceae (Nyffeler et al. 2008). Carolin (1987) described the growth habit of *Phemeranthus* as "suffruticose and passive chamaephytes", in which "the perennating buds are held close to the ground on weak, more or less decumbent or short branch systems". Some *Phemeranthus* would be better described as "active chamaephytes or protohemicryptophytes", in which "the perennating buds are held at or below ground level on prostrate stems or stolons" (Carolin 1987). The tuberous roots or rhizomes and the lower, perennial portions of the stems store large amounts of starch. The leaves have slightly sunken, ellipsoidal stomatal guard cells and are covered with a waxy cuticle (Harshberger 1897). The leaves and young vegetative stems may feature unicellular epidermal papillae (Bogle 1969).

The cymose inflorescences of *Phemeranthus* have sometimes been described as scorpiod cymes (e.g., Ware 1969b), but this terminology is inaccurate. In fact, they are dichasia (or polychasia) that may appear monochasial distally (Harshberger 1897; Carolin 1987). Other genera of Portulacaceae exhibit regularly monochasial cymes that could properly be called scorpioid. The inflorescences often appear terminal, but actually they are borne in leaf axils.

Phemeranthus pollen is pancolpate with a few broad colpi (ca. 3–4 times as long as broad) and usually numerous irregular papillae scattered over the aperture surface (Carolin 1987). The pollen of *P. teretifolius* has 12 more or less circular apertures distributed evenly around the surface of the pollen grain, three of the colpi being larger than the rest (Bogle 1969). *Phemeranthus* seeds are enclosed in a membranous aril that develops from the funicle (Bogle 1969), which is loose and wrinkled in some species and tightly adherent to the testa in others (Fig. 1.4). This chartaceous aril or pellicle may be evanescent, rubbing or flaking away when the seeds are released from the fruit.

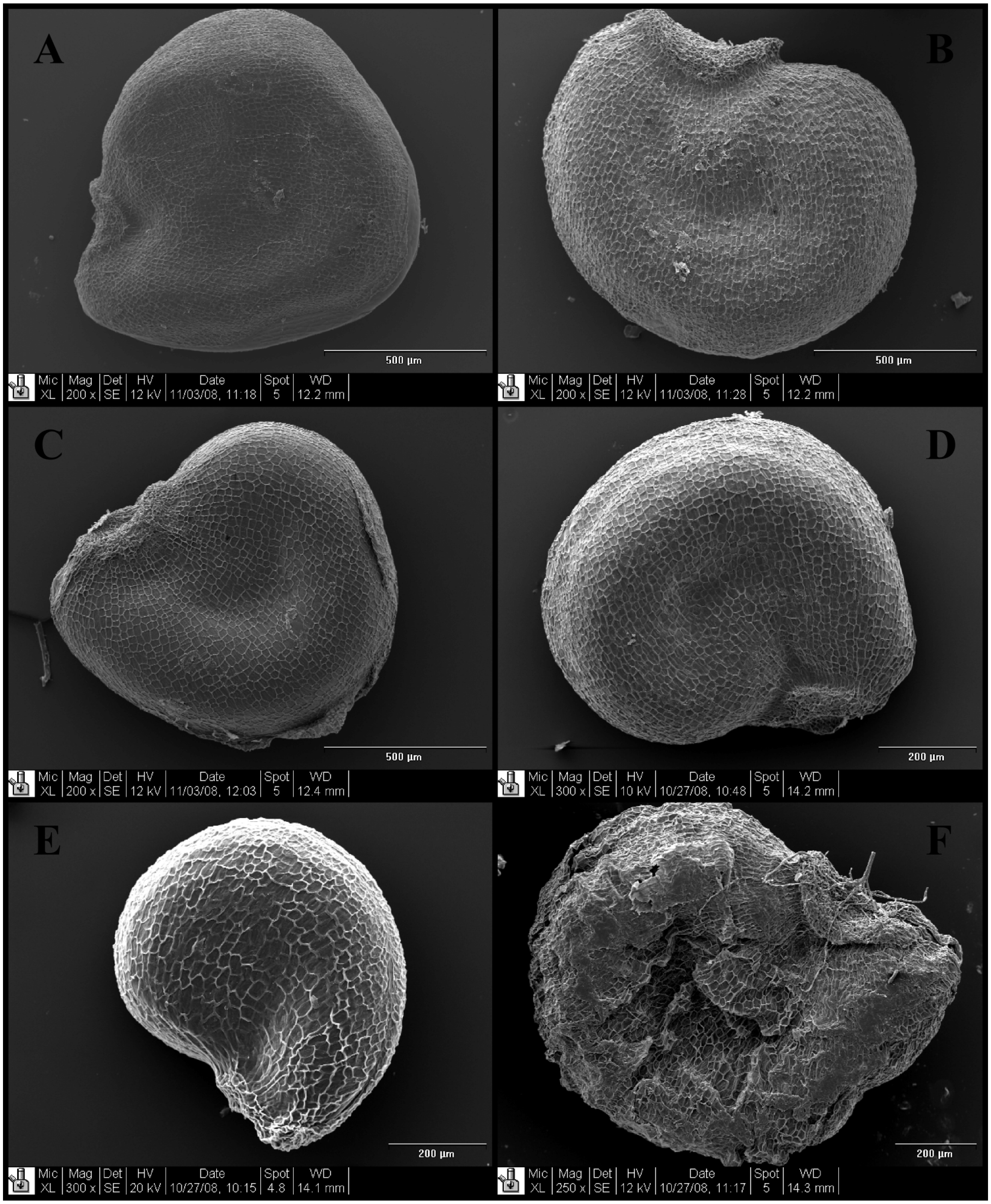

FIGURE 1.4. Scanning electron micrographs of *Phemeranthus* seeds. A) *P. brevicaulis*; B) *P. calcaricus*; C) *P. mengesii*; D) *P. parviflorus*; E) *P. punae*; F) *P. rugospermus*. Note differing scale bars.

Examination of flowers, fruit, and seeds is often necessary to identify *Phemeranthus* species (Kiger 2003). The diagnostic characters of *Phemeranthus* species, such as flower color and size, fruit shape and size, sepal persistence, stamen number, style length, and stigma lobes are often difficult or impossible to evaluate in pressed specimens. Thus, examination of living materials, especially those grown under common conditions in the greenhouse, is necessary to understanding these species (Holzinger 1900; Ware 1967, 2011).

Within *Phemeranthus*, a group of relatively tall, pink- or white-flowered species is broadly distributed in patchy xeric habitats across the Midwestern and Southeastern United States. This eastern North American (ENA) group includes *P. confertiflorus*, *P. parviflorus*, *P. calycinus*, *P. calcaricus*, *P. mengesii*, *P. teretifolius*, and *P. rugospermus*. ENA *Phemeranthus* is a morphologically cohesive group distinguished by erect, distinctly cauline habit; long leaves; multi-branched inflorescences borne on long, erect peduncles; and usually bright pink flowers. Chloroplast and nuclear sequence data indicate close relationships among all of the ENA species of *Phemeranthus*, but show very little divergence among species.

ENA *Phemeranthus* are especially characteristic of granite outcrops in central Texas (Walters and Wyatt 1982) (Fig. 1.2C), rock outcrop plant communities (glades) in the Ozarks (Baskin and Baskin 2000; Ware 2002) (Fig. 1.2E), limestone glades in the Central Basin of Tennessee (Harper 1926) and northern Alabama (Baskin et al. 1995) (Fig. 1.2G), granite outcrops of southern Appalachia and the Piedmont of Georgia and the Carolinas (McVaugh 1943; Murdy 1968; Wyatt 1997) (Fig. 1.2H), and the serpentine barrens of Pennsylvania (Baskin and Baskin 1988; Tyndall and Hull 1999). The plants occupy a similar niche in each of these rock outcrop systems: very shallow soil, typically at the ecotone between bare rock and dense vegetation at the edges of outcrops and of soil pits or depressions on the outcrops. They are typically the only vascular plant actively growing, flowering, and setting seed in this zone during the hottest, driest part of the summer. ENA *Phemeranthus* are also found in open barrens or savannas in sandy prairies from the upper Midwest south to Texas.

Within the ENA group, intriguing intraspecific disjunctions occur among populations of *P. rugospermus* and *P. parviflorus*. The latter species is distributed almost entirely west of the Mississippi River, with populations just across the river in southern Illinois, but a disjunct population grows on bluffs above the Coosa River in central Alabama. The species may have first entered Alabama at a time when the bare-rock habitat on exposed Pottsville sandstone was more widespread and continuous than at present, subsequently becoming confined to remote, isolated outcrops as forest communities encroached upon the gradually deepening soil (Wolf 1939). The prairie fameflower, *P. rugospermus* (Holz.) Kiger, also shows striking population disjunctions. While the main part of this species' range is in the upper Midwest, populations have been found in central Nebraska, central Kansas, southern Oklahoma, and east Texas and adjacent Louisiana (Holzinger 1899a; Nixon et al. 1980; Cochrane 1993; MacRoberts and MacRoberts 1997). Several hypotheses have been proposed to explain this widely disconnected distribution. *P. rugospermus* may have arrived in its present localities via post-glacial long-distance dispersal (Cochrane 1993). Its distribution may be a remnant of a previously widespread range (Harshberger 1897). Or the *P. rugospermus* morphology may have arisen multiple times via hybridization between its co-distributed relatives. Its morphology is intermediate in several respects between that of the small-flowered sunbright, *P. parviflorus*, and that of the large-flowered fameflower, *P. calycinus*. These two species are broadly sympatric and often syntopic across the range of *P. rugospermus*.

Beginning with Harshberger's (1897) "Ecological study of the genus *Talinum*", the ENA group has been relatively well studied. A wealth of morphological, ecological, cytological, genetic, and reproductive studies have been performed on the glade and rock outcrop species, including allozyme surveys, chromosome counts, and substrate specificity experiments (e.g., Harshberger, 1897; Wolf, 1939; Steiner, 1944; Ware, 1967; Ware, 1968; Montgomery & Blake, 1969; Ware, 1969; Ware & Quarterman, 1969; Murdy et al., 1970; Krebs, 1971; Black & Murdy, 1972; Carter, 1983; Carter & Murdy, 1985; Murdy & Carter, 1985; Carter & Murdy, 1986; Reinhard & Ware, 1989; Ware & Pinion, 1990; Harris & Martin, 1991; Ware, 1991; Murdy & Carter, 2001). The findings of these studies are summarized below.

Menges' fameflower (*P. mengesii*) is typical of ENA *Phemeranthus* in its natural history. It is found most often on sandstone outcrops exposed along streams. The strongly sloped outcrops often receive heavy runoff from adjacent woods during winter rains, making them susceptible to erosion. This soil erosion is probably a limiting factor in the establishment of *P. mengesii* seedlings (Ware 1969b). A few long, elastic roots anchor the perennial tuberous rhizome to the soil. Following winter dormancy, the rhizomes resume growth in early April as new green leaves emerge from the scale leaves surrounding the winter bud. The new fleshy stems grow quickly, and an extensive branching root system arises along with them. In older plants, several large, branched stems bearing numerous inflorescences may arise from the winter buds in a single growing season. Flower buds become visible in mature plants as early as three weeks after growth resumes, and flowers and fruits are produced throughout the summer, typically from mid-May to mid-September or even October. Capsules develop quickly—the seeds ripen in about 20 days in *P. calcaricus*, *P. teretifolius*, and *P. mengesii* (Ware 1968)—so plants can produce seed throughout the season. At the end of the season, clusters of awl-shaped scale leaves form at the base of the stem or on the upper surface of the rhizome, surrounding the winter buds, although plants may continue to flower for several weeks after these buds develop. Soon after flowering ceases, the plants die back to the rhizome. Non-flowering stems may develop thick corky skins, their apical buds become protected by scale leaves and become winter buds, and they become incorporated into the perennial rhizome (Ware 1969b). Though plants usually do not flower their first year as seedlings in the field, they can do so in the greenhouse (Ware 1968; pers. obs.).

The daily periodicity of flowering in *Phemeranthus* is well known (Harshberger 1897; Holzinger 1899b; Wolf 1939). The flowers open at a particular time each day, which varies among species and populations. Each flower opens for just a few hours on a single day, but large individuals may have dozens of flowers open at one time when conditions are favorable. In the morning, when the flowers are not open, the plants tend to be inconspicuous against their background of rock, lichens, and mosses. However, they become quite conspicuous when the flowers open in the afternoon, as their showy pink flowers on tall, wiry peduncles rise above the surrounding vegetation (Ware 1969b, 1969a).

Relatively little information is available concerning the pollination ecology of *Phemeranthus*. Harshberger (1897) observed that *P. rugospermus* (as *T. teretifolium*) flowers were visited by *Calliopsis andreniformis* (Hymenoptera), a small, short-tongued bee. In the Piedmont of Georgia, the most frequently observed pollinators on *P. mengesii* and *P. teretifolius* were the small native bees *Auglochora* and *Lasioglossum* and the larger *Bombus* and *Apis* (Carter and Murdy 1986). Sweat bees (Halictidae) are the primary pollinators of *P. mengesii*, *P. teretifolius*, *P. calcaricus*, and *P. calycinus* (Ware 1968; Krebs 1971; pers. obs.). These small, dark bees visit the flowers in linear sequence, often beginning their activity before the flowers have opened for the day (pers. obs.) and frequently effecting pollination of the stigmas before the corollas have fully opened (Ware, 1968). The bees do not discriminate between *P. mengesii* and *P. teretifolius* where those species are sympatric, and hybrids are known (Carter and Murdy 1986). These species produce a tiny amount of nectar (Krebs, 1971) but are not fragrant; and Halictid bees are pollen eaters. In the western United States, *P. brevifolius* has a strong, pleasantly sweet fragrance at anthesis (Ferguson, pers. comm.; pers. obs.), but it is not known whether this contributes to pollination. *P. sediformis* of the inland Northwest and *P. napiforme* of Mexico (and probably all other *Phemeranthus* species) possess a small nectary at the base of the innermost stamens (Vanvinckenroye and Smets 1996), but the role of this structure in pollinator attraction has not been studied.

ENA *Phemeranthus* usually grow in very shallow (2–5 cm), sandy or rocky soil, with the rhizome often resting on bedrock and its top exposed above the soil surface. Nevertheless, the plants withstand severe drought. They can continue flowering for several days even after the leaves wilt, and the leaves promptly regain turgidity and flowering resumes after rain (Ware 1969b). When uprooted, *P. mengesii* plants are slow to wilt; left unpotted, they may continue to flower for a day or two and can recover fully upon potting even after a week or more without soil or water. Furthermore, given sufficiently frequent watering, broken-off branches can produce adventitious roots and thus continue to flower (Harshberger 1897; Wolf 1939; Ware 1969b).

Glade and rock-outcrop *Phemeranthus* may be confined to the shallowest soil zones because they are poor competitors for light and nutrients but can exploit marginal habitats where drought stress excludes their potential competitors (Ware 1969a; Baskin and Baskin 1988; Ware 1991). In cedar glades, soil a bit deeper than that occupied by *P. calcaricus* is dominated by annual grasses such as *Sporobolus vaginiflorus* (Torr.) Wood (Quarterman 1950; Ware 1969a). Although *Phemeranthus* plants are most dense in shallower soil where grasses are absent, a few large, vigorous *Phemeranthus* are typically found in deeper soil (pers. obs.), suggesting that the slow-growing seedlings of *Phemeranthus* are unable to compete with faster-growing annual grass seedlings, limiting their establishment in deeper soil. In controlled growth experiments, *P. mengesii* and *P. calcaricus* were inhibited by whole-plant and/or root competition from the grass *Poa pratensis*. Decreased light intensity also inhibited the growth of *P. calcaricus*. Although drought stress reduced the growth of *Phemeranthus* plants, the grass was much more strongly affected by low moisture, giving *Phemeranthus* a competitive advantage under these conditions (Ware 1991).

Indeed, *Phemeranthus* of the southeastern United States are somewhat legend among those who know them for their extreme temperature and drought tolerance. For example, *P. calcaricus* is the only indigenous vascular plant that actively grows and flowers during the hot, dry summer in the shallow soil bordering bare limestone in cedar glades (Ware 1967; Ware and Quarterman 1969). The succulent leaves may wilt during extended drought, but the plants continue to flower and produce seeds. The plants can withstand soil-surface temperatures measured at more than 50°C (Wyatt 1997). In Mexico, *P. humilis* and *P. napiformis* thrive on exposed volcanic rocks at arid, high-elevation sites (Harshberger 1897). Characteristics that promote drought resilience in *Phemeranthus* species include their succulent stems and leaves, terete leaves, sunken stomata, low stomatal number, thick cuticle, profusely branched summer root system, and ability to flower even with a water deficit in the leaves (Harshberger 1897; Guptill 1947; Ware 1968). Some species also possess long, elastic roots that penetrate deep into the rocky substrate and/or swollen, tuberous roots protected by corky scales.

Additionally, although *Phemeranthus* are primarily C_3 plants, some species apparently utilize a facultative CAM-cycling mode of photosynthesis in which atmospheric CO_2 is taken up and fixed via the C_3 pathway during the day and respiratory CO_2 is recaptured at night via the CAM pathway to form malic acid (Guralnick and Jackson 2001). This CO_2 recycling process enables plants to reduce atmospheric CO_2 uptake and transpiration during the day, thus limiting transpirational water losses. Conceivably, drought-stressed plants could continue to utilize recycled CO_2 from accumulated malic acid even while keeping the stomata closed throughout the day ("CAM-idling"), thus maintaining the activity of photosynthetic enzymes during drought and enabling plant growth to rebound quickly when water becomes available. This pathway has been reported to occur in at least 15 plant families, especially in succulent herbs found in xeric microenvironments (Martin et al. 1988).

Researchers have studied this phenomenon in eastern and Midwestern *Phemeranthus* species (Martin et al. 1982; Martin and Zee 1983; Martin et al. 1988;

Harris and Martin 1991a; Harris and Martin 1991b; Harris et al. 1993). In one set of experiments, Harris and Martin (1991a; 1991b) measured photosynthetic gas exchange and malic acid fluctuations in *P. teretifolius*, *P. parviflorus*, *P. mengesii*, *P. calycinus*, and *P. calcaricus*. They hypothesized that high CAM-cycling activity decreases daytime transpiration and increases water-use efficiency under non-drought conditions. The data showed similar CAM-cycling patterns in all five species; the plants took up CO_2 during the day using the typical C_3 pathway and accumulated malic acid at night. However, the species differed significantly in their rates of gas exchange and average malic acid fluctuations. Day-night fluctuations in leaf malic acid content were positively correlated with net overnight CO_2 exchange for all individuals combined and within three species and negatively correlated with net daytime CO_2 uptake for all individuals combined and within one species (*P. parviflorus*). Also, the extent of CO_2 recycling via malic acid was negatively correlated with daytime transpirational water loss (Harris and Martin 1991a; Harris and Martin 1991b). The trend of increasing water-use efficiency with increasing overnight malic acid fluctuation levels was non-significant. Nevertheless, according to Martin et al. (1988), *P. calycinus* might effect a daily water savings of up to 43% via CAM-cycling.

Geological substrate is important in determining the distribution and occurrence of *Phemeranthus* species (Harshberger 1897; Reinhard and Ware 1989; Ware and Pinion 1990). While some *Phemeranthus* species occur on a range of geologic substrates, other species show some degree of substrate specificity. According to Ware and Pinion (1990), *P. teretifolius, P. mengesii*, and *P. calcaricus* are each characteristic of a major rock outcrop system in the southeastern United States. *P. teretifolius* grows on granite outcrops of the Piedmont from Virginia to Georgia and on serpentinite in Maryland and Pennsylvania, and occasionally on sandstone. *P. mengesii* is found on Pottsville sandstone outcrops of northern Alabama and adjacent Georgia and Tennessee, occasionally on granite in north-central Georgia, and in the Altamaha Grit region of the Coastal Plain of Georgia (Montgomery and Blake 1969). *P. calcaricus* is endemic to limestone cedar glades of the Central Basin of Tennessee and Moulton Valley of northern Alabama. Related species are rarely found on calcareous substrates. Germination and growth experiments indicate that *P. calcaricus* can tolerate greater variation in soil pH than its relative *P. mengesii* (Ware 1969b; Krebs 1971). Growth experiments on different soil types indicate that all three southeastern species, including *P. calcaricus*, grow best on more acidic substrates, but only *P. calcaricus* grows uninhibited on calcareous soil (Ware 1969b; Reinhard and Ware 1989; Ware and Pinion 1990). In contrast, several species in the southwestern United States are found on calcareous substrates.

The broad range of substrates occupied by *P. teretifolius* (granite, serpentinite) is apparently due to broad edaphic tolerance rather than to ecotypic adaptation. Plants from serpentinite in Maryland grew better on limestone soil than on serpentine soil but exhibited abnormal coloration on limestone. They grew better on sandstone and granite than on either limestone or serpentinite, defying the common assumption that plants found on serpentine soils are physiologically adapted to this soil type. The limited competition in the shallow soil of serpentine barrens ensures that the slow-growing *P. teretifolius* can survive and reproduce (Ware and Pinion 1990).

Whereas different types of rock outcrop systems in the Southeast are geographically separated, outcrops of different rock types occur in close proximity in the

Interior Highlands (Ozarks and Ouachitas). Two species are broadly co-distributed in this region: *P. calycinus* and *P. parviflorus*. The former species was regarded as substrate indifferent (Steyermark 1963), having been recorded from limestone, sandstone, granite, shale, chert, syenite, and other igneous rocks. The latter species had also been recorded on siliceous and igneous rock types, but not on limestone. When seeds and plants from multiple populations of these species were grown in soil collected from their native outcrops and from outcrops of different geological types, *P. parviflorus* from sandstone outcrops grew well on either shale or sandstone soils but very poorly on soils from calcareous outcrops, showing abnormal pigmentation, poor growth, and high mortality. All *P. calycinus* populations also grew well on non-calcareous substrates, including sandstone, shale, granite, and syenite, but very poorly on calcareous soils. However, one population collected from a limestone outcrop did not display abnormal coloration when grown on calcareous soil, as plants from other outcrop types did, suggesting that some ecotypic adaptation had occurred to extend the limit of tolerance and permit these plants to grow on calcareous substrate. Like *P. calcaricus*, this *P. calycinus* population was tetraploid (Reinhard and Ware 1989).

Different populations of *P. calycinus* exhibit morphological differences, although most of these differences are difficult to detect in herbarium specimens and can be clearly observed only in living plants. These differences persist in plants grown from seed under controlled conditions in the greenhouse (Reinhard and Ware 1989). For example, plants from shale and syenite outcrops in three counties in northwestern Arkansas were smaller overall, had proportionally longer stigmas relative to the style, had quickly deciduous sepals, and had smaller black seeds than other populations. Plants from the tetraploid population on limestone were consistently larger in both vegetative and reproductive parts, and plants from a Missouri population on granite had stamens equal in length to the styles. Their stigmas were also dorsiventrally flattened and pink at the base where they joined the style. However, there was no clear correlation between the morphological differences and the responses of various populations to different types of soil substrate (Reinhard and Ware 1989).

Fameflower species vary in breeding system and in ploidy level (Kiger, 2001; Murdy & Carter 2001). Some species show pronounced herkogamy, which promotes outcrossing. Others, particularly the small-flowered *P. parviflorus* and *P. confertiflorus*, have stigmas equal to the stamens and can self-pollinate when the flowers close in the afternoon. Species are occasionally found in sympatry with close relatives, and some hybridization is known. Furthermore, allopolyploid and autopolyploid speciation have apparently been important in the evolution of ENA *Phemeranthus*. Tetraploid *P. teretifolius* is derived from hybridization between *P. parviflorus* and *P. mengesii*, while *P. calcaricus* is apparently an autotetraploid derivative of *P. calycinus* (Murdy and Carter, 2001). Chromosome numbers, hybridization, and polyploid speciation are further discussed below.

Phemeranthus species fit a simple polyploid series based on a chromosome number of x=12 (Steiner 1944) or x=6 (Black and Murdy 1972). All species and populations examined to date are either diploid or tetraploid, although some cortical cells in *P. parviflorus* root tips contain 96 chromosomes, a feature not observed in other species studied (Steiner 1944). *P. calcaricus* (Krebs 1971) and *P. teretifolius* are tetraploid ($2n$=48) (Fig. 1.5), the latter behaving as an amphidiploid (Murdy 1968; Black and Murdy 1972). *P. mengesii* is diploid, except for an outlying population in the Altamaha Grit region of the Georgia Coastal Plain, which is tetraploid (Montgomery and Blake, 1969; Murdy et al., 1970). Chromosome counts are also available for a few other species (Table 1.3).

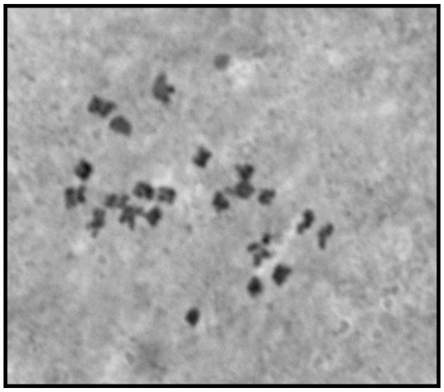

FIGURE 1.5. Meiotic chromosome squash of *P. teretifolius* from Wake Co., NC (TMP 272).

TABLE 1.3. Chromosome numbers of *Phemeranthus* species

Species	Locality	Chromosome No.	Reference
P. brevicaulis	Harding County, NM	2*n*=24	8
P. calcaricus	Central TN, northern AL	2*n*=48	5, 9
P. calycinus	Various	2*n*=24, 48	9
P. confertiflorus	Valencia & Harding Counties, NM	2*n*=48	8
P. mengesii	29+ populations	2*n*=24	1, 2, 4
P. mengesii	Altamaha Grit region, GA	2*n*=48	3, 6
P. parviflorus	Various	2*n*=24	1, 7
P. parviflorus	Springdale, AR	2*n*=48	1
P. teretifolius	32+ populations	2*n*=48	1, 2, 4, 6

*References: 1. (Steiner 1944); 2. (Murdy 1968); 3. (Montgomery and Blake 1969); 4. (Murdy et al. 1970); 5. (Krebs 1971); 6. (Black and Murdy 1972); 7. (Carter and Murdy 1985); 8. (Ward and Spellenberg 1986); 9. (Murdy and Carter 2001)

P. mengesii and *P. calcaricus* have pistils longer than the stamens and are dependent on pollinators to effect fertilization, though they are apparently not self-incompatible (Ware 1967; Murdy and Carter 2001). Most *P. calycinus* populations have stigmas exceeding the stamens, but plants from one Missouri population on granite had stamens equal in length to the styles and were able to self-pollinate to some extent without a vector (Reinhard and Ware 1989). Manual crosses between *P. calcaricus* or *P. mengesii* plants from different populations produced seed set comparable to that observed in the field (Ware 1967). Similarly, various Missouri and Arkansas *P. calycinus* populations were inter-fertile, despite pronounced differences in vegetative and reproductive proportions (Reinhard and Ware 1989). Four *P. teretifolius* populations from different substrates were also fully inter-fertile, although plants from serpentinite in Maryland produced fewer seeds per capsule than those from other populations (Ware and Pinion 1990). Crosses between *P. calcaricus* and either *P. mengesii* or *P. calycinus* from Arkansas resulted in no or very low fruit and seed production (Ware 1967), and crosses between *P. calcaricus* and *P. teretifolius* yielded vigorous but sterile hybrids (Murdy and Carter 2001). Crosses between diploids of different species or between diploid and tetraploid *P. calycinus* also yielded sterile hybrids. However, crosses between *P. calcaricus* and tetraploid *P. calycinus* later yielded fertile hybrids (Murdy and Carter 2001). Crosses between *P. parviflorus* and *P. teretifolius* and between *P. parviflorus* and *Talinum aurantiacum* were unsuccessful (Steiner 1944).

Several studies have examined polyploid speciation processes in ENA *Phemeranthus*. Wolf (1939) noted that *P. teretifolius* appeared to be morphologically intermediate between *Talinum appalachianum* (a central Alabama taxon similar to *P. parviflorus*) and *P. mengesii* and accordingly proposed that the former species occupied an intermediate phylogenetic position between the latter two. Based on this observation and on Steiner's (Steiner 1944) report that *P. teretifolius* had twice the chromosome number of *P. mengesii*, Murdy (Murdy 1968) hypothesized that *P. teretifolius* had originated as an amphidiploid, one of whose parents was *P. mengesii*. Black and Murdy

(1972) tested this hypothesis by generating artificial hybrids between *P. teretifolius* and diploid and tetraploid *P. mengesii* and observing their chromosome-pairing behavior. Both triploid and tetraploid hybrids were sterile with abnormal pollen. Triploid hybrids exhibited 18–24 meiotic associations per cell, while tetraploid hybrids exhibited 24–30. These observations reinforced the idea that *P. teretifolius* originated as an amphidiploid hybrid of *P. mengesii* and another species; *T. appalachianum* met all the morphological and cytological requirements to be the second parent. Black and Murdy (1972) proposed a model to explain this meiotic behavior in which *P. mengesii* and the other parent of *P. teretifolius* also began as amphidiploids that shared one genome in common; this hypothesis has not been further tested.

Later, Carter and Murdy (1985) succeeded in generating artificial hybrids between *P. mengesii* and *P. parviflorus* and compared them to *P. teretifolius*. Although the hybrids were sterile, their floral morphology and time of diurnal anthesis were intermediate between the parental species and similar to those of *P. teretifolius*. When the hybrids were polyploidized by colchicine treatment, they were able to generate fertile offspring by selfing, sib-crossing or crossing to natural *P. teretifolius*. Isozyme data showed that *P. teretifolius* populations were genetically uniform and that their alleles were a combination of alleles found in the putative parents. The enzyme data ruled out the alternative hypothesis that *P. calycinus*, rather than *P. mengesii*, was one parent of *P. teretifolius* (Murdy and Carter 1985). Electrophoretic polymorphism was high in *P. calycinus* and *P. mengesii*, low in *P. parviflorus*, and none in *P. teretifolius*. Most of the variation was between rather than within populations (Murdy and Carter 1985). The genetic uniformity of *P. teretifolius* suggests a recent origin; it must have migrated north to the serpentine barrens of eastern Pennsylvania since the last glaciation retreated from the area around 12 kya (Murdy and Carter 2001).

Carter and Murdy (1985) also compared *T. appalachianum* to several populations of *P. parviflorus* and concluded that the former was synonymous with the latter, overlapping in all measured traits and being fully inter-fertile. Isozyme data reinforced the conclusion that *T. appalachianum* was merely a disjunct population of *P. parviflorus*. The average genetic identity between populations of these taxa was higher than that between populations of *P. calycinus* or *P. mengesii* (Murdy and Carter 1985). The Alabama population may represent a remnant of a formerly more extensive distribution of *P. parviflorus* east of the Mississippi (Carter and Murdy 1985).

Murdy and Carter (2001) added additional morphological, isozyme, and crossing data on *P. calcaricus* and *P. calycinus* to their previous work on speciation in *P. teretifolius*, *P. mengesii*, and *P. parviflorus*. They found that diploid and tetraploid *P. calycinus* did not differ in floral traits and that *P. calcaricus* shared the persistent sepals and darker purple flower color of *P. calycinus*. Crosses between *P. calcaricus* and tetraploid *P. calycinus* yielded fertile hybrids. Enzyme data also supported the hypothesis that *P. calcaricus* is derived from autotetraploid *P. calycinus*.

On granite outcrops in the Piedmont of Georgia, where the ranges of *P. teretifolius* and *P. mengesii* meet and overlap, *P. teretifolius* appears to competitively replace its parent species (Murdy et al. 1970). The two species can be distinguished by petal size and shape, stamen number, relative length of style and stamens, and time of diurnal anthesis. *P. teretifolius* possesses a competitive advantage due to its greater dessication tolerance in the seedling stage and to the difference in breeding system.

Because its stamens are held at the same level as the stigma, *P. teretifolius* can set seed without pollinators by self-pollinating upon flower closure. The flowers of *P. mengesii* have stigmas held well above the anthers, so they do not set seed without pollinators (although they are not self-incompatible). Thus, *P. teretifolius* can both self and outcross, whereas *P. mengesii* depends mostly on cross-pollination, making *P. teretifolius* a more effective colonizer and making *P. mengesii* more subject to deleterious fitness effects of hybridization.

Where *P. mengesii* and *P. teretifolius* are found in sympatry, triploid hybrids sometimes occur (Murdy et al. 1970). In such populations, the former species (but not the latter) exhibits divergence in sexual and asexual reproductive characters, including larger flowers, longer styles, and earlier time of diurnal anthesis (Carter 1983; Carter and Murdy 1986). These traits might help to reduce interspecific hybridization and thus gamete wastage, providing a selective advantage under the threat of hybridization with *P. teretifolius*. For example, earlier flowering would provide an increased opportunity for intraspecific pollination in *P. mengesii* prior to the opening of *P. teretifolius* flowers. Plants in sympatric populations of *P. mengesii* also form asexual propagules, while those in allopatric populations do not. All of these traits had high heritability in experimental crosses, and the divergence was not due to ecotypic or clinal variation (Carter 1983; Carter and Murdy 1986).

Geographic Context: Xeric North America—

Phemeranthus species are almost exclusively North American in distribution. The one exception is *P. punae* (R.E. Fr.) Eggli & Nyffeler, which is narrowly restricted to the puna region of northern Argentina and southern Bolivia, approximately 5500 km from the southern limit of its congeners in Oaxaca and Puebla, Mexico. Another disjunction occurs in the inland Northwest: *P. spinescens* (Torr.) Hershkovitz is found in the Columbia Plateau of northern Oregon and central Washington, while *P. sediformis* (Poelln.) Kiger is restricted to the Okanagan region of northern Washington and adjacent British Columbia. The nearest congeners are found across the Rocky Mountains in the Great Plains of eastern Montana. *Phemeranthus* exhibits a biogeographic pattern similar to that of numerous other taxa of arid western North America. Like other elements of the so-called Madro-Tertiary Geoflora (Axelrod 1958), its center of diversity is in the Chihuahuan region of northern Mexico and the southwestern United States. Fameflowers in this region occur mostly in mid-elevation pinyon-juniper or xeric grassland habitats. The biogeography of western North American deserts is more extensively reviewed in Chapter II. Here, I focus on *Phemeranthus* habitats in the midwestern and southeastern United States, which can be viewed as micro-deserts for their dry, xeric conditions.

The distribution of *Phemeranthus* in ENA is unique within Montiaceae, most of whose genera are distributed primarily in western North America and Australia. *Lewisia*, *Cistanthe,* and *Calandrinia* are diverse in the West but absent from the East. *Claytonia* has two widespread species and one narrow endemic in ENA, and *Montia* has about five species in ENA, most occurring at the southern extent of a boreal/arctic distribution. *Phemeranthus*, however, has apparently speciated in the midwestern and southeastern United States, giving rise to the seven named species of the ENA group. Major areas of ENA *Phemeranthus* habitat include sand blows or dunes in the Midwest (Cochrane 1993); Ozark glades in Missouri, Arkansas, and adjacent states; granite flatrocks in the

Piedmont from Georgia to Virginia; limestone cedar glades in central Tennessee and adjacent Alabama and Kentucky; mid-Appalachian shale barrens in Virginia, West Virginia, and Pennsylvania; serpentine barrens in the Piedmont of Pennsylvania and Maryland; and sandstone outcrops in northern Alabama (Ware 2002).

Glades and flatrocks form where bedrock is exposed at or near the soil surface, resulting in moisture stress and limiting tree establishment. Glades may form on a variety of substrates, including limestone, dolomite, sandstone, granite, rhyolite, chert, and shale (Ware 2002). The glade environment is characterized by intense sunlight throughout the year; winter moisture and summer drought; daily temperature extremes; shallow, bare soil with low water-holding capacity; and soil chemistry closely linked to the rocky substrate (Baskin and Baskin 2000; Ware 2002; Baskin and Baskin 2003). Glade plants encounter much greater drought stress during summer and potentially greater cold stress during winter than may be experienced by surrounding vegetation. The shallowest soils of glades and flatrocks are mostly dominated by bryophytes and small winter annual plants (Baskin and Baskin 2000, 2003). Southeastern rock outcrops feature level terrain and moderate erosion, resulting in distinct vegetational zonation from bare rock outward through increasing soil depth, whereas Ozark glades are often strongly sloping, resulting in substantial soil erosion and a mosaic of different soil depths and associated plant species in small patches. Ozark glades are maintained by periodic fire, supported by the fuel load created by perennial grasses, which suppresses the invasion of woody plants (Ware 2002).

The relatively xeric habitats occupied by ENA *Phemeranthus* now exist as islands within a matrix of more mesic deciduous forest vegetation, but may have been more widespread during earlier periods. Pollen data from Missouri, Kentucky, and Tennessee indicate that warm and dry climates with low groundwater tables also prevailed throughout the Ozark Plateau and Interior Low Plateaus from about 30,000 to 24,000 BP, and prairie and glade habitats may have been widespread during this interstadial period (Delcourt et al. 1986). The ancestors of ENA *Phemeranthus* may have spread from the Southwest into Midwestern prairies and into the Southeast via the Ozarks during this period of warming and drying (Walters and Wyatt 1982; Baskin and Baskin 1986). Subsequently, cool and wet climates associated with the Late Wisconsonian glaciation promoted the development of boreal coniferous forest throughout the region, probably eliminating suitable habitats for characteristic glade species north of about 34°N. However, suitable habitats probably persisted in the southern portion of the present range. Alternatively, small, isolated patches may have supported winter-wet, summer-dry microclimates throughout the full-glacial interval, even while the surrounding vegetation changed dramatically (Baskin and Baskin 1986). As the climate warmed during the Pleistocene-Holocene transition, glade species may have colonized newly available habitats to the north from their full-glacial refuges in the south. Glade habitats probably reached their maximum extent during the mid-Holocene Hypsithermal (ca. 10,000–4,500 BP), when temperatures in inland North Temperate regions were 1°–4°C warmer than at present (Delcourt et al. 1986). Glade plant populations in the Ozarks and Interior Low Plateaus likely had increased gene flow during this period. More recently, increasingly mesic conditions have resulted in the encroachment of closed deciduous forest, decreasing the connectivity of glade habitats and possibly leading to genetic isolation (Delcourt et al. 1986).

Emerging Questions—

The phylogenetic and geographic context of *Phemeranthus* raise several intriguing questions. If, as previous studies suggest, *Phemeranthus* is sister to the remainder of Montiaceae (Applequist and Wallace 2001; Nyffeler and Eggli 2010), then understanding its biogeography and character evolution is an important key to understanding those of the family as a whole. Phylogenetic analyses using DNA sequence data from a large sample of *Phemeranthus* species will show whether the genus is monophyletic as presently circumscribed and clarify its position within Montiaceae.

Given the overall concentration of Montiaceae in western North America and western South America, *Phemeranthus*' center of origin is relevant to the biogeography of the family as a whole. Fameflowers seem to exemplify a biogeographic pattern of origin and diversification in the arid southwestern United States and northern Mexico, with expansion north and east into patchy, isolated xeric habitats within more mesic biomes.

The dramatic geographic disjunctions in *Phemeranthus* raise further questions. The phylogenetic positions of the Argentinean *P. punae* and of the northwestern *P. sediformis* and *P. spinescens* are particularly interesting. Do these species occupy cladistically basal positions, suggesting long-distance dispersal or vicariance early in the diversification of the group, or are they deeply nested in the tree, indicating a recent origin? Within *P. rugospermus* and *P. parviflorus*, do the population disjunctions correspond to divergent lineages?

Furthermore, *Phemeranthus* includes several rare and endemic taxa whose relationships are not well understood, and species boundaries are unclear in many cases.

Sampling multiple exemplars from across the distribution of widespread species will make it possible to evaluate whether named taxa correspond to evolutionary lineages. The morphological, cytological, and enzyme evidence for allopolyploid speciation in ENA *Phemeranthus* raises the question of how prevalent this process has been throughout the genus. By sequencing multiple chloroplast and nuclear regions and reconstructing gene trees and species trees, the role of hybridization in the evolution of the genus can be assessed.

Due to their unique habitat requirements, fameflowers grow in widely scattered patches across wide areas. The extreme microclimates of their habitats seem likely to impose strong selection pressure on life-history traits such as the timing of seed germination, possibly resulting in clinal variation within widespread species. This possibility has implications for conservation planning and horticulture. Researchers and designers of water-conservative and green-roof plantings have shown increasing interest in Midwestern *Phemeranthus* species (e.g., Getter et al. 2009; Dvorak 2010), and the success of these efforts may be affected by clinal variation in the seed sources used.

These emerging questions will be addressed in the following chapters. Chapter II utilizes multiple chloroplast loci to infer the phylogeny of *Phemeranthus* and to assess the role of hybridization in its evolution. The phylogeny provides a framework to examine the biogeographical history of the genus. Chapter III reports an experiment designed to detect latitudinal variation in seed germination requirements. A preliminary taxonomic treatment of the genus is given as an appendix.

Literature Cited—

Anderson, C. L., K. Bremer, and E. M. Friis. 2005. Dating phylogenetically basal eudicots using *rbcL* sequences and multiple fossil reference points. *American Journal of Botany* 92: 1737-1748.

Applequist, W. L. and R. S. Wallace. 2001. Phylogeny of the portulacaceous cohort based on *ndhF* sequence data. *Systematic Botany* 26: 406-419.

Applequist, W. L., W. Wagner, E. A. Zimmer, and M. Nepokroeff. 2006. Molecular evidence resolving the systematic position of *Hectorella* (Portulacaceae). *Systematic Botany* 31: 310-319.

Axelrod, D. I. 1958. Evolution of the Madro-Tertiary geoflora. *Botanical Review* 24: 433-509.

Axelrod, D. I. 1979. Age and origin of Sonoran Desert vegetation. *Occasional Papers of the California Academy of Sciences* 132: 1-74.

Axelrod, D. I. 1983. Paleobotanical history of the western deserts. Pp. 113-129 in *Origin and Evolution of Deserts*, ed. S. G. Wells and D. R. Haragan. Albuquerque, NM: University of New Mexico Press.

Baskin, J. M. and C. C. Baskin. 1986. Distribution and geographical/evolutionary relationships of cedar glade endemics in southeastern United States. *ASB Bulletin* 33: 138-154.

Baskin, J. M. and C. C. Baskin. 1988. Endemism in rock outcrop plant communities of unglaciated eastern United States: an evaluation of the roles of the edaphic, genetic and light factors. *Journal of Biogeography* 15: 829-840.

Baskin, J. M. and C. C. Baskin. 2000. Vegetation of limestone and dolomite glades in the Ozarks and Midwest regions of the United States. *Annals of the Missouri Botanical Garden* 87: 286-294.

Baskin, J. M. and C. C. Baskin. 2003. The vascular flora of cedar glades of the southeastern United States and its phytogeographical relationships. *Journal of the Torrey Botanical Society* 130: 101-118.

Baskin, J. M., D. H. Webb, and C. C. Baskin. 1995. A floristic plant ecology study of the limestone glades of northern Alabama. *Bulletin of the Torrey Botanical Club* 122: 226-242.

Black, C. and W. H. Murdy. 1972. The evolutionary origin of *Talinum teretifolium* Pursh. *Botanical Gazette* 133: 405-410.

Bogle, A. L. 1969. The genera of Portulacaceae and Basellaceae in the southeastern United States. *Journal of the Arnold Arboretum* 50: 566-598.

Brockington, Samuel F., R. Alexandre, J. Ramdial, Michael J. Moore, S. Crawley, A. Dhingra, K. Hilu, D. E. Soltis, and Pamela S. Soltis. 2009. Phylogeny of the Caryophyllales Sensu Lato: Revisiting Hypotheses on Pollination Biology and Perianth Differentiation in the Core Caryophyllales. *International Journal of Plant Sciences* 170: 627-643.

Brown, J. H., G. C. Stevens, and D. M. Kaufman. 1996. The geographic range: Size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics* 27: 597-623.

Carlquist, S. 2010. Caryophyllales: a key group for understanding wood anatomy character states and their evolution. *Botanical Journal of the Linnean Society* 164: 342-393.

Carolin, R. 1987. A review of the family Portulacaceae. *Australian Journal of Botany* 35: 383-412.

Carter, M. E. B. 1983. *Character displacement in* Talinum mengesii *(Portulacaceae)*. Ph.D. Dissertation. Atlanta, GA: Emory University.

Carter, M. E. B. and W. H. Murdy. 1985. Systematics of *Talinum parviflorum* Nutt. and the origin of *T. teretifolium* Pursh (Portulacaceae). *Rhodora* 87: 121-130.

Carter, M. E. B. and W. H. Murdy. 1986. Divergence for sexual and asexual reproductive characters in *Talinum mengesii* (Portulacaceae). *Bulletin of the Torrey Botanical Club* 113: 259-267.

Coates, D. J., S. Carstairs, and V. L. Hamley. 2003. Evolutionary patterns and genetic structure in localized and widespread species in the *Sylidium caricifolium* complex (Stylidiaceae). *American Journal of Botany* 90: 997-1008.

Cochrane, T. S. 1993. Status and distribution of *Talinum rugospermum* Holz. (Portulacaceae). *Natural Areas Journal* 13: 33-41.

Cronquist, A. 1981. *An Integrated System of Classification of Flowering Plants*. New York, NY: Columbia University Press.

Cronquist, A. 1988. *The Evolution and Classification of Flowering Plants*. Second Edition. New York, NY: The New York Botanical Garden.

Cuenoud, P., V. Savolainen, L. W. Chatrou, M. Powell, R. Grayer, and M. Chase. 2002. Molecular phylogenetics of Caryophyllales based on nuclear 18S rDNA and plastid *rbcL*, *atpB*, and *matK* DNA sequences. *American Journal of Botany* 89: 132-144.

Dahlgren, R. 1975. A system of classification of the angiosperms to be used to demonstrate the distribution of characters. *Botaniska Notiser* 128: 119-147.

Davis, M. B. and R. G. Shaw. 2001. Range shifts and adaptive responses to Quaternary climate change. *Science* 292: 673-679.

Delcourt, H. R., P. A. Delcourt, G. R. Wilkins, and E. N. Smith, Jr. 1986. Vegetational history of the cedar glades regions of Tennessee, Kentucky, and Missouri during the past 30,000 years. *ASB Bulletin* 33: 128-137.

Downie, S., D. KatzDownie, and K. Cho. 1997. Relationships in the caryophyllales as suggested by phylogenetic analyses of partial chloroplast DNA ORF2280 homolog sequences. *American Journal of Botany* 84: 253-273.

Downie, S. R. and J. D. Palmer. 1994. A chloroplast DNA phylogeny of the Caryophyllales based on structural and inverted repeat restriction site variation. *Systematic Botany* 19: 236-252.

Dvorak, B. 2010. Rooftop membrane temperature reductions with green roof technology in south-central Texas. 17th Symposium for Improving Building Systems in Hot and Humid Climates, Austin, Texas, ESL-HH-10-08-23: 1-7.

Ehrendorfer, F. 1976. Closing remarks: systematics and evolution of centrospermous families. *Plant Systematics and Evolution* 126: 99-106.

Gaston, K. J. 1996. Species-range-size distributions: patterns, mechanisms and implications. *Trends in Ecology & Evolution* 11: 197-201.

Gaston, K. J. 1998. Species-range size distributions: products of speciation, extinction and transformation. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* 353: 219-230.

Gaston, K. J. 2008. Biodiversity and extinction: the dynamics of geographic range size. *Progress in Physical Geography* 32: 678-683.

Gaston, K. J. and F. He. 2002. The distribution of species range size: a stochastic process. *Proceedings of the Royal Society B: Biological Sciences* 269: 1079.

Getter, K. L., D. B. Rowe, and B. M. Cregg. 2009. Solar radiation intensity influences extensive green roof plant communities. *Urban Forestry & Urban Greening* 8: 269-281.

Gitzendanner, M. A. and P. S. Soltis. 2000. Patterns of genetic variation in rare and widespread plant congeners. *American Journal of Botany* 87: 783-792.

Greene, E. L. 1912. Miscellaneous specific types - VI. *Leaflets of Botanical Observation and Criticism* 2: 270-272.

Guptill, P. L. 1947. *The morphology and life cycle of* Talinum teretifolium *Pursh*. M.A. Thesis. Atlanta, GA: Emory University.

Guralnick, L. C. and M. D. Jackson. 2001. The occurrence and phylogenetics of Crassulacean Acid Metabolism in the Portulacaceae. *International Journal of Plant Sciences* 162: 257-262.

Hamrick, J. L. and M. J. W. Godt. 1989. Allozyme diversity in plant species. Pp. 43-63 in *Plant Population Genetics, Breeding, and Genetic Resources,* ed. A. H. D. Brown, M. T. Clegg, A. L. Kahler, and B. S. Weir. Sunderland, MA: Sinauer Associates.

Harper, R. M. 1926. The cedar glades of middle Tennessee. *Ecology* 7: 48-54.

Harris, F. and C. Martin. 1991a. Correlation between CAM-Cycling and Photosynthetic Gas Exchange in Five Species of *Talinum* (Portulacaceae). *Plant Physiology* 96: 1118-1124.

Harris, F. and C. E. Martin. 1991b. Plasticity in the degree of CAM-cycling and its relationship to drought stress in 5 species of *Talinum* (Portulacaceae). *Oecologia* 86: 575-584.

Harris, F., M. E. B. Carter, and C. E. Martin. 1993. Relationship between ploidal level and CAM in 5 species of *Talinum* (Portulacaceae). *American Journal of Botany* 80: 533-536.

Harshberger, J. 1897. An ecological study of the genus *Talinum* with descriptions of two species. *Bulletin of the Torrey Botanical Club* 24: 178-188.

Hershkovitz, M. A. 1993. Revised circumscriptions and subgeneric taxonomies of *Calandrinia* and *Montiopsis* (Portulacaceae) with notes on phylogeny of the portulacaceous alliance. *Annals of the Missouri Botanical Garden* 80: 333-365.

Hershkovitz, M. A. 2006. Ribosomal and chloroplast DNA evidence for diversification of western American Portulacaceae in the Andean region. *Gayana Botanica* 63: 13-74.

Hershkovitz, M. A. and E. A. Zimmer. 1997. On the evolutionary origins of the cacti. *Taxon* 46: 217-232.

Hershkovitz, M. A. and E. A. Zimmer. 2000. Ribosomal DNA evidence and disjunctions of Western American Portulacaceae. *Molecular Phylogenetics and Evolution* 15: 419-439.

Hoffmann, A. A. and C. M. Sgrò. 2011. Climate change and evolutionary adaptation. *Nature* 470: 479-485.

Holzinger, J. M. 1899a. *Talinum rugospermum*, n. sp. *The Asa Gray Bulletin* 7: 115-117.

Holzinger, J. M. 1899b. Some notes from my flower garden. *The Asa Gray Bulletin* 7: 80-81.

Holzinger, J. M. 1900. The geographical distribution of the *Teretifolium* group of *Talinum*. *The Asa Gray Bulletin* 8: 36-39.

Iverson, L. and A. Prasad. 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. *Ecological Monographs* 68: 465-485.

Judd, W. S., C. S. Campbell, E. A. Kellogg, and P. F. Stevens. 1999. *Plant Systematics: a Phylogenetic Approach*. Sunderland, MA: Sinauer Associates.

Kiger, R. W. 2001. New combinations in *Phemeranthus* Rafinesque (Portulacaceae). *Novon* 11: 319-321.

Kiger, R. W. 2003. *Phemeranthus*. Pp. 488-495 in *Flora of North America North of Mexico* vol. 4, ed. Flora of North America Editorial Committee. New York, NY and Oxford, UK: Oxford University Press.

Krebs, S. M. 1971. *A systematic study of* Talinum calcaricum *Ware*. M.S. Thesis. Atlanta, GA: Emory University.

Kruckeberg, A. R. and D. Rabinowitz. 1985. Biological aspects of endemism in higher plants. *Annual Review of Ecology and Systematics* 16: 447-479.

MacRoberts, M. H. and B. R. MacRoberts. 1997. *Talinum rugospermum* Holz., new to Louisiana with notes on terete-leaved *Talinum* in Louisiana. *Phytologia* 82: 86-93.

Magallón, S. A. and A. Castillo. 2009. Angiosperm diversification through time. *American Journal of Botany* 96: 349-365.

Martin, C. E. and A. K. Zee. 1983. C-3 photosynthesis and Crassulacean acid metabolism in a Kansas rock outcrop succulent, *Talinum calycinum* Engelm. (Portulacaceae). *Plant Physiology* 73: 718-723.

Martin, C. E., A. E. Lubbers, and J. A. Teeri. 1982. Variability in Crassulacean acid metabolism: A survey of North Carolina succulent species. *Botanical Gazette* 143: 491-497.

Martin, C. E., M. Higley, and W. Z. Wang. 1988. Ecophysiological significance of CO_2-recycling via Crassulacean acid metabolism in *Talinum calycinum* Engelm. (Portulacaceae). *Plant Physiology* 86: 562-568.

McVaugh, R. 1943. The vegetation of the granitic flat-rocks of the southeastern United States. *Ecological Monographs* 13: 119-166.

Montgomery, F. and D. Blake. 1969. *Talinum mengesii* Wolf from a new physiographic province. *Bulletin of the Torrey Botanical Club* 96: 719-720.

Moyle, L. C. 2006. Correlates of genetic differentiation and isolation by distance in 17 congeneric *Silene* species. *Molecular Ecology* 15: 1067-1081.

Muller, J. 1981. Fossil pollen records of extant angiosperms. *Botanical Review* 47: 1-146.

Murdy, W. H. 1968. Plant speciation associated with granite outcrop communities of the southeastern Piedmont. *Rhodora* 70: 394-407.

Murdy, W. H. and M. E. B. Carter. 1985. Electrophoretic study of the allopolyploidal origin of *Talinum teretifolium* and the specific status of *T. appalachianum* (Portulacaceae). *American Journal of Botany* 72: 1590-1597.

Murdy, W. H. and M. E. B. Carter. 2001. Speciation in *Talinum* in the southeastern United States. *Castanea* 66: 145-153.

Murdy, W. H., T. Johnson, and V. Wright. 1970. Competitive replacement of *Talinum mengesii* by *T. teretifolium* in granite outcrop communities of Georgia. *Botanical Gazette* 131: 186-192.

Nixon, E. S., K. L. Marietta, and M. McCrary. 1980. *Brachyelytrum erectum* and *Talinum rugospermum*, new species to Texas and notes on *Schoenolirion wrightii*. *Sida* 8: 355-356.

Nowicke, J. 1996. Pollen morphology, exine structure and the relationships of Basellaceae and Didiereaceae to Portulacaceae. *Systematic Botany*: 187-208.

Nyananyo, B. and S. Mensah. 2004. Distribution and origins of members of the family Portulacaceae (Centrospermae). *Journal of Applied Science & Environmental Management* 8: 59-62.

Nyffeler, R. 2007. The closest relatives of cacti: insights from phylogenetic analyses of chloroplast and mitochondrial sequences with special emphasis on relationships in the tribe Anacampseroteae. *American Journal of Botany* 94: 89-101.

Nyffeler, R. and U. Eggli. 2010. Disintegrating Portulacaceae: A new familial classification of the suborder Portulacineae (Caryophyllales) based on molecular and morphological data. *Taxon* 59: 227-240.

Nyffeler, R., U. Eggli, R. M. Ogburn, and E. J. Edwards. 2008. Variations on a theme: repeated evolution of succulent life forms in the Portulacineae (Caryophyllales). *Haseltonia* 14: 26-36.

Ocampo, G. 2002. Transferencia de tres especies Mexicanas de *Talinum* Adans. a *Phemeranthus* Raf. (Portulacaceae). *Acta Botanica Mexicana* 59: 75-80.

Ocampo, G. 2003. Una combinación nueva en *Phemeranthus* (Portulacaceae). *Acta Botanica Mexicana* 63: 55-57.

Ocampo, G. and J. T. Columbus. 2010. Molecular phylogenetics of suborder Cactineae (Caryophyllales), including insights into photosynthetic diversification and historical biogeography. *American Journal of Botany* 97: 1827-1847.

Paleontology, U. o. C. M. o. 1994-2007. Caryophyllids: Fossil Record, *History of Life Through Time*: the Regents of the University of California.

Quarterman, E. 1950. Major plant communities of the Tennessee cedar glades. *Ecology* 31: 234-254.

Raven, P. H. 1963. Amphitropical relationships in the floras of North and South America. *Quarterly Review of Biology* 38: 151-177.

Raven, P. H. and D. A. Axelrod. 1974. Angiosperm biogeography and past continental movements. *Annals of the Missouri Botanical Garden* 61: 539-673.

Raven, P. H. and D. A. Axelrod. 1978. Origin and relationships of the California flora. *University of California Publications in Botany* 72: 1-134.

Ravn, R. L. 1987. *Montiapollis* n. gen., possible Portulacaceae pollen from the Cenomanian of Iowa. *Grana* 26: 243-247.

Reinhard, R. and S. Ware. 1989. Adaptation to substrate in rock outcrop plants: interior highlands *Talinum* (Portulacaceae). *Botanical Gazette* 150: 449-453.

Rettig, J. H., H. D. Wilson, and J. R. Manhart. 1992. Phylogeny of the Caryophyllales: Gene sequence data. *Taxon* 41: 201-209.

Reusch, T. B. H. and T. E. Wood. 2007. Molecular ecology of global change. *Molecular Ecology* 16: 3973-3992.

Rose, J. N. and P. C. Standley. 1911. The genus *Talinum* in Mexico. *Contributions from the United States National Herbarium* 13: 281-288.

Schaal, B. A., D. A. Hayworth, K. M. Olsen, J. T. Rauscher, and W. A. Smith. 1998. Phylogeographic studies in plants: problems and prospects. *Molecular Ecology* 7: 465-474.

Sexton, J. P., P. J. McIntyre, A. L. Angert, and K. J. Rice. 2009. Evolution and Ecology of Species Range Limits. *Annual Review of Ecology, Evolution and Systematics* 40: 415-436.

Soltis, D. E., S. A. Smith, N. Cellinese, K. J. Wurdack, D. C. Tank, S. F. Brockington, N. F. Refulio-Rodriguez, J. B. Walker, M. J. Moore, B. S. Carlsward, C. D. Bell, M. Latvis,

S. Crawley, C. Black, D. Diouf, Z. Xi, C. A. Rushworth, M. A. Gitzendanner, K. J. Sytsma, Y.-L. Qiu, K. W. Hilu, C. C. Davis, M. J. Sanderson, R. S. Beaman, R. G. Olmstead, W. S. Judd, M. J. Donoghue, and P. S. Soltis. 2011. Angiosperm phylogeny: 17 genes, 640 taxa. *American Journal of Botany*: 1-27.

Stebbins, G. L. 1942. The genetic approach to problems of rare and endemic species. *Madrono* 6: 241-258.

Stebbins, G. L. 1980. Rarity of plant species: A synthetic viewpoint. *Rhodora* 82: 77-86.

Steiner, E. 1944. Cytogenetic studies on *Talinum* and *Portulaca*. *Botanical Gazette* 105: 374-379.

Stevens, P. F. 2001 onwards. Angiosperm Phylogeny Website. Version 9, June 2008 [and more or less continually updated since]. http://www.mobot.org/MOBOT/research/APweb/.

Steyermark, A. J. 1963. *Flora of Missouri*. Ames, Iowa: Iowa State University Press.

Takhtajan, A. 1980. Outline of the classification of flowering plants (Magnoliophyta). *Botanical Review* 46: 225-359.

Takhtajan, A. 1997. *Diversity and classification of flowering plants*. New York: Columbia University Press.

The Angiosperm Phylogeny Group. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society* 161: 105-121.

Thorne, R. F. 1968. Synopsis of a putatively phylogenetic classification of the flowering plants. *Aliso* 6: 57-66.

Thorne, R. F. 1976. A phylogenetic classification of the Angiospermae. *Evolutionary Biology* 9: 35-106.

Thorne, R. F. 2000. The classification and geography of the flowering plants: Dicotyledons of the class Angiospermae (subclasses Magnoliidae, Ranunculidae, Caryophyllidae, Dilleniidae, Rosidae, Asteridae, and Lamiidae). *Botanical Review* 66.

Tyndall, R. W. and J. C. Hull. 1999. Vegetation, flora, and plant physiological ecology of serpentine barrens of Eastern North America. Pp. 67-82 in *Savannas, Barrens, and Rock Outcrop Plant Communities of North America* vol., ed. R. C. Anderson, J. S. Fralish, and Jerry M Baskin. New York: Cambridge University Press.

University of California Museum of Paleontology. 1994–2007. Caryophyllids: Fossil Record. *History of Life Through Time* (web site). Copyright 1994–2007 by the Regents of the University of California, all rights reserved. Available online at http://www.ucmp.berkeley.edu/anthophyta/caryos/caryophyllidfr.html. Accessed 11/12/07.

Vanvinckenroye, P. and E. Smets. 1996. Floral ontogeny of five species of *Talinum* and of related taxa (Portulacaceae). *Journal of Plant Research* 109: 387-402.

von Poellnitz, V. K. 1934. Monographie der Gattung *Talinum* Adans. *Repertorium Specierum Novarum Regni Vegetabilis* 35: 1-34.

Walters, T. W. and R. Wyatt. 1982. The vascular flora of granite outcrops in the Central Mineral Region of Texas. *Bulletin of the Torrey Botanical Club* 109: 344-364.

Ward, D. E. and R. W. Spellenberg. 1986. Chromosome counts of angiosperms of western North America. *Phytologia* 61: 119-125.

Ware, S. 1967. A new *Talinum* (Portulacaceae) from the cedar glades of middle Tennessee. *Rhodora* 69: 466-475.

Ware, S. 1969a. Ecological role of *Talinum* (Portulacaceae) in cedar glade vegetation. *Bulletin of the Torrey Botanical Club* 96: 163-175.

Ware, S. 1969b. On the ecology of *Talinum mengesii* (Portulacaceae). *Bulletin of the Torrey Botanical Club* 96: 4-10.

Ware, S. 1972. Growth and dormancy in *Talinum* rhizomes. *Ecology* 53: 1195-1199.

Ware, S. 1991. Influence of interspecific competition, light and moisture levels on growth of rock outcrop *Talinum* (Portulacaceae). *Bulletin of the Torrey Botanical Club* 118: 1-5.

Ware, S. 2002. Rock outcrop plant communities (glades) in the Ozarks: a synthesis. *The Southwestern Naturalist* 47: 585-597.

Ware, S. 2011. A new *Phemeranthus* (Portulacaceae) from the Piedmont of Virginia and North Carolina. *Journal of the Botanical Research Institute of Texas* 5: 1-7.

Ware, S. and E. Quarterman. 1969. Seed germination in cedar glade *Talinum*. *Ecology* 50: 137-140.

Ware, S. and G. Pinion. 1990. Substrate adaptation in rock outcrop plants: eastern United States *Talinum* (Portulacaceae). *Bulletin of the Torrey Botanical Club* 117: 284-290.

Ware, S. A. 1968. *Responses and adaptations of a cedar glade endemic (*Talinum calcaricum*, Portulacaceae) to factors of its habitat*. Ph.D. thesis. Nashville, TN: Vanderbilt University.

Wikstrom, N., V. Savolainen, and M. W. Chase. 2001. Evolution of the angiosperms: calibrating the family tree. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 268: 2211-2220.

Wolf, W. 1939. The status of *Talinum* in Alabama. *American Midland Naturalist* 22: 315-332.

Wyatt, R. 1997. Reproductive ecology of granite outcrop plants from the south-eastern United States. *Journal of the Royal Society of Western Australia* 80: 123-129.

CHAPTER II. PHYLOGENY AND EVOLUTION OF *PHEMERANTHUS* IN NORTH AMERICAN XERIC HABITATS BASED ON CHLOROPLAST DNA SEQUENCES

Abstract—The center of diversity of *Phemeranthus* is in northern Mexico and the southwestern United States, but several species occur in the glade and flat-rock ecosystems of the Midwestern and Southeastern United States, and others are disjunct from the remainder of the genus in the inland Northwest or the southern Andes. Here, the phylogenetic relationships of *Phemeranthus* species are inferred from DNA sequences of the chloroplast regions *ndhF* and *matK-trnK*, and geographic patterns within the genus are examined in the context of other North American desert biota. *Phemeranthus* (excluding *P. aurantiacus*) is monophyletic and is likely sister to the remainder of Montiaceae. The genus contains two geographically structured clades: a southern clade centered in Mexico and a northern clade distributed primarily in the United States. Plant habit and flower color distinguish the northern and southern clades, but seed coat morphology does not reliably separate groups within *Phemeranthus*. A geographically disjunct lineage is sister to the remainder of each clade: *P. punae* of Argentina is sister to the Mexican species, while *P. spinescens* and *P. sediformis* of the inland Northwest are sister to the remaining northern species, suggesting broad-scale movements early in the diversification of the genus. The current distribution indicates an origin in the southwestern United States and northern Mexico, followed by northward and eastward expansion with accompanying speciation. The placement of certain species and populations highlights the probable role of hybridization in the evolution of this xerophytic genus.

Introduction: Biogeography of North American Deserts**—**Species diversification in North Temperate arid zones, such as the American Southwest, is of great interest to evolutionary biologists, especially as climate-change models predict increasing aridity and an expansion of xeric conditions in mid-latitude regions throughout the world (IPCC 2007; Seager et al. 2007; Fawcett et al. 2011). Landscape heterogeneity and extreme climatic conditions are associated with the evolution of many endemic species in arid zones (e.g., Moore and Jansen 2006). Harsh environmental conditions may promote adaptation to narrowly restricted microhabitats, while landscape heterogeneity may enforce isolation of populations in fragmented habitats such as mountain ranges, desert springs, and geologic outcroppings. Severe climatic conditions of intense insolation, high air and soil temperature, and drought can impose strong natural selection. Dramatic seasonal differences in temperature and soil moisture are an additional challenge.

The classic pattern of post-glacial migration in eastern North America (ENA) has been extensively studied with fossil pollen and molecular phylogeography (e.g., Hewitt 1996; Comes and Kadereit 1998; Soltis et al. 2006), and many European taxa exhibit common genetic patterns due to classical refugial dynamics during the Quaternary (e.g., Hewitt 1996; Comes and Kadereit 1998; Hewitt 2004). However, the biogeographic patterns of xerophytic Southwestern plants are less well understood. According to Axelrod (1958), the desert and semi-desert vegetative communities of southwestern North America first began to form during late Tertiary (Miocene) aridification, reaching their widest distribution in the early Pliocene and shrinking during wetter and cooler intervals in the late Pliocene and throughout the Pleistocene. During pluvial periods, arid-adapted vegetation was confined to western and southern refugia (Rebernig et al. 2010b; and references therein).

The regional deserts of today developed as a result of dramatic aridification following the Last Glacial Maximum, covering their maximum area during the Hypsithermal interval ca. 9,000–5,000 BP (Riddle and Hafner 2006). This Holocene aridification proceeded from west to east, beginning in the Sonoran Desert (van Devender and Spaulding 1979; McAuliffe and Van Devender 1998; Holmgren et al. 2007). During mid-Pleistocene interglacials, parts of the Southwestern United States went through periods of high temperatures and increased aridity lasting centuries to millennia (Fawcett et al. 2011). Thus, arid-adapted taxa are expected to show genetic signatures reflecting late Miocene to Pliocene vicariance due to mountain building, plateau uplift, and rifting; Pleistocene fragmentation and divergence due to cyclical isolation in desert refugia; and Holocene range expansion and secondary contact (Riddle and Hafner 2006; Rebernig et al. 2010a; Bryson et al. 2011; and references therein).

Biogeographic studies of arid ecosystems are hampered by the scarcity of fossil evidence. The main sources of biogeographic hypotheses have been contemporary species' distributions and the geological record. In addition to these indirect data, numerous studies have used packrat middens and pollen cores to reconstruct dramatic vegetation shifts in the Southwest (e.g., McAuliffe and Van Devender 1998; Metcalfe et al. 2000; Thompson and Anderson 2000; Holmgren et al. 2003; Holmgren et al. 2007). These records, however, extend back only to the mid-Pleistocene; hypotheses about earlier conditions rely on geology and, increasingly, on phylogenetic evidence.

Hypotheses about the biogeography of the arid Southwest have been tested against phylogeographic data in numerous animal groups, and certain common patterns have emerged. Perhaps the most general pattern is a pronounced east-west split between species or intraspecific phylogroups. Often, molecular dating techniques indicate that this divergence is associated with Late Miocene to Pliocene Cordilleran uplift. Vicariance between eastern (Chihuahuan) and western (Sonoran and Mojave) continental deserts due to the uplift of the Sierra Madres and Mexican Plateau has been inferred for rodents (e.g., Riddle 1995), insects (e.g., Wilson and Pitts 2010), amphibians (e.g., Jaeger et al. 2005), snakes (e.g., Castoe et al. 2007; Fontanella et al. 2008; Bryson et al. 2010; Bryson et al. 2011), and lizards (e.g., Morafka 1977; Haenel 2007). In many groups, however, east-west divergence across the Continental Divide dates to the Pleistocene and may be associated with climatic oscillations (e.g., Zink and Blackwell 1998; Pook et al. 2000; Ashton and de Queiroz 2001; Reeder and Montanucci 2001; Ayoub and Riechert 2004; Leaché and McGuire 2006; Leaché and Reeder 2006). In many cases, both intraspecific differentiation attributed to Pleistocene refugial dynamics and deeper divergences associated with Neogene formation of geographical barriers can be detected simultaneously.

During the Holocene and likely during some earlier interglacials, climatic warming has permitted migration across the Continental Divide, particularly through the Cochise Filter Barrier, a narrow region in southern New Mexico and Arizona where the Chihuahuan and Sonoran desert biotas come into contact. High species, clade, and haplotype diversity in this contact zone is the result of post-Pleistocene expansion from separate desert refugia located east and west of the Divide (e.g., Morafka 1977; Jaeger et al. 2005; Castoe et al. 2007). Commonly, eastern phylogroups exhibit more dramatic Holocene range expansion compared to western phylogroups, with evidence for northward, eastward, and even westward (into the Colorado Plateau and/or Rockies) movement from refugia located in the southern Chihuahuan desert and elsewhere east of the Continental Divide (e.g., Ayoub and Riechert 2004; Jaeger et al. 2005; Smith and Farrell 2005a; Castoe et al. 2007; Haenel 2007; Fontanella et al. 2008).

In contrast to highly arid-adapted lowland taxa, the more mesic and cold-tolerant biota of southwestern mountain ranges may have expanded their ranges downward and southward during glacials and contracted during interglacials. Depending upon taxon-specific factors such as dispersal ability, these fluctuations could result in differentiation among isolated sky islands or in the presence of northern phylogroups unexpectedly far to the south (e.g., Masta 2000; Knowles 2001; Smith and Farrell 2005b; Moore and Jansen 2006; McCormack et al. 2008; Burbrink et al. 2011).

Despite these advances in understanding the phylogeography of southwestern fauna, comparable studies in plants have been rare until recently, and general patterns are less clear. Several studies have focused on plant taxa that are distributed only west of the Continental Divide, in the Mojave, Sonoran, and/or Peninsular deserts (e.g., Nason et al. 2002; Clark-Tapia and Molina-Freaner 2003; Fehlberg and Ranker 2007, 2009; Garrick et al. 2009). These studies have found evidence for Miocene-Pliocene vicariant events largely congruent with those inferred for co-distributed animal groups and have also reported dramatic northward (and, to a lesser extent, southward) post-Pleistocene range expansion. Sosa et al. (2009) studied a xerophytic plant from the opposite side of the Continental Divide, the Mexican tulip poppy, which is centered in the Sierra Madre

Oriental. They too detected the signatures of historical isolation and post-glacial range expansion.

Among plants found on both sides of the Continental Divide, some exhibit a broad east-west split like that seen in many animal groups, with glacial refugia located both west and east of the Continental Divide (e.g., Moreno-Letelier and Piñero 2009; Rebernig et al. 2010b; Sanchez-del Pino and Motley 2010). Refugial areas inferred for both animals (e.g., Riddle and Hafner 2006; Castoe et al. 2007) and plants include the lower Colorado basin (Hunter et al. 2001; Fehlberg and Ranker 2007; Rebernig et al. 2010b), the central or southern Chihuahuan Desert (Hunter et al. 2001), and the Tamaulipan plains (Rebernig et al. 2010a). Post-Pleistocene range expansion from separate desert refugia has produced contemporary contact zones and opportunities for hybridization (e.g., Rebernig et al. 2010b). At a broader scale, dispersion out of a southwestern center of diversity is a general pattern in xeric-adapted plant groups (Moore and Jansen 2006; Moore et al. 2006; Douglas and Manos 2007; Marlowe and Hufford 2007; Evans et al. 2009; Rebernig et al. 2010a; Yang and Berry 2011).

As in animals, sky islands have played an important role in the phylogeography of southwestern plants. For example, some coniferous taxa that originated in cooler regions to the north migrated southward along the Cordillera during glacial epochs and became isolated in mountainous regions during warmer periods (Moreno-Letelier and Piñero 2009; Gugger et al. 2010b; Gugger et al. 2010a). Clearly, a nuanced and thorough understanding of the influence of recent and ancient events on Southwestern biota will require studies of additional plant groups.

Phemeranthus: A Case Study for North American Xerophytic Plants—Xeric habitats in North America are not restricted to the desert Southwest. In the glade and flat-rock ecosystems of the interior highlands and the southeastern United States, local patches of extreme desert-like habitats are surrounded by deeper-soil forest communities (Quarterman et al., 1993). The flora and fauna of these glade ecosystems include numerous species whose closest relatives occur to the west, including animals (e.g., scorpions, tarantulas, lichen grasshoppers, collared lizards, and roadrunners) and plants (e.g., prickly pear cacti, evening primroses, and bladderpods). Numerous endemic species are found in these open, rocky habitats (Baskin and Baskin 1988, 2000). *Phemeranthus* Raf. (Montiaceae; fameflowers, rockpinks, sunbrights) exemplifies this distributional pattern, forming part of the characteristic flora of many glade and rock-outcrop ecosystems. Even among glade plants, fameflowers stand out for their extreme xerophytic adaptation, actively growing and flowering in the shallowest soils throughout the height of summer, seemingly heedless of drought and temperature stress.

The genus *Phemeranthus* comprises about 25 species of succulent, herbaceous perennials with terete leaves, most of which grow in patchy xeric habitats such as rock outcrops and sand barrens (Figs. 1.1, 1.2). Formerly included in *Talinum* Adans., *Phemeranthus* has been segregated on the basis of molecular (Hershkovitz and Zimmer 1997, 2000) and morphological evidence (Carolin 1987; Hershkovitz 1993).

Phemeranthus species are almost exclusively North American in distribution (Table 1.1; Fig. 2.1), with a center of diversity in northern Mexico and the southwestern United States; one disjunct species is found in northern Argentina. Several species extend northward and eastward across the Great Plains and into the interior highlands and the southeastern United States. This distributional pattern suggests a biogeographic origin in the Southwest followed by northward and eastward movement into arid habitats elsewhere.

Phemeranthus species vary widely in geographic range size and habitat specificity. For example, *P. calcaricus* (S.Ware) Kiger is restricted to limestone cedar glades in the central basin of Tennessee; *P. brevifolius* (Torr.) Hershk. is widespread in a single geographic region, the Colorado Plateau; and *P. parviflorus* (Nutt.) Kiger ranges from Texas to the Dakotas and from Colorado east to Illinois, with a disjunct population in central Alabama. Some species appear to be edaphic specialists, while others occur on a wide range of soil types (Ware 1967, 1969a, 1969b; Reinhard and Ware 1989; Ware and Pinion 1990). This variation in geographic distribution, range size, and habitat specificity makes *Phemeranthus* an ideal study system for research regarding diversification in arid habitats and the origins of glade endemics.

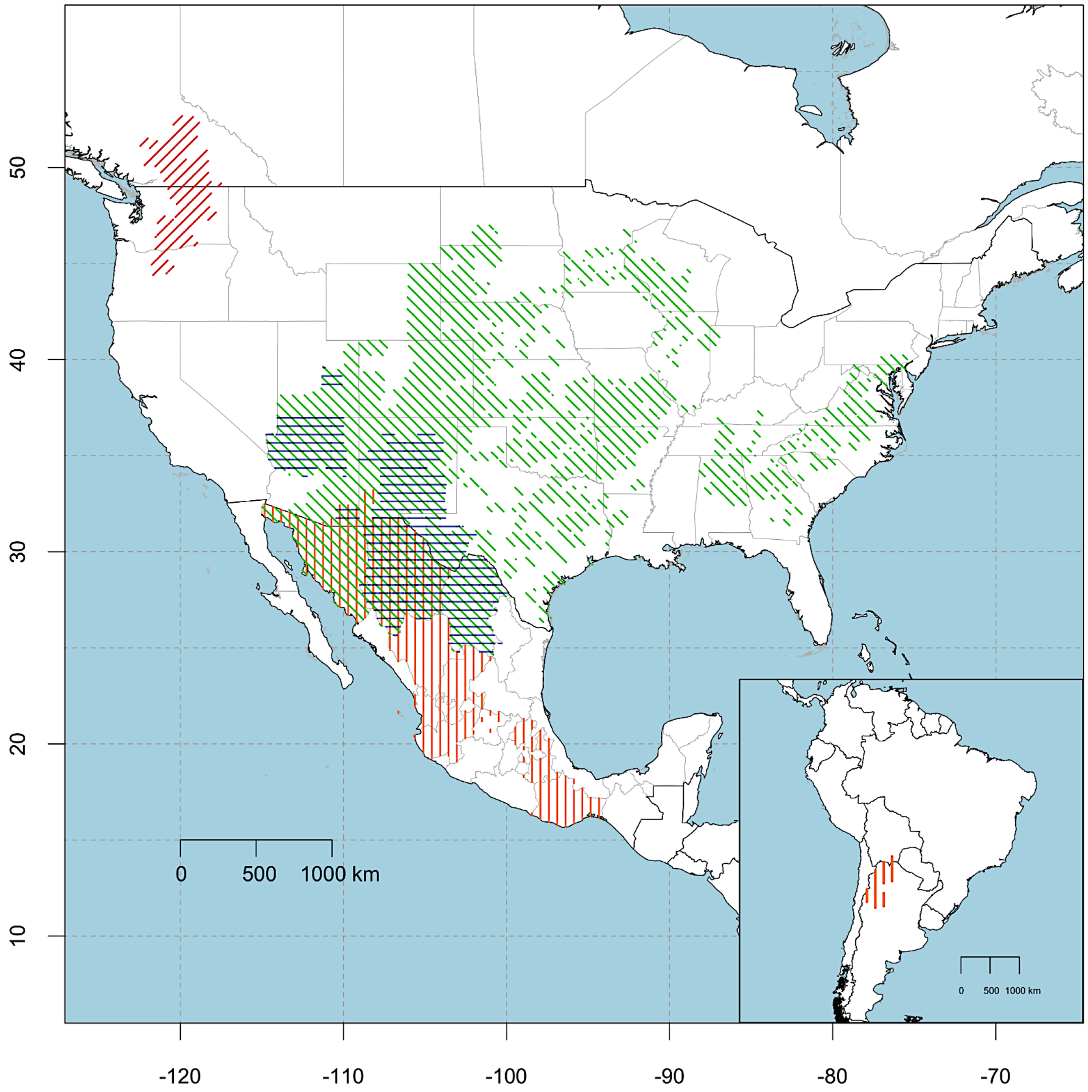

FIGURE 2.1. Distribution map for *Phemeranthus*, showing the approximate ranges of each major clade. Colors correspond to the clades labeled in Fig. 2.2 (below): Clade 1A, red; Clade 1B, blue; Clade 1C, green; Clade 2, orange. Highlighted areas in the United States are based on county-level occurrence data, while those in Mexico and Argentina are based on departamento (state)-level occurrence data.

The families that constitute the suborder Portulacineae (Cactaceae, Didiereaceae, Basellaceae, Halophytaceae, and the various lineages of the traditional Portulacaceae, including Montiaceae) provide many opportunities to study the evolution of xeric-adapted plant taxa; most members of the group exhibit some type of succulence (Nyffeler et al. 2008). The relationships among these families have been clarified by recent analyses of both morphological and molecular data (Fig. 1.3). Notably, Cactaceae is derived from within the traditional Portulacaceae, necessitating the division of the latter family into several smaller families (Nyffeler and Eggli 2010). Most members of the former Portulacaceae found in temperate North and South America, including *Phemeranthus*, are now classified in Montiaceae, the largest family segregated from Portulacaceae and the possible sister group to the remainder of Portulacineae. However, although major clades within Portulacineae have been identified and are mostly well supported, many details of their relationships remain poorly resolved. Furthermore, lower-level relationships within Montiaceae have yet to be examined in depth. The present study examines an important lineage within Montiaceae that also exemplifies the evolution of xeric-adapted plant groups in temperate North America.

The goals of this study were to evaluate the monophyly of *Phemeranthus* as treated in the *Flora of North America* and to assess its relationships with other lineages of Montiaceae and Portulacineae; to discern geographic patterns among *Phemeranthus* clades in the context of plant biogeographic patterns in xeric North America; and to examine whether certain morphological traits, especially seed testa ornamentation, reliably distinguish clades.

Materials and Methods—

Taxon Sampling and Field Studies**—***Phemeranthus* species were collected throughout the southwestern, midwestern, and southeastern United States, with multiple accessions from across the geographic ranges of widely distributed species. For this study, 55 *Phemeranthus* accessions representing 15 taxa were collected at 50 sites. Collections were documented with digital photographs and voucher specimens (deposited at MO). Leaf material was desiccated in silica gel for DNA extraction. When possible, live plants and/or seeds were brought back to the greenhouse and grown under controlled conditions to provide fresh leaf material for higher quality DNA extracts. Material representing species from Argentina, Mexico, and the United States was generously provided by colleagues, and additional accessions of five species (seed or live plants) were obtained from commercial rock-garden and succulent nurseries. In all, 68 *Phemeranthus* accessions were newly sequenced for this study.

Outgroup selection was guided by recent phylogenetic analyses (e.g., Nyffeler and Eggli 2010; Ocampo and Columbus 2010) that have clarified relationships within suborder Portulacineae (see Fig. 1.3). Nine outgroup samples were collected in the field, including three *Claytonia* L. and one *Lewisia* Pursh (Montiaceae), two *Portulaca* L. (Portulacaceae), and three accessions of *Talinum aurantiacum* Engelm. [= *Phemeranthus aurantiacus* (Engelm.) Kiger; Talinaceae]. In addition, DNA was extracted and sequences generated from silica-dried tissue of three other *Talinum* and *Talinella* Baill. species supplied by M. Ogburn of the University of Missouri, St. Louis. In all, five additional Montiaceae, two Portulacaceae, and six Talinaceae accessions were newly sequenced for this study (see APPENDIX 1 for taxon sampling).

Additional sequences were downloaded from GenBank, including the *ndhF* sequences for *P. mengesii* (W.Wolf) Kiger and *T. angustissimum* Wooton & Standl. generated by Applequist and colleagues (Applequist and Wallace 2001; Applequist et al.

2006) and *ndhF* and *matK* sequences for 30 other taxa (ten Montiaceae, four Talinaceae, four Portulacaceae, three Cactaceae, one Anacampserotaceae, five Didiereaceae, two Basellaceae, and one Molluginaceae). An *ndhF* sequence was available for every terminal taxon used in the final dataset, but *matK* sequences were not available for some taxa (see Appendix). *Mollugo verticillata* L., which is not a member of Portulacineae but has been implicated as a possible sister group in previous studies (e.g., Applequist et al. 2006), was used as a more distant outgroup to root the trees.

DNA Regions and Phylogenetic Analyses—Genomic DNA was extracted from either silica-dried or liquid nitrogen-frozen leaves using a modified CTAB protocol. For most accessions, either a 1:10 or a 1:100 dilution of genomic DNA extract was used for PCR.

To place *Phemeranthus* within its phylogenetic context in Montiaceae (Nyffeler and Eggli 2010), the chloroplast gene *ndhF* was sequenced. This region has been used in previous studies of Portulacinae (Applequist and Wallace 2001; Applequist et al. 2006; Nyffeler and Eggli 2010), making sequences available for a broad sampling of outgroup taxa. In addition, the chloroplast region *matK–trnK* was sequenced using primers from Johnson and Soltis (1995) and Hilu et al. (2003). These two regions consistently amplified in *Phemeranthus* species and produced high-quality, readily alignable sequence data. In the search for better phylogenetic resolution, we surveyed several additional chloroplast intergenic spacer regions (e.g., Small et al. 1998; Shaw et al. 2005; Shaw et al. 2007). However, most primer sets either did not amplify reliably in *Phemeranthus* or produced poor sequence data due to the presence of lengthy poly-A/T regions.

The primers NYmatK480F (Borsch et al. 2003) and trnK2R (Johnson and Soltis

1995) were used to amplify *matK*, and the primers 1B, 8B, 5C, and 16D of Applequist and Wallace (2001) were used to amplify *ndhF* (Table 2.1). The complete *ndhF* region was typically amplified in two overlapping segments using the primer pairs 1B-8B and 5C-16D. For some taxa in which PCR or sequencing reactions using these primers were unsuccessful, the alternative forward primer ndhF20F (substituted for 1B) and the alternative reverse primer ndhF2047R (substituted for 16D) were employed.

TABLE 2.1. Primers used to amplify and sequence chloroplast regions

Primer	**Sequence**	**Reference**
NYmatK480F	5'-CATCTGGAAATCTTGSTTC-3'	Borsch et al., 2003
trnK2R	5'-AACTAGTCGGATGGAGTAG-3'	Johnson & Soltis, 1995
1B	5'-CCTTYATTCCRCTTCCAGTTCC-3'	Applequist & Wallace, 2001
8B	5'-ATAGATTCGACACATATAAAATGCAGTT-3'	Applequist & Wallace, 2001
5C	5'-CTTCTTCCTCTTTTCGTAGTTATACC-3'	Applequist & Wallace, 2001
16D	5'-CCTCCTRYATAYTTGATACCTTCTCC-3'	Applequist & Wallace, 2001
ndhF20F	5'-GTTAATAGGAGTGGGACTTC-3	This study
ndhF2047R	5'-AACACCAAAACCATTCGGA-3'	This study

For both *matK* and *ndhF*, PCR amplifications were performed in a total volume of 10.0 µL containing 1× Taq buffer [Qiagen CoralLoad (Qiagen Inc., Valencia, California) or Promega GoTaq Green (Promega Corporation, Fitchburg, Wisconsin)], 1.5–2.5 mM $MgCl_2$ (contained in the buffer and/or added separately), 0.2 mM each dNTP, 0.2 µM forward primer, 0.2 µM reverse primer, 0.25 U Taq DNA polymerase (Qiagen or Promega GoTaq), and 1.0 µL genomic DNA (usually a 1:10 dilution of the genomic DNA extract). For *ndhF*, the PCR thermal-cycling profile consisted of a 1-min initial denaturation at 94ºC; 36 cycles of 1 min at 94ºC, 1 min at 53ºC, and 2 min 10 sec at 72ºC; and a 10-min final extension at 72ºC. For *matK*, the PCR thermal-cycling profile consisted of a 3-min initial denaturation at 94ºC; 30 cycles of 30 sec at 94ºC, 30 sec at 53ºC, and 2 min at 72ºC; and a 10-min final extension at 72ºC.

Amplified products were purified by treatment with exonuclease I and either shrimp alkaline phosphatase or Antarctic phosphatase. Cycle-sequencing reactions used the same primers used for amplification and BigDye Terminator v1.1 or v3.1 (Applied Biosystems Inc., Foster City, California). Amplicons were sequenced in both directions on an ABI 3130xl DNA sequencer at Washington University in St. Louis or on an ABI 3730xl DNA sequencer at the Institute for Genome Sciences & Policy DNA Sequencing Facility at Duke University. Sequence chromatograms were examined and contigs constructed in Sequencher v4.10.1 (Gene Codes Corporation, Ann Arbor, Michigan). Additional outgroup sequences were downloaded from GenBank, and sequences were manually aligned using Se-Al v2.0a11 (Rambaut 1996). Single-nucleotide-repeat gaps were removed, and informative gaps were coded using simple gap coding (Simmons and Ochoterena 2000; Simmons et al. 2001). For combined analyses, the two data sets were concatenated using Phyutility (Smith and Dunn 2008). ALTER (Glez-Peña et al. 2010) was also used to convert data sets to the formatting requirements of different programs.

Maximum-parsimony (MP) phylogeny reconstruction was performed in PAUP* version 4.0a114 (Swofford 2003). Heuristic tree searches included 20 replicates using random addition sequence and tree-bisection-reconnection (TBR) branch swapping. A maximum of 100,000 trees were saved during each replicate to ease computational constraints. Gaps were treated as missing data. To assess branch support, 1,000 bootstrap replicates were performed, each consisting of a single random addition sequence with TBR branch swapping and the maximum number of trees to be saved set at 5,000. To assess the contribution of each cpDNA region, the analysis was repeated for *matK* alone, *ndhF* alone, and both regions combined; all three datasets were analyzed with and without indels.

The phylogeny was also inferred under the criterion of maximum likelihood (ML) using GARLI (Zwickl 2006). For this analysis, the binary indel data were excluded and only the nucleotide sequences were used. Program default parameters were used, and the run was automatically terminated after 10,000 generations without significant improvement in topology. The program was allowed to estimate the optimum model of sequence evolution, and a random starting tree was used. To assess branch support, 1,000 repetitions of bootstrap resampling were performed. For each bootstrap repetition, the termination condition was set at 5,000 generations without significant improvement in topology. For comparison, jModelTest v0.1 (Guindon and Gascuel 2003; Posada 2008) was also used to determine the model of sequence evolution that best fit the data. The program was allowed to optimize the topology rather than being supplied with a fixed topology. The jModelTest analysis was run separately on the *matK*, *ndhF,* and combined datasets. The GARLI analysis was then repeated with the sequence evolution model parameters fixed according to the optimum model selected by the corrected Akaike information criterion (AICc) in jModelTest.

Finally, MrBayes 3.1 (Carolin 1987; Kiger 2003) was used to perform Bayesian inference of phylogeny (BI). MrBayes was also set up to optimize the sequence-evolution model parameters. Two parallel MCMC runs of four chains each were run for 10,000,000 generations, sampling every 1,000 generations. The temperature parameter was set at 0.08. To improve convergence, a starting tree obtained by neighbor joining was supplied. To assess convergence, the standard deviations of splits frequencies were examined and the first 2,500 trees were discarded as burn-in, leaving a sample of 7,500 trees in the set, from which a majority-rule consensus was computed.

Results—A total of 113 terminal taxa were included in the analyses (APPENDIX 1). Of these, 68 *Phemeranthus* accessions, five additional Montiaceae, two Portulacaceae, and six Talinaceae accessions were newly sequenced for this study. Thirty-two *ndhF* sequences and 15 *matK* sequences were obtained from GenBank. Thus, the final dataset contained 162 sequences generated for this study and 47 from GenBank, or approximately 78% new data.

After gap insertion, the aligned length of the *ndhF* region was 2,028 base pairs, while that of the *matK* region was 1,251 base pairs. Eight *ndhF* indels (6–12 bp) and nine *matK* indels (3–22 bp) were coded as binary characters. Of these 3,296 total characters, 590 were parsimony-informative. See Table 2.2 for additional details about each region. The heuristic tree search in PAUP* using the total data set yielded 22 MP trees. The differences among these 22 trees were confined to relationships among the three sampled Cactaceae and the placement of certain subgroups of Talinaceae.

Excluding the binary indel data from the analysis did not alter the topology nor substantially affect branch support values in the MP bootstrap consensus tree. When the two regions were analyzed separately, the *ndhF* data provided substantially more resolution and overall branch support than did the *matK* data, but the combined data set yielded more resolution and higher branch supports than the *ndhF* data alone (Table 2.2). Although the *matK* tree was less resolved, its topology mostly did not conflict with that of the *ndhF* tree, except as noted below. The *matK* dataset alone provided no support for backbone relationships within Portulacineae.

The sequence evolution models selected for each region and for the combined data set according to the corrected Akaike information criterion (AICc) in jModelTest are summarized in Table 2.3. In the ML analyses using GARLI, constraining the sequence-evolution model parameters according to the results obtained from jModelTest did not alter the resulting topology, nor did it noticeably affect the inferred branch lengths in any part of the tree, although the likelihood was improved slightly. Furthermore, the sequence-evolution models inferred by GARLI were generally similar to those chosen by jModelTest, except that GARLI tended to yield larger gamma shape parameter values (see Table 2.3). Only the results of the unconstrained GARLI analyses are presented here.

Table 2.2. Sequence regions and summary of maximum parsimony results. †Number of terminal taxa in the dataset / number obtained from GenBank. *Number of clades with MP bootstrap support >50% within *Phemeranthus*.

region	**†accessions**	**length**	**variable characters**	**parsimony informative**	**# MP trees**	**MP tree length**	**CI**	**RI**	**RC**	***nodes resolved**
ndhF	113 / 32	2,028 bp	668	415	11,938	1,365	0.649	0.860	0.558	24
(w/ indels)		8 indels	676	422	12,019	1,381	0.647	0.859	0.556	24
matK	94 / 15	1,251 bp	298	166	12,853	476	0.754	0.888	0.670	16
(w/ indels)		9 indels	306	168	12,861	484	0.758	0.888	0.674	16
ndhF + *matK*	113 / 32	3,279 bp	966	581	22	1,850	0.673	0.865	0.582	29
(w/ indels)		17 indels	982	590	22	1,874	0.673	0.864	0.581	29

Table 2.3. Sequence evolution model and maximum likelihood results for each region. *For each region, the top row shows the model selected by jModelTest according to the corrected Akaike information criterion (AICc); the bottom row shows the model estimated by GARLI simultaneously with the topology and branch lengths.

region	***model**	**-lnL**	**freqA**	**freqC**	**freqG**	**freqT**	**R[AC]**	**R[AG]**	**R[AT]**	**R[CG]**	**R[CT]**	**p-inv**	**gamma shape**
ndhF	TVM+I+G	10,937.8	0.287	0.148	0.156	0.409	1.726	1.631	0.434	1.470	1.631	0.325	0.676
	GTR+I+G	10,933.7	0.292	0.143	0.159	0.405	1.772	1.483	0.433	1.495	1.801	0.331	0.758
matK	GTR+G	4,576.6	0.379	0.167	0.158	0.296	0.670	1.519	0.178	1.109	1.015	n/a	0.387
	GTR+I+G	4,572.9	0.379	0.166	0.158	0.296	0.682	1.556	0.177	1.128	1.046	0.237	0.779
both	TVM+I+G	15,669.1	0.322	0.154	0.159	0.366	1.290	1.491	0.357	1.328	1.491	0.290	0.624
	GTR+I+G	15,665.4	0.323	0.153	0.159	0.365	1.306	1.483	0.356	1.336	1.510	0.327	0.783

Relationships Within Portulacineae—The ML bootstrap consensus topology is presented in Fig. 2.2 with MP, ML, and BI branch support values, and the ML tree with branch lengths is shown in Fig. 2.3. In general, this analysis recovered the relationships within Portulacineae that other authors have reported (summarized in Fig. 1.3). However, the chloroplast regions used here provided only weak or equivocal support for some of these relationships, and there were some topological differences along the backbone of the tree depending upon the method of tree reconstruction. Specifically, the positions of members of Didiereaceae and Basellaceae differed between parsimony and model-based trees. *Ceraria fruticulosa* Pearson & Stephens and *Portulacaria afra* Jacq. (Didiereaceae) formed a clade with 100% support under all methods of tree reconstruction. All 22 MP trees placed this clade as sister to all remaining Portulacineae, although the clade encompassing all Portulacineae except *C. fruticulosa* and *P. afra* received only 58% bootstrap support (Fig. 2.4). In turn, a clade encompassing the remaining Didiereaceae (*Didierea trollii* Capuron & Rauh, *Decarya madagascariensis* Choux, and *Calyptrotheca somalensis* Gilg) plus Basellaceae (*Basella alba* L. and *Ullucus tuberosus* Caldas) was sister to core Portulacineae in the strict consensus of MP trees, albeit with less than 50% bootstrap support. In contrast, maximum likelihood recovered *Ceraria* + *Portulacaria* as sister (with 76% bootstrap support) to the clade consisting of the remaining Didiereaceae plus Basellaceae (see Fig. 2.2). In the ML analysis, this Didiereaceae sens. lat. + Basellaceae clade in turn was sister (also with 76% bootstrap support) to the ACPT clade (Anacampserotaceae, Cactaceae, Portulacaceae sens. str., Talinaceae). Didiereaceae sensu Nyffeler & Eggli was never recovered as monophyletic.

Analysis of the *matK* data alone differed from *ndhF* in the anomalous placement of the two sampled *Portulaca* species within a very weakly supported (MP bootstrap: 52) clade with *Maihuenia patagonica* (Phil.) Britton & Rose and *Quiabentia verticillata* (Vaupel) Vaupel ex Berger (Cactaceae), while the other sampled representative of Cactaceae, *Pereskia aculeata* Mill., appeared alongside this group as part of a large, unresolved basal polytomy (not shown).

In the analysis of the full data set, all methods of tree reconstruction supported the monophyly of the ACPT clade (81 MP, 97 ML, 1.0 BI). Within this clade, Portulacaceae sens. str. (represented by six species of *Portulaca*) and Cactaceae (represented by *Pereskia aculeata*, *Quiabentia verticillata*, and *Maihuenia patagonica*) were each strongly supported as monophyletic. Talinaceae was recovered as monophyletic by all methods of tree reconstruction, but with weak support (57 MP, 72 ML, 0.97 BI). Only one representative of Anacampserotaceae (*Grahamia bracteata* Gill.) was included. Relationships among the four families making up the ACPT clade were unresolved.

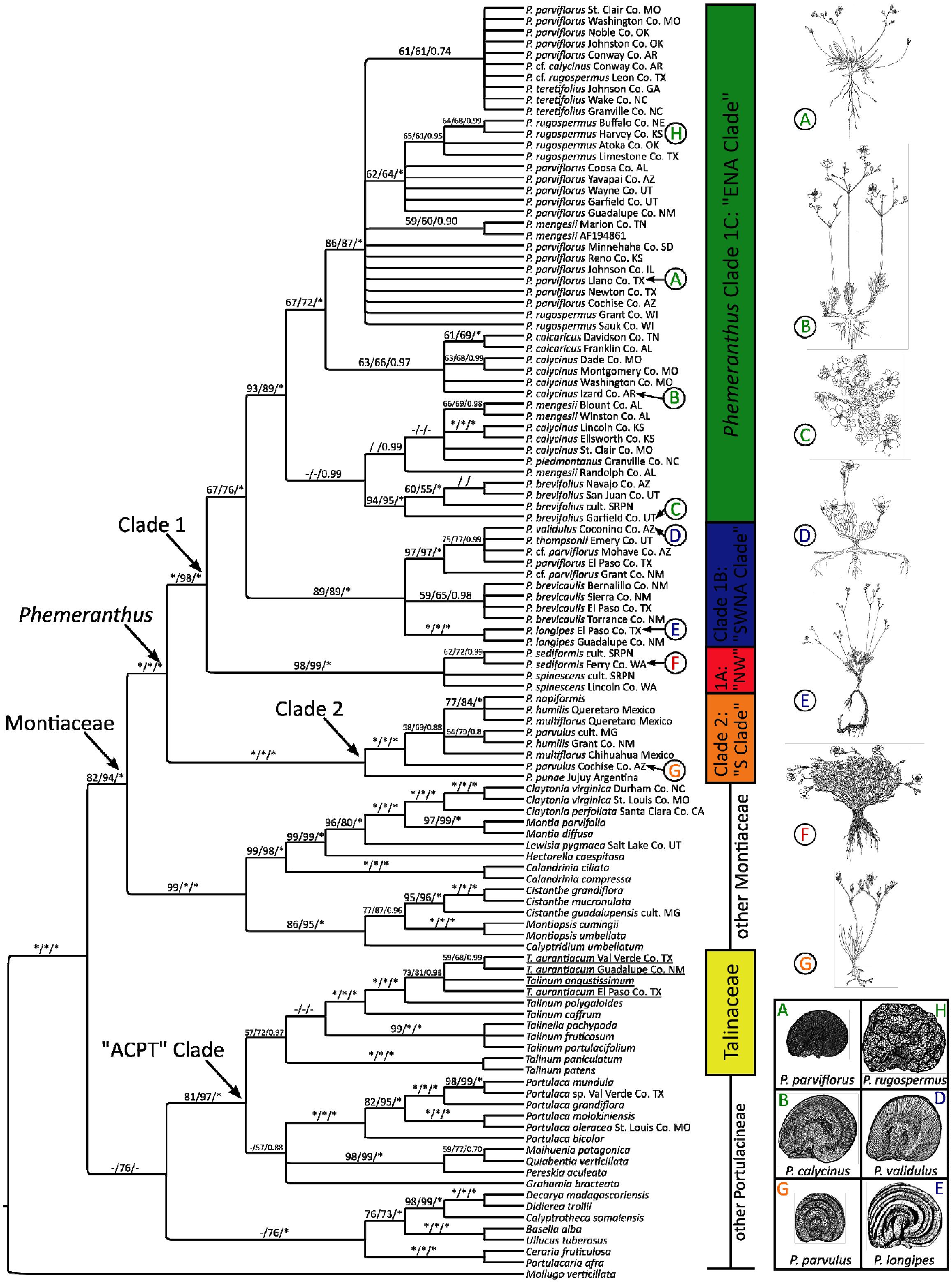

FIGURE 2.2. See caption on following page.

FIGURE 2.2. Maximum likelihood bootstrap consensus topology with branch support values (MP bootstrap / ML bootstrap / BI posterior probability). *: Bootstrap value of 100 / posterior probability of 1.0. -: Bootstrap value < 50 or posterior probability < 0.50. Major clades are labeled with arrows at the nodes. Major subclades within *Phemeranthus* are labeled on the sidebar; colors correspond to those used in Fig. 2.1. Talinaceae is also labeled on the sidebar, and *Talinum* accessions classified as *Phemeranthus aurantiacus* by Kiger (2001, 2003) are underlined. The diversity of growth habits in *Phemeranthus* is shown by line drawings of selected species in each clade, drawn from specimens corresponding to the accessions labeled with circled letters. The seeds of selected *Phemeranthus* species are depicted at the lower right.

Montiaceae were recovered as monophyletic, although support for the clade was only moderately strong (82 MP, 94 ML, 1.0 BI). The sister group of Montiaceae was equivocal. In the strict consensus of MP trees, Montiaceae were sister to the ACPT clade. However, no sister-group relationship for Montiaceae received greater than 50% MP bootstrap support. In the ML tree, Montiaceae were sister to the remainder of Portulacineae (i.e., the ACPT clade plus the paraphyletic Didiereaceae + Basellaceae clade).

FIGURE 2.3. Maximum likelihood phylogenetic tree with branch lengths from the GARLI analysis of the full data set. The full tree with outgroups is shown at the upper left, with major clades/ families labeled. *Phemeranthus*, marked by the large black diamond at its crown node, is expanded to the right. Major clades discussed in the text (1A, 1B, 1C, 2) are marked with arrowed circles. The geographic origin of each accession is noted on the sidebar with shading corresponding to the areas marked on the inset maps. SW/MX = Mexico and the southwestern United States; MW = the midwestern United States; NW = the northwestern United States; and SE = the southeastern United States. *P. confertiflorus* accessions in bold type are discussed in the text.

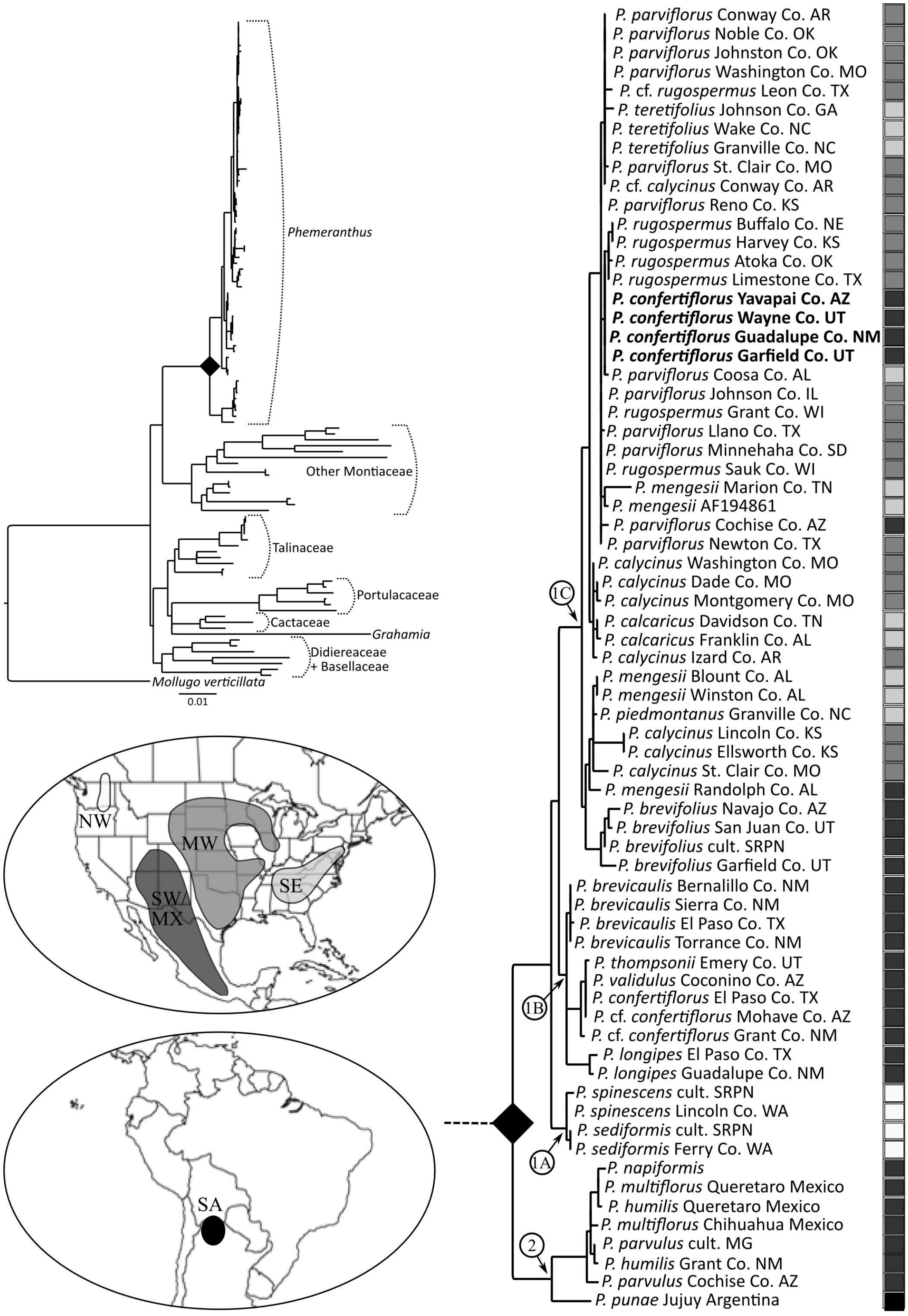

FIGURE 2.3. See caption on previous page.

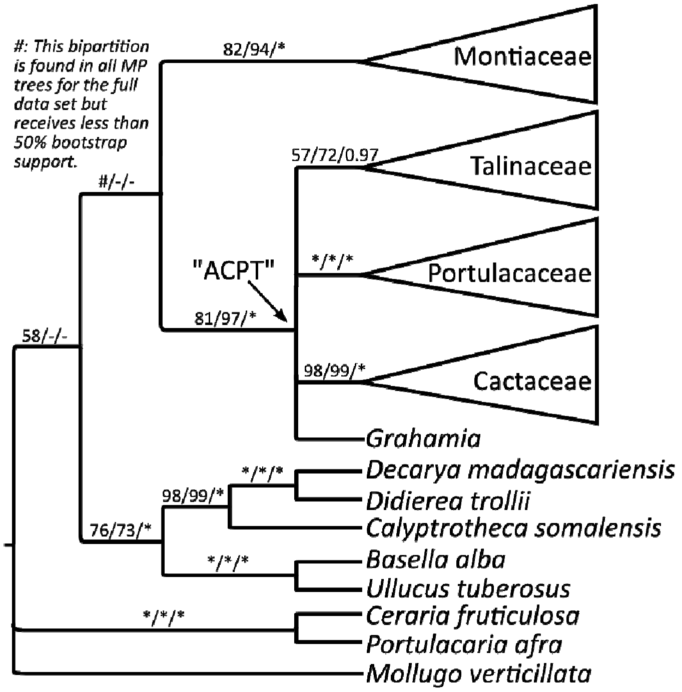

FIGURE 2.4. Condensed cladogram showing the alternative outgroup topology supported by the maximum parsimony analysis, with *Ceraria* + *Portulacaria* falling outside the Didiereaceae + Basellaceae clade. Support values are shown as in Fig. 2.2.

Monophyly of *Phemeranthus*—Excluding *Talinum aurantiacum* / *angustissimum*, all sampled accessions of *Phemeranthus* formed a monophyletic group with maximum support under all three methods of tree reconstruction (MP, ML, and BI). Including the three sampled accessions of *Talinum aurantiacum* (Texas, New Mexico) and the *T. angustissimum* sequences from GenBank in *Phemeranthus* would make the genus polyphyletic; these accessions formed a strongly supported clade with *T. polygaloides* Gill. ex Arn. (Argentina, Bolivia, Paraguay) and *T. caffrum* Eckl. & Zeyh. (South Africa, Tanzania). This clade, in turn, was part of the relatively weakly supported Talinaceae within the ACPT clade, along with other *Talinum* and *Talinella* species from the Old and New World. *Phemeranthus* formed a strongly supported monophyletic group with the remainder of Montiaceae (82 MP, 94 ML, 1.0 BI), being sister to a strongly supported clade (99.9 MP, 100 ML, 1.0 BI) consisting of all other sampled taxa.

Relationships Within *Phemeranthus*—Within *Phemeranthus*, two strongly supported clades were found (Fig. 2.2). The pink- to white-flowered, distinctly caulescent species primarily found in the United States (and extending into British Columbia, Canada, and northern Mexico) formed a clade (Clade 1) with 100% support under MP and BI and 98% under ML. Its sister group (Clade 2), which had 100% support under MP, ML, and BI, consisted of yellow- to white-flowered, ±acaulescent species from Mexico (extending into southern Arizona and New Mexico) and Argentina.

Within both clades, the deepest divergence was between a disjunct species or species pair and the remaining species in the clade. *P. sediformis* (Poelln.) Kiger of the Okanagan region in northern Washington and southern British Columbia and *P. spinescens* (Torr.) Hershk. of the Columbia Plateau in eastern Washington formed a strongly supported clade (Clade 1A) that was sister to the remainder of Clade 1 (which otherwise occurs only east and south of the Great Basin) in analyses of the full data set, although this sister-group relationship received only modest bootstrap support under MP and ML. Analysis of *ndhF* alone placed the NW species as sister to the SW clade (Clade 1B; see below), but with weak support. Similarly, *P. punae* (R.E.Fr.) Eggli & Nyffeler of the Puna region in the southern Andes was unequivocally supported as sister to the remainder of Clade 2 (which otherwise occurs only north of the Isthmus of Tehuantepec in Mexico).

Clade 1 included three major subclades. Clade 1A, discussed above, is distributed in the inland Northwest. The southwestern species *P. validulus* (Greene) Kiger, *P. thompsonii* (N.D. Atwood & S.L. Welsh) Kiger, *P. brevicaulis* (S.Watson) Kiger, and *P.*

longipes (Wooton & Standl.) Kiger formed the moderately strongly supported Clade 1B (along with three accessions of *P.* cf. *parviflorus* that grouped with *P. validulus* and *P. thompsonii*; see Discussion). The remaining species, which are predominantly distributed throughout the Midwestern and Southeastern United States (hereafter Eastern United States, ENA) but also extend to the Southwest and northern Mexico, made up Clade 1C (Fig. 2.2). This clade encompasses two-thirds of the sampled *Phemeranthus* accessions.

Relationships within Clade 1C generally lacked strong support; branch lengths were extremely short, and most species' haplotypes did not form monophyletic groups (Fig. 2.3). However, a few notable patterns were evident. First, except for the three accessions that grouped with Clade 1B, all *P. parviflorus* (from Utah, Arizona, New Mexico, Texas, Oklahoma, Arkansas, Kansas, Missouri, Illinois, South Dakota, and Alabama) formed a large, moderately well supported (MP: 86, ML: 88, BI: 100) comb that also included all *P. rugospermus* (Holz.) Kiger (Texas, Oklahoma, Kansas, Nebraska, and Wisconsin) and *P. teretifolius* (Pursh) Raf. (Georgia, North Carolina), two *P. mengesii* (Tennessee), and one morphologically unusual accession identified as *P.* cf. *calycinus* (Engelm.) Kiger from Conway Co., Arkansas. Second, *P. calycinus* accessions (excluding the aforementioned *P.* cf. *calycinus* from Conway Co.) formed two groups: one group of Missouri and Arkansas plants formed a clade along with *P. calcaricus* (S.Ware) Kiger (Tennessee, Alabama) that was weakly supported as sister to the *P. parviflorus* + *P. rugospermus* + *P. teretifolius* clade, while another group of Kansas and Missouri *P. calycinus* accessions formed a weakly supported clade along with three *P. mengesii* (Alabama) individuals and *P. piedmontanus* Ware (North Carolina). This latter group was sister to *P. brevifolius*, a dwarf species of the Colorado Plateau, in all MP trees; this relationship was also supported by BI but did not receive greater than 50% bootstrap support in either MP or ML analyses. The four accessions of *P. brevifolius* formed a strongly supported clade.

***Discussion*—**This phylogenetic analysis of chloroplast DNA sequences clearly supports the monophyly of *Phemeranthus* (excluding *P. aurantiacus*) and reinforces its separation from *Talinum* and its relationship to other predominantly western North American taxa within Portulacineae. Disparities between certain relationships predicted from morphology and those recovered from molecular data suggest complex speciation processes. The data also resolve two major geographically structured and morphologically distinct clades within the genus and strongly suggest that two dramatic geographical disjunctions within the group predate the diversification of the extant species. The biogeographic history suggested by the phylogeny is similar to those of other xeric-adapted taxa centered in the American Southwest and northern Mexico, with a pattern of origin in the Southwest followed by northward and eastward movement within North America. This study supports previous findings concerning deeper-level relationships within Portulacineae (e.g., the ACPT clade), although further work is needed to resolve remaining ambiguities.

Taxonomic History and Placement of *Phemeranthus*— Although *ndhF* and *matK–trnK* exhibit little variation within portions of *Phemeranthus* (particularly the ENA group), the phylogenetic signal present strongly supports the monophyly of *Phemeranthus* if *P. aurantiacus* is excluded (Fig. 2.2). The data also reinforce *Phemeranthus*' relationship to predominantly western North American genera such as *Lewisia*, *Montia* L., and *Cistanthe* Spach, as opposed to African-centered *Talinum*, in which *Phemeranthus* was long included. Rafinesque erected *Phemeranthus* in 1814 to accommodate *T. teretifolium* Pursh, the first terete-leaved *Talinum* species to be described. However, other taxonomists did not recognize *Phemeranthus* at the generic level, even though this group is distinguished from *Talinum* sens. str. by numerous morphological characters, notably terete leaves and a funicular aril or pellicle surrounding the seed. Beginning with de Candolle, who described the second terete-leaved species, *T. napiforme* DC, in 1828, the terete-leaved members of the genus were recognized as *Talinum* sect. *Phemeranthus*.

The relationship between sections *Talinum* and *Phemeranthus* began to be questioned when cladistic analyses of morphological characters by Carolin (1987) and Hershkovitz (1993) found that the two sections did not form a clade. Subsequently, molecular data have reinforced the conclusion that the two groups are not closely related (Hershkovitz and Zimmer 1997, 2000; Applequist and Wallace 2001; Applequist et al. 2006; Hershkovitz 2006). *Talinum* (and *Talinella*, which is nested within *Talinum*) is now placed in its own family, Talinaceae, which is more closely related to *Portulaca*, *Anacampseros* and its relatives, and Cactaceae (The Angiosperm Phylogeny Group 2009; Nyffeler and Eggli 2010). *Phemeranthus* species have been recovered as sister to the remaining genera of Montiaceae, which contains most of the diversity of traditional Portulacaceae.

Hershkovitz initiated the resurrection of *Phemeranthus* by publishing combinations for the three species sampled in a molecular phylogenetic analysis focusing on the relationships of Cactaceae (Hershkovitz and Zimmer 1997). Subsequently, Kiger

(2001) transferred the remaining terete-leaved *Talinum* species distributed in the United States in preparation for his treatment in the *Flora of North America* (Kiger 2003). However, Kiger also treated the non-terete-leaved *Talinum aurantiacum* (including *T. angustissimum* and *T. whitei* I.M.Johnst.) as *P. aurantiacus* on the basis of their seeds with strong concentric ridges and fruit morphology. This taxonomic decision was contradicted by molecular evidence from Applequist and Wallace (2001) and Hershkovitz and Zimmer (1997, 2000), and Kiger (2003) noted that it might prove untenable. The present study provides definitive evidence that the non-terete-leaved *T. aurantiacum* and similar species should be retained in *Talinum*. As noted by Kiger, these plants lack the terete leaves and seed pellicle that characterize *Phemeranthus*, and their general growth habit also unites them with *Talinum* rather than *Phemeranthus*.

Geographic and Morphological Correlates of Major Lineages within *Phemeranthus*—*Phemeranthus* contains two monophyletic subgenera: a southern clade distributed primarily in Mexico (Clade 2) and a northern clade distributed primarily in the United States (Clade 1) (Fig. 2.2). These clades are geographically distinct (Fig. 2.1, Fig. 2.3), overlapping only in a relatively small area of the southwestern United States and northern Mexico. The maximum distributional overlap of clades (clades 1B, 1C, and 2) occurs in the state of Chihuahua, Mexico, and adjacent Cochise County, Arizona (Fig. 2.1). At some sites in this region, species from Clade 2 can be found growing alongside species of Clade 1B or 1C.

Within each clade, the deepest divergence is between a geographically disjunct lineage and the remainder of the group. Within Clade 1, the northwestern disjunct species

P. sediformis and *P. spinescens* (Clade 1A), which are also distinguished by their woody growth habit, are moderately supported as sister to the rest of the clade (Fig. 2.2). This result suggests a single, early dispersion of a Clade 1 ancestor into the Northwest, followed by divergence and speciation in isolation due to geographical and/or climatic barriers formed by the northern Rocky Mountains and glacial Cordilleran ice sheets. Within Clade 2, the single South American species, *P. punae*, is sister to the remaining species, suggesting ancient long-distance dispersal by a Clade 2 ancestor.

Seed coat morphology has been suggested as an important taxonomic character in the group. Most members of Clade 2 possess seed coats with strong concentric ridges, whereas most members of Clade 1 lack these ridges. However, this character does not reliably distinguish the clades. Just as concentric ridges on the seed were misleading in the incorrect placement of *Talinum aurantiacum* within *Phemeranthus*, this character would mislead an attempt to classify groups within the genus. Notably, *P. longipes*, a diminutive species of limestone substrates in trans-Pecos Texas, New Mexico, and adjacent Mexico, features strongly ridged seeds like those found in Clade 2 (Fig. 2.2, lower right). However, the molecular data indicate that *P. longipes* belongs to Clade 1B. Other members of Clade 1 have non-ridged seeds that variously appear smooth due to a thin, tightly fitting pellicle or rough due to a loose, wrinkled pellicle.

Nevertheless, morphology provides some obvious characters to distinguish the major clades. Members of Clade 1 are distinctly caulescent, have tapering taproots or amorphous to spreading rhizomatous rootstocks, and have dark pink to white flowers. Members of Clade 2 are basically acaulescent, have tuberous rootstocks, and have yellow to white flowers. Within Clade 1, members of Clade 1A are distinguished by their highly branched, spiny, suffrutescent bases.

Species Relationships Within Clades—The southwestern species *P. brevicaulis, P. validulus,* and *P. longipes* form Clade 1B (Fig. 2.2). The placement of *P. longipes* in this clade is unexpected, albeit well supported. Often mistaken for depauperate individuals of *P. parviflorus* (though it is quite distinctive in floral and seed morphology), the diminutive *P. longipes* lacks the decumbent habit, extensive subterranean caudex, and long, tapered, recurved sepals of other Clade 1B species. The relatively narrow range of this clade, centered on New Mexico and parts of adjoining states (Fig. 2.1, Fig. 2.3), suggests that this lineage evolved in isolation from the lineage that would give rise to the widespread Clade 1C. However, species of Clades 1B and 1C frequently co-occur throughout their current area of overlap in Utah, Arizona, New Mexico, and Texas, suggesting more recent expansion of one or both groups. The anomalous placement of certain *P. parviflorus* individuals in Clade 1B suggests hybridization/ chloroplast introgression, but this hypothesis requires further exploration using nuclear markers.

Hybridization and polyploidy have played a role in speciation within Clade 1C, the widely distributed but poorly resolved group of species distributed in ENA. All sampled accessions of *P. teretifolius*, an allotetraploid derivative of *P. parviflorus* and *P. mengesii* (Black and Murdy 1972; Carter and Murdy 1985; Murdy and Carter 1985), share a chloroplast haplotype with Missouri, Oklahoma, and Arkansas *P. parviflorus*. This haplotype is also found in *P.* cf. *calycinus* from Conway Co., AR, suggesting hitherto undocumented hybridization between *P. parviflorus* and *P. calycinus*.

The close relationship of *P. brevifolius* with *P. calycinus* and *P. mengesii* is also unexpected. A dwarf species with small leaves, short internodes, and nearly sessile flowers, *P. brevifolius* is endemic to the Colorado Plateau. In contrast, *P. calycinus* and *P. mengesii* are tall, erect plants with relatively long leaves, visible internodes, long peduncles, and well-branched inflorescences, and are distributed in ENA. However, *P. calycinus* is highly variable; three or more species may deserve recognition (D.J. Ferguson, pers. comm.). Some populations have shorter leaves, stems, internodes, and peduncles and a more rhizomatous habit. Some western populations of *P. calycinus* also have a distinctive, sweet floral scent (D. J. Ferguson, pers. comm.), a trait that is otherwise known in the genus only from *P. brevifolius* (pers. obs.), although it has not been exhaustively surveyed and may be present in other species. The taxonomic status of *P. calycinus* and its relationships to *P. brevifolius*, *P. mengesii*, and other ENA species require further study.

<u>Plant Biogeographical Patterns in Xeric North America</u>**—** The evident correspondence between the phylogenetic and geographic structure suggests an "out of the Southwest" history for the genus (Fig. 2.3). Mexican and southwestern areas unite deeper-level branches, while midwestern and southeastern accessions appear at the tips of the tree, with extremely short branch lengths and poorly resolved species relationships. Ancestral character state reconstruction of distributional area using Mesquite (Maddison and Maddison 2011) (not shown) or MacClade (Maddison and Maddison 2000) (Fig. 2.5) supports the southwestern United States and northern Mexico as *Phemeranthus*' center of origin.

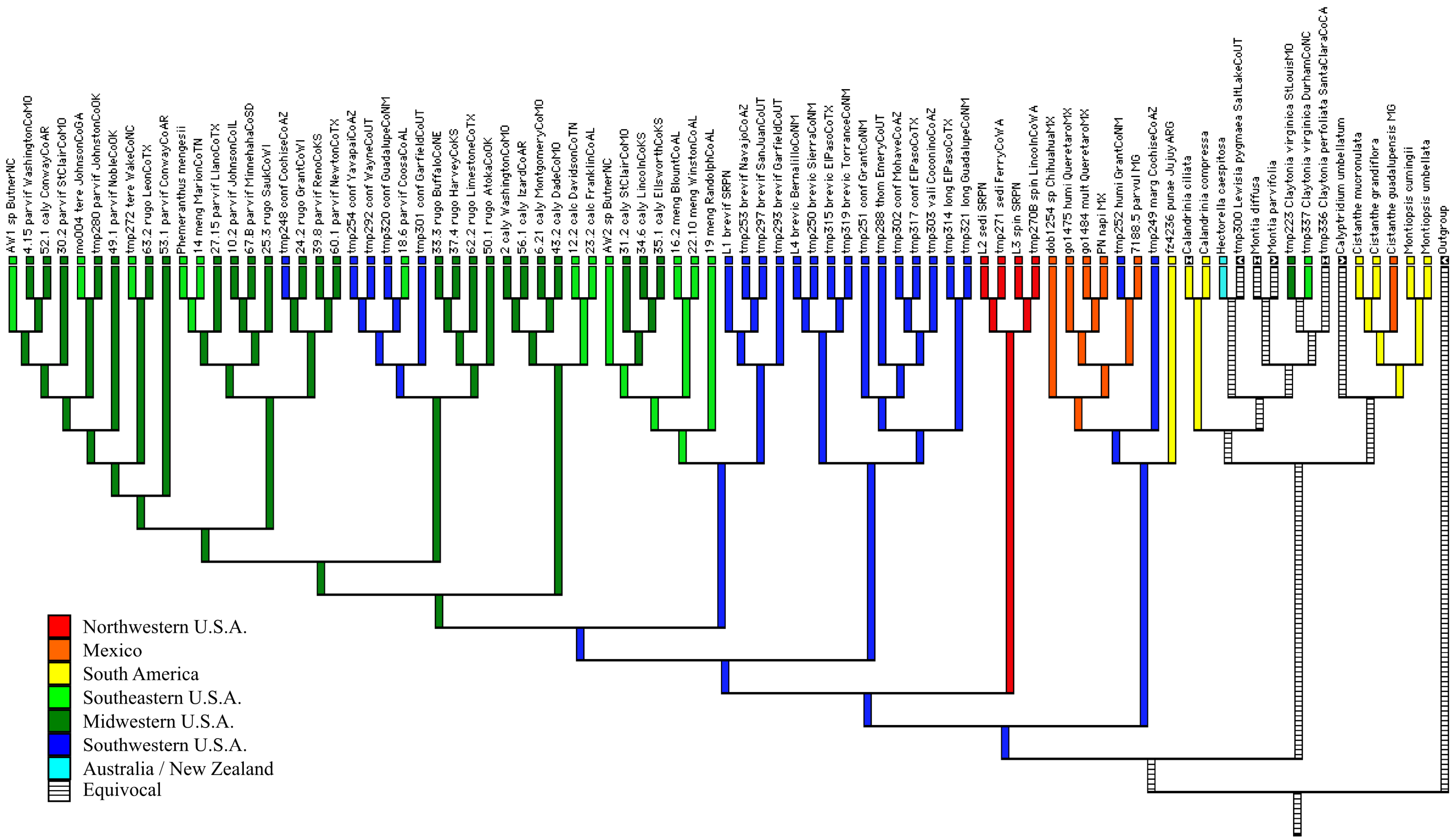

FIGURE 2.5. Parsimony-based ancestral character state reconstruction of geographic range using MacClade. Only Montiaceae is included; other Portulacineae are reduced to a single "outgroup" coded as occurring in every area. ACCTRAN optimization was used.

In a phylogenetic study of suborder Portulacineae, Ocampo and Columbus (2010) estimated divergence times based on two indirect calibration points (island ages) for endemic Hawaiian *Portulaca* species. Their BEAST chronogram (Drummond and Rambaut 2007) and S-DIVA biogeographical reconstruction (Yu et al. 2010) indicated that the suborder originated in the Americas ca. 18.8 (6.7–33.7) million years (Myr) ago and that Montiaceae originated in North America ca. 13 (3.4–25.4) Myr years ago, consistent with the 8–16 Myr estimate of Hershkovitz and Zimmer (2000). Although these dates must be interpreted with extreme caution, applying these mean age estimates in a BEAST analysis of the data set used here (Fig. 2.6) yields dates of ca. 10.4–12.5 Myr for the root node of *Phemeranthus*, ca. 8.6–10.4 Myr for Clade 1, and ca. 6.2–7.5 Myr for Clade 2. These dates fall within the mid- to late Miocene, a period of global cooling and drying with expanding grasslands and mountain building in western North America.

The character-state distribution suggests that at least one *Phemeranthus* lineage has re-invaded the Southwest from the Midwest or Southeast: four *P. parviflorus* accessions from Arizona, New Mexico, and Utah form a clade with *P. parviflorus* from Alabama and with *P. rugospermus* accessions from Nebraska, Kansas, Oklahoma, and Texas. This clade is nested within the predominantly midwestern Clade 1C. Although branch lengths and support are low throughout Clade 1C, chloroplast genotypes within this group also appear to have crossed the Mississippi Embayment into the Southeast on multiple occasions, with *P. calcaricus*, *P. mengesii*, *P. parviflorus* (Alabama), *P. piedmontanus*, and *P. teretifolius* accessions scattered across the clade. The current gene pools of *P. mengesii* and *P. calycinus* may reflect incomplete sorting of ancestral polymorphism or may indicate that these species comprise multiple distinct lineages.

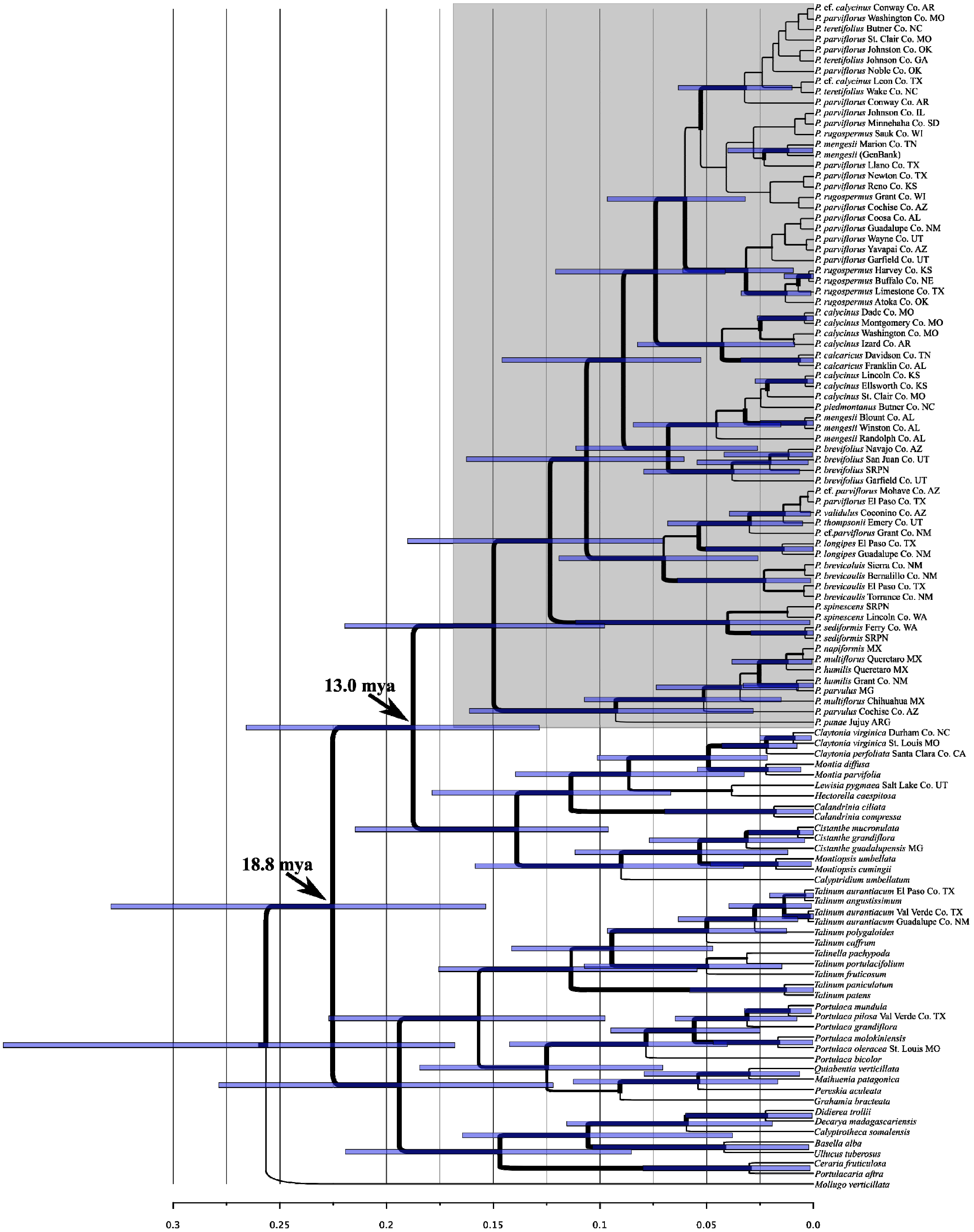

FIGURE 2.6. BEAST chronogram showing relative ages of divergences in *Phemeranthus* and related groups. *Phemeranthus* is highlighted in gray. Branch thicknesses correspond to Bayesian posterior probability values (thicker branch = stronger support). Horizontal blue bars on nodes represent 95% credibility intervals for node height (= relative age). Mean dates inferred by Ocampo and Columbus (2010) for Portulacineae and Montiaceae are indicated at the respective nodes.

An origin and initial diversification of the genus in northern Mexico and allied habitats in the American Southwest during the Miocene, followed by a more recent spread northward and eastward, is consistent with general patterns observed in other North American xeric-adapted plant groups (Moore and Jansen 2006; Moore et al. 2006; Douglas and Manos 2007; Marlowe and Hufford 2007; Evans et al. 2009; Rebernig et al. 2010a; Yang and Berry 2011). For example, *Gaillardia* Foug. (blanket flowers; Asteraceae) originated in the Chihuahuan region, with lineages subsequently spreading east through Texas, northwest, and north into the Great Plains (Marlowe and Hufford 2007). The North American xerophytic clade within Nyctaginaceae, which includes such genera as *Abronia*, *Boerhavia*, and *Mirabilis* (Douglas and Manos 2007), and the Chamaesyce clade within *Euphorbia* (Yang and Berry 2011) likely originated in the desert regions of western North America and subsequently dispersed elsewhere. At a finer scale, the pattern of historical isolation and post-glacial range expansion found for the Mexican tulip poppy in the Sierra Madre Oriental, Chihuahuan Desert, and central Mexico (Sosa et al. 2009) may provide an instructive comparison to Mexican *Phemeranthus* when additional sampling of Clade 2 can be obtained, particularly from the region of the Mexican Transvolcanic Belt.

Phemeranthus also exemplifies another general pattern exhibited by many North American xeric-adapted plant groups: amphitropical disjunctions between arid zones of North and South America (Raven 1963; Wen and Ickert-Bond 2009). *Phemeranthus punae* is one of several such disjunctions within Montiaceae alone (Hershkovitz and Zimmer 2000; Hershkovitz 2006). It appears that *P. punae* is the result of a long-distance dispersal event from the Mexican Cordillera to the southern Andes. Likewise, Moore and colleagues (2006) have found evidence for a North American origin of *Tiquilia* Pers. subgenus *Tiquilia* (Boraginaceae), with a complex history of long-distance dispersal events. According to Simpson and colleagues (2006), the current distribution of *Pomaria* Cav. (Fabaceae) can be explained by two long-distance dispersals from southwestern North America, one to South America and one to southern Africa. *Gaillardia* also parallels *Phemeranthus* in having a small group of species in northern Argentina, but Marlowe and Hufford (2007) were unable to include the South American taxa in their analysis.

Some *Phemeranthus* species, including *P. validulus*, *P. humilis*, *P. multiflorus* and *P. parvulus*, are associated with higher-elevation habitats in coniferous forests and might be expected to exhibit sky-island phylogeographic patterns (Moreno-Letelier and Piñero 2009; Gugger et al. 2010b; Gugger et al. 2010a). Other *Phemeranthus* species, such as *P. brevicaulis* and *P. longipes*, are found in lower elevation desert habitats and might have distributional histories more like those reported by Rebernig et al. (2010b; 2010a). Chloroplast loci are typically too slowly evolving to address such fine-scale phylogeographic questions (Schaal et al. 1998); further studies of individual subclades within *Phemeranthus* using population-level sampling and more variable markers would help to clarify the Pleistocene and recent history of these groups.

Further Directions**—** The molecular phylogenetic analysis presented here provides a foundation to address a variety of questions regarding the evolution of *Phemeranthus*. Further study is needed to examine the possibility of hybridization between populations included in Clades 1B and 1C and reticulate evolution elsewhere in the genus. Additional sampling of Clade 2 is needed to clarify the relationships of species in this group and to elucidate the biogeographic history of *Phemeranthus*. Finally, species boundaries and phylogeographic history in Clade 1C merit further study using population-level sampling and genotyping markers.

The relationships among the families that constitute the suborder Portulacineae have been substantially clarified in recent years (Fig. 1.3) (Nyffeler and Eggli 2010; Ocampo and Columbus 2010). However, the backbone relationships among the major lineages of Portulacineae remain poorly resolved. In this study, parsimony and model-based methods differed in the sister-group relationship of Montiaceae; all MP trees placed Montiaceae as sister to the ACPT clade (albeit without support) (Fig. 2.4), while the ML analysis placed Montiaceae as sister to the remainder of Portulacineae. Furthermore, the relationships of Didiereaceae and Basellaceae were unclear. For included samples of these taxa, the ML analysis recovered the same topology reported by Hershkovitz and Zimmer (1997) but conflicted with that found by Applequist and Wallace (2001), in which *Ceraria* + *Portulacaria* were sister to *Alluaudia ascendens* Drake + *Didierea* + *Calyptrotheca*. Didiereaceae sensu Nyffeler and Eggli were never recovered as monophyletic (Fig. 2.4). The limited sampling employed here precludes any confident conclusions; further studies employing nuclear and/or genomic data are needed to clarify the backbone relationships of Portulacineae.

As suggested by previous studies and based on the extensive taxon sampling here, *Phemeranthus* is likely sister to the remainder of the clade now recognized as Montiaceae. Understanding the complete biogeographic history and intricacies of trait evolution within Montiaceae and relative to the ACPT clade will require enhanced sampling of such ecologically diverse and geographically disjunct taxa as *Calyptridium* Nutt. and *Lewisiopsis* Govaerts (North America); *Calandrinia* Kunth, *Cistanthe*, and *Montia* (North and South America); *Lenzia* Phil., *Montiopsis* Kuntze, and *Philippiamra* Kuntze (South America); *Parakeelya* Hershk. (Australia; = Australian *Calandrinia*); *Hectorella* Hook. f. (New Zealand); and *Lyallia* Hook. f. (Kerguelen Islands).

Literature Cited—

Applequist, W. L. and R. S. Wallace. 2001. Phylogeny of the portulacaceous cohort based on *ndhF* sequence data. *Systematic Botany* 26: 406-419.

Applequist, W. L., W. Wagner, E. A. Zimmer, and M. Nepokroeff. 2006. Molecular evidence resolving the systematic position of *Hectorella* (Portulacaceae). *Systematic Botany* 31: 310-319.

Ashton, K. G. and A. de Queiroz. 2001. Molecular systematics of the western rattlesnake, *Crotalus viridis* (Viperidae), with comments on the utility of the D-loop in phylogenetic studies of snakes. *Molecular Phylogenetics and Evolution* 21: 176-189.

Axelrod, D. I. 1958. Evolution of the Madro-Tertiary geoflora. *Botanical Review* 24: 433-509.

Axelrod, D. I. 1979. Age and origin of Sonoran Desert vegetation. *Occasional Papers of the California Academy of Sciences* 132: 1-74.

Axelrod, D. I. 1983. Paleobotanical history of the western deserts. Pp. 113-129 in *Origin and Evolution of Deserts*, ed. S. G. Wells and D. R. Haragan. Albuquerque, NM: University of New Mexico Press.

Ayoub, N. A. and S. E. Riechert. 2004. Molecular evidence for Pleistocene glacial cycles driving diversification of a North American desert spider, *Agelenopsis aperta*. *Molecular Ecology* 13: 3453-3465.

Baskin, J. M. and C. C. Baskin. 1988. Endemism in rock outcrop plant communities of unglaciated eastern United States: an evaluation of the roles of the edaphic, genetic and light factors. *Journal of Biogeography* 15: 829-840.

Baskin, J. M. and C. C. Baskin. 2000. Vegetation of limestone and dolomite glades in the Ozarks and Midwest regions of the United States. *Annals of the Missouri Botanical Garden* 87: 286-294.

Black, C. and W. H. Murdy. 1972. The evolutionary origin of *Talinum teretifolium* Pursh. *Botanical Gazette* 133: 405-410.

Borsch, T., K. Hilu, D. Quandt, V. Wilde, C. Neinhuis, and W. Barthlott. 2003. Noncoding plastid *trnT–trnF* sequences reveal a well resolved phylogeny of basal angiosperms. *Journal of Evolutionary Biology* 16: 558-576.

Bryson, R. W., U. O. García-Vázquez, and B. R. Riddle. 2011. Phylogeography of Middle American gophersnakes: mixed responses to biogeographical barriers across the Mexican Transition Zone. *Journal of Biogeography* 38: 1570-1584.

Bryson, R. W., R. W. Murphy, A. Lathrop, and D. Lazcano-Villareal. 2010. Evolutionary drivers of phylogeographical diversity in the highlands of Mexico: a case study of the *Crotalus triseriatus* species group of montane rattlesnakes. *Journal of Biogeography* 38: 697-710.

Burbrink, F. T., H. Yao, M. Ingrasci, R. W. B. Jr, T. J. Guiher, and S. Ruane. 2011. Speciation at the Mogollon Rim in the Arizona Mountain Kingsnake (*Lampropeltis pyromelana*). *Molecular Phylogenetics and Evolution* 60: 445-454.

Carolin, R. 1987. A review of the family Portulacaceae. *Australian Journal of Botany* 35: 383-412.

Carter, M. E. B. and W. H. Murdy. 1985. Systematics of *Talinum parviflorum* Nutt. and the origin of *T. teretifolium* Pursh (Portulacaceae). *Rhodora* 87: 121-130.

Castoe, T. A., C. L. Spencer, and C. L. Parkinson. 2007. Phylogeographic structure and historical demography of the western diamondback rattlesnake (*Crotalus atrox*): A perspective on North American desert biogeography. *Molecular Phylogenetics and Evolution* 42: 193-212.

Clark-Tapia, R. and F. Molina-Freaner. 2003. The genetic structure of a columnar cactus with a disjunct distribution: *Stenocereus gummosus* in the Sonoran desert. *Heredity* 90: 443-450.

Comes, H. P. and J. W. Kadereit. 1998. The effect of quaternary climatic changes on plant distribution and evolution. *Trends in Plant Science* 3: 432-438.

Douglas, N. and P. S. Manos. 2007. Molecular phylogeny of Nyctaginaceae: taxonomy, biogeography, and characters associated with a radiation of xerophytic genera in North America. *American Journal of Botany* 94: 856-872.

Drummond, A. J. and A. Rambaut. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* 7: 214.

Evans, M. E. K., S. A. Smith, R. S. Flynn, and M. J. Donoghue. 2009. Climate, niche evolution, and diversification of the “bird‐cage” evening primroses (*Oenothera*, sections *Anogra* and *Kleinia*). *The American Naturalist* 173: 225-240.

Fawcett, P. J., J. P. Werne, R. S. Anderson, J. M. Heikoop, E. T. Brown, M. A. Berke, S. J. Smith, F. Goff, L. Donohoo-Hurley, L. M. Cisneros-Dozal, S. Schouten, J. S. S. Damsté, Y. Huang, J. Toney, J. Fessenden, G. Woldegabriel, V. Atudorei, J. W. Geissman, and C. D. Allen. 2011. Extended megadroughts in the southwestern United States during Pleistocene interglacials. *Nature* 470: 518-521.

Fehlberg, S. D. and T. A. Ranker. 2007. Phylogeny and biogeography of *Encelia* (Asteraceae) in the Sonoran and Peninsular deserts based on multiple DNA sequences. *Systematic Botany* 32: 692-699.

Fehlberg, S. D. and T. A. Ranker. 2009. Evolutionary history and phylogeography of *Encelia farinosa* (Asteraceae) from the Sonoran, Mojave, and Peninsular Deserts. *Molecular Phylogenetics and Evolution* 50: 326-335.

Fontanella, F. M., C. R. Feldman, M. E. Siddall, and F. T. Burbrink. 2008. Phylogeography of *Diadophis punctatus*: Extensive lineage diversity and repeated patterns of historical demography in a trans-continental snake. *Molecular Phylogenetics and Evolution* 46: 1049-1070.

Garrick, R. C., J. D. Nason, C. A. Meadows, and R. J. Dyer. 2009. Not just vicariance: phylogeography of a Sonoran Desert euphorb indicates a major role of range expansion along the Baja peninsula. *Molecular Ecology* 18: 1916-1931.

Glez-Peña, D., D. Gómez-Blanco, M. Reboiro-Jato, F. Fdez-Riverola, and D. Posada. 2010. ALTER: program-oriented conversion of DNA and protein alignments. *Nucleic Acids Research* 38: W14-18.

Gugger, P. F., S. Sugita, and J. Cavender-Bares. 2010a. Phylogeography of Douglas-fir based on mitochondrial and chloroplast DNA sequences: testing hypotheses from the fossil record. *Molecular Ecology* 19: 1877-1897.

Gugger, P. F., A. González-Rodríguez, H. Rodríguez-Correa, S. Sugita, and J. Cavender-Bares. 2010b. Southward Pleistocene migration of Douglas-fir into Mexico: phylogeography, ecological niche modeling, and conservation of ‘rear edge’ populations. *New Phytologist* 189: 1185-1199.

Guindon, S. and O. Gascuel. 2003. A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Systematic Biology* 52: 696-704.

Haenel, G. J. 2007. Phylogeography of the tree lizard, *Urosaurus ornatus*: responses of populations to past climate change. *Molecular Ecology* 16: 4321-4334.

Hershkovitz, M. A. 1993. Revised circumscriptions and subgeneric taxonomies of *Calandrinia* and *Montiopsis* (Portulacaceae) with notes on phylogeny of the portulacaceous alliance. *Annals of the Missouri Botanical Garden* 80: 333-365.

Hershkovitz, M. A. 2006. Ribosomal and chloroplast DNA evidence for diversification of western American Portulacaceae in the Andean region. *Gayana Botanica* 63: 13-74.

Hershkovitz, M. A. and E. A. Zimmer. 1997. On the evolutionary origins of the cacti. *Taxon* 46: 217-232.

Hershkovitz, M. A. and E. A. Zimmer. 2000. Ribosomal DNA evidence and disjunctions of Western American Portulacaceae. *Molecular Phylogenetics and Evolution* 15: 419-439.

Hewitt, G. 1996. Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society* 58: 247-276.

Hewitt, G. 2004. Genetic consequences of climatic oscillations in the Quaternary. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* 359: 183-195.

Hilu, K., T. Borsch, K. Muller, D. Soltis, P. Soltis, V. Savolainen, M. Chase, M. Powell, L. Alice, and R. Evans. 2003. Angiosperm phylogeny based on *matK* sequence information. *American Journal of Botany* 90: 1758.

Holmgren, C., M. Penalba, K. Rylander, and J. L. Betancourt. 2003. A 16,000 14C yr BP packrat midden series from the USA–Mexico Borderlands. *Quaternary Research* 60: 319-329.

Holmgren, C. A., J. Norris, and J. L. Betancourt. 2007. Inferences about winter temperatures and summer rains from the late Quaternary record of C-4 perennial grasses and C-3 desert shrubs in the northern Chihuahuan Desert. *Journal of Quaternary Sciences* 22: 141-161.

Hunter, K. L., J. L. Betancourt, B. Riddle, T. R. van Devender, K. L. Cole, and W. G. Spaulding. 2001. Ploidy race distributions since the Last Glacial Maximum in the North American desert shrub, *Larrea tridentata*. *Global Ecology and Biogeography* 10: 521-533.

IPCC. 2007. *Working Group II Contribution to the Intergovernmental Panel of Climate Change Fourth Assessment Report: Climate Change 2007: Climate Change Impacts, Adaptation and Vulnerability. Summary for Policymakers.*

Jaeger, J., B. Riddle, and D. Bradford. 2005. Cryptic Neogene vicariance and Quaternary dispersal of the red-spotted toad (*Bufo punctatus*): insights on the evolution of North American warm desert biotas. *Molecular Ecology* 14: 3033-3048.

Johnson, L. and D. Soltis. 1995. Phylogenetic inference in Saxifragaceae sensu stricto and *Gilia* (Polemoniaceae) using *matK* sequences. *Annals of the Missouri Botanical Garden* 82: 149-175.

Kiger, R. W. 2001. New combinations in *Phemeranthus* Rafinesque (Portulacaceae). *Novon* 11: 319-321.

Kiger, R. W. 2003. *Phemeranthus*. Pp. 488-495 in *Flora of North America North of Mexico* vol. 4, ed. Flora of North America Editorial Committee. New York, NY and Oxford, UK: Oxford University Press.

Knowles, L. 2001. Did the Pleistocene glaciations promote divergence? Tests of explicit refugial models in montane grasshoppers. *Molecular Ecology* 10: 691-701.

Leaché, A. D. and T. W. Reeder. 2006. Molecular systematics of the eastern fence lizard (*Sceloporus undulatus*): a comparison of parsimony, likelihood, and Bayesian approaches. *Systematic Biology* 51: 44-68.

Leaché, A. D. and J. A. McGuire. 2006. Phylogenetic relationships of horned lizards (*Phrynosoma*) based on nuclear and mitochondrial data: Evidence for a misleading mitochondrial gene tree. *Molecular Phylogenetics and Evolution* 39: 628-644.

Maddison, D. R. and W. P. Maddison. 2000. MacClade 4: Analysis of phylogeny and character evolution. Version 4.0. Sunderland, MA: Sinauer Associates.

Maddison, W. P. and D. R. Maddison. 2011. Mesquite: a modular system for evolutionary analysis. Available at http://mesquiteproject.org.

Marlowe, K. and L. Hufford. 2007. Taxonomy and biogeography of *Gaillardia* (Asteraceae): A phylogenetic analysis. *Systematic Botany* 32: 208-226.

Masta, S. 2000. Phylogeography of the jumping spider *Habronattus pugillis* (Araneae: Salticidae): recent vicariance of sky island populations? *Evolution* 54: 1699-1711.

McAuliffe, J. and T. Van Devender. 1998. A 22,000-year record of vegetation change in the north-central Sonoran Desert. *Palaeogeography, Palaeoclimatology, Palaeoecology* 141: 253-275.

McCormack, J. E., B. S. Bowen, and T. B. Smith. 2008. Integrating paleoecology and genetics of bird populations in two sky island archipelagos. *BMC Biology* 6: 28.

Metcalfe, S., S. O'Hara, M. Caballero, and S. Davies. 2000. Records of Late Pleistocene-Holocene climatic change in Mexico—a review. *Quaternary Sci Rev* 19: 699-721.

Moore, M. and R. Jansen. 2006. Molecular evidence for the age, origin, and evolutionary history of the American desert plant genus *Tiquilia* (Boraginaceae). *Molecular Phylogenetics and Evolution* 39: 668-687.

Moore, M., A. Tye, and R. Jansen. 2006. Patterns of long-distance dispersal in *Tiquilia* subg. *Tiquilia* (Boraginaceae): implications for the origins of amphitropical disjuncts and Galapagos Islands endemics. *American Journal of Botany* 93: 1163-1177.

Morafka, D. J. 1977. *A Biogeographical Analysis of the Chihuahuan Desert through its Herpetofauna*. The Hague, Netherlands: Dr. W. Junk B.V., Publishers.

Moreno-Letelier, A. and D. Piñero. 2009. Phylogeographic structure of *Pinus strobiformis* Engelm. across the Chihuahuan Desert filter-barrier. *Journal of Biogeography* 36: 121-131.

Murdy, W. H. and M. E. B. Carter. 1985. Electrophoretic study of the allopolyploidal origin of *Talinum teretifolium* and the specific status of *T. appalachianum* (Portulacaceae). *American Journal of Botany* 72: 1590-1597.

Nason, J. D., J. L. Hamrick, and T. H. Fleming. 2002. Historical vicariance and postglacial colonization effects on the evolution of genetic structure in *Lophocereus*, a Sonoran desert columnar cactus. *Evolution* 56: 2214-2226.

Nyffeler, R. and U. Eggli. 2010. Disintegrating Portulacaceae: A new familial classification of the suborder Portulacineae (Caryophyllales) based on molecular and morphological data. *Taxon* 59: 227-240.

Nyffeler, R., U. Eggli, R. M. Ogburn, and E. J. Edwards. 2008. Variations on a theme: repeated evolution of succulent life forms in the Portulacineae (Caryophyllales). *Haseltonia* 14: 26-36.

Ocampo, G. and J. T. Columbus. 2010. Molecular phylogenetics of suborder Cactineae (Caryophyllales), including insights into photosynthetic diversification and historical biogeography. *American Journal of Botany* 97: 1827-1847.

Pook, C. E., W. Wuster, and R. S. Thorpe. 2000. Historical biogeography of the western rattlesnake (Serpentes: Viperidae: *Crotalus viridis*) inferred from mitochondrial DNA sequence information. *Molecular Phylogenetics and Evolution* 15: 269-282.

Posada, D. 2008. jModelTest: Phylogenetic model averaging. *Molecular Biology and Evolution* 25: 1253-1256.

Rambaut, A. 1996. Se-Al: Sequence Alignment Editor. Available at http://tree.bio.ed.ac.uk/software/seal/.

Raven, P. H. 1963. Amphitropical relationships in the floras of North and South America. *Quarterly Review of Biology* 38: 151-177.

Rebernig, C. A., H. Weiss-Schneeweiss, G. M. Schneeweiss, P. Schoenswetter, R. Obermayer, J. L. Villaseñor, and T. F. Stuessy. 2010a. Quaternary range dynamics and polyploid evolution in an arid brushland plant species (*Melampodium cinereum*, Asteraceae). *Molecular Phylogenetics and Evolution* 54: 594-606.

Rebernig, C. A., G. M. Schneeweiss, K. E. Bardy, P. Schoenswetter, J. L. Villaseñor, R. Obermayer, T. F. Stuessy, and H. Weiss-Schneeweiss. 2010b. Multiple Pleistocene refugia and Holocene range expansion of an abundant southwestern American desert plant species (*Melampodium leucanthum*, Asteraceae). *Molecular Ecology* 19: 3421-3443.

Reeder, T. W. and R. R. Montanucci. 2001. A phylogenetic analysis of the horned lizards (Phrynosomatidae: *Phrynosoma*): Evidence from mitochondrial DNA and morphology. *Copeia* 2: 309-323.

Reinhard, R. and S. Ware. 1989. Adaptation to substrate in rock outcrop plants: interior highlands *Talinum* (Portulacaceae). *Botanical Gazette* 150: 449-453.

Riddle, B. 1995. Molecular biogeography in the pocket mice (*Perognathus* and *Chaetodipus*) and grasshopper mice (*Onychomys*)—the Late Cenozoic development of a North American aridlands rodent guild. *Journal of Mammalogy* 76: 283-301.

Riddle, B. and D. Hafner. 2006. A step-wise approach to integrating phylogeographic and phylogenetic biogeographic perspectives on the history of a core North American warm deserts biota. *Journal of Arid Environments* 66: 435-461.

Sanchez-del Pino, I. and T. J. Motley. 2010. Evolution of *Tidestromia* (Amaranthaceae) in the deserts of the southwestern United States and Mexico. *Taxon* 59: 38-48.

Schaal, B. A., D. A. Hayworth, K. M. Olsen, J. T. Rauscher, and W. A. Smith. 1998. Phylogeographic studies in plants: problems and prospects. *Molecular Ecology* 7: 465-474.

Seager, R., M. Ting, I. Held, Y. Kushnir, J. Lu, G. Vecchi, H.-P. Huang, N. Harnik, A. Leetmaa, N.-C. Lau, C. Li, J. Velez, and N. Naik. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. *Science* 316: 1181-1184.

Shaw, J., E. B. Lickey, E. E. Schilling, and R. L. Small. 2007. Comparison of whole chloroplast genome sequences to choose noncoding regions for phylogenetic studies in angiosperms: the tortoise and the hare III. *American Journal of Botany* 94: 275-288.

Shaw, J., E. B. Lickey, J. Beck, S. Farmer, W. Liu, J. Miller, K. Siripun, C. Winder, E. E. Schilling, and R. L. Small. 2005. The tortoise and the hare II: relative utility of 21 noncoding chloroplast DNA sequences for phylogenetic analysis. *American Journal of Botany* 92: 142-166.

Simmons, M. and H. Ochoterena. 2000. Gaps as characters in sequence-based phylogenetic analyses. *Systematic Biology* 49: 369-381.

Simmons, M., H. Ochoterena, and T. Carr. 2001. Incorporation, relative homoplasy, and effect of gap characters in sequence-based phylogenetic analyses. *Systematic Biology* 50: 454-462.

Simpson, B., L. Larkin, A. Weeks, and J. McDill. 2006. Phylogeny and biogeography of *Pomaria* (Caesalpinioideae: Leguminosae). *Systematic Botany* 31: 792-804.

Small, R. L., J. Ryburn, R. Cronn, T. Seelanan, and J. Wendel. 1998. The tortoise and the hare: choosing between noncoding plastome and nuclear *Adh* sequences for phylogeny reconstruction in a recently diverged plant group. *American Journal of Botany* 85: 1301-1315.

Smith, C. I. and B. D. Farrell. 2005a. Range expansions in the flightless longhorn cactus beetles, *Moneilema gigas* and *Moneilema armatum*, in response to Pleistocene climate changes. *Molecular Ecology* 14: 1025-1044.

Smith, C. I. and B. D. Farrell. 2005b. Phylogeography of the Longhorn cactus beetle *Moneilema appressum* LeConte (Coleoptera: Cerambycidae): was the differentiation of the Madrean sky islands driven by Pleistocene climate changes? *Molecular Ecology* 14: 3049-3065.

Smith, S. A. and C. W. Dunn. 2008. Phyutility: a phyloinformatics tool for trees, alignments and molecular data. *Bioinformatics* 24: 715-716.

Soltis, D., A. B. Morris, J. S. McLachlan, P. S. Manos, and P. Soltis. 2006. Comparative phylogeography of unglaciated eastern North America. *Molecular Ecology* 15: 4261-4293.

Sosa, V., E. Ruiz-Sanchez, and F. C. Rodriguez-Gomez. 2009. Hidden phylogeographic complexity in the Sierra Madre Oriental: the case of the Mexican tulip poppy *Hunnemannia fumariifolia* (Papaveraceae). *Journal of Biogeography* 36: 18-27.

Swofford, D. L. 2003. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sunderland, MA: Sinauer Associates.

The Angiosperm Phylogeny Group. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society* 161: 105-121.

Thompson, R. S. and K. H. Anderson. 2000. Biomes of western North America at 18,000, 6000 and 0 14C yr B.P. reconstructed from pollen and packrat midden data. *Journal of Biogeography* 27: 555-584.

van Devender, T. R. and W. G. Spaulding. 1979. Development of vegetation and climate in the southwestern United States. *Science* 204: 701-710.

Ware, S. 1967. A new *Talinum* (Portulacaceae) from the cedar glades of middle Tennessee. *Rhodora* 69: 466-475.

Ware, S. 1969a. On the ecology of *Talinum mengesii* (Portulacaceae). *Bulletin of the Torrey Botanical Club* 96: 4-10.

Ware, S. 1969b. Ecological role of *Talinum* (Portulacaceae) in cedar glade vegetation. *Bulletin of the Torrey Botanical Club* 96: 163-175.

Ware, S. and G. Pinion. 1990. Substrate adaptation in rock outcrop plants: eastern United States *Talinum* (Portulacaceae). *Bulletin of the Torrey Botanical Club* 117: 284-290.

Wen, J. and S. M. Ickert-Bond. 2009. Evolution of the Madrean-Tethyan disjunctions and the North and South American amphitropical disjunctions in plants. *Journal of Systematics and Evolution* 47: 331-348.

Wilson, J. S. and J. P. Pitts. 2010. Phylogeographic analysis of the nocturnal velvet ant genus *Dilophotopsis* (Hymenoptera: Mutillidae) provides insights into diversification in the Nearctic deserts. *Biological Journal of the Linnean Society* 101: 360-375.

Yang, Y. and P. E. Berry. 2011. Phylogenetics of the Chamaesyce clade (*Euphorbia*, Euphorbiaceae): Reticulate evolution and long-distance dispersal in a prominent C_4 lineage. *American Journal of Botany* 98: 1486-1503.

Yu, Y., A. J. Harris, and X. He. 2010. S-DIVA (Statistical Dispersal-Vicariance Analysis): A tool for inferring biogeographic histories. *Molecular Phylogenetics and Evolution* 56: 848-850.

Zink, R. M. and R. C. Blackwell. 1998. Molecular systematics of the scaled quail complex (genus *Callipepla*). *The Auk* 115: 349-403.

Zwickl, D. J. 2006. *Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion*. Ph.D. dissertation. Austin, TX: The University of Texas at Austin.

CHAPTER III. GERMINATION RESPONSE TO CHILLING DURATION SUGGESTS LOCAL ADAPTATION IN *PHEMERANTHUS PARVIFLORUS*

Abstract—Seed germination requirements have important consequences for the successful use of native species in conservation or horticultural plantings; mismatches between these requirements and local environmental conditions can result in failure to germinate, seedling death, and/or reproductive failure. *Phemeranthus parviflorus* (Montiaceae) is a widespread succulent perennial that occurs in dry, open, rocky or sandy habitats from northern Mexico to the Dakotas. The flowering period extends throughout the summer, with more or less continuous production of flowers and fruits from late spring to early fall. I examined the chilling requirement for seed germination in twelve natural populations from across the broad latitudinal range of this species. Field-collected seeds were subjected to moist chilling for zero to twelve weeks, and their subsequent germination rates were tracked under common conditions in the greenhouse. Populations differed strongly in their responses to different chilling durations. Seeds from the southernmost populations were capable of germinating without chilling and reached their peak germination rates at shorter chilling durations. Seeds from the northernmost populations failed to germinate with no or brief chilling and required longer chilling periods to achieve maximum germination. In a subsequent experiment using greenhouse-grown seeds, the results showed a less pronounced pattern, suggesting that maternal effects played a role. Seed chilling also affected adult life history; except in the southernmost population, chilling was necessary for the plants to flower in their first season of growth.

Introduction—

Species with large geographic ranges encounter a broad range of environmental conditions. Temperature and light, water and nutrient availability all have direct consequences for growth and reproduction, and all vary predictably with season and latitude. If inter-population gene flow is limited, natural selection can cause local adaptation, leading to differences among populations in morphology, physiology, phenology, and other traits. If individuals from different populations meet and mate, the offspring may be poorly adapted to either parental environment, resulting in a loss of fitness (Templeton 1997). Even without hybridization, local adaptation is a matter of great concern to conservation biologists in planning any kind of translocation and in anticipating how populations and species may respond to environmental change. For successful translocation of threatened species and for use of native species in restoration, reclamation, or landscaping projects, it is important that the individuals used be appropriately adapted to the target environment. Therefore, source populations must be chosen with care to match the conditions of the target environment as closely as possible, and ideally to be in close geographic proximity.

The sunbright, *Phemeranthus parviflorus* (Nutt.) Kiger, and the large-flowered fameflower, *Phemeranthus calycinus* (Engelm.) Kiger, are widespread in the Midwestern United States and have recently attracted greater horticultural attention for their potential use in green-roof plantings (Getter and Rowe 2008; Getter et al. 2009; Dvorak 2010). As highly drought-tolerant, succulent plants with attractive floral displays, these species can be a valuable component of green roofs and other water-conservative landscaping designs. These species may also be used in re-vegetation of restored glade habitats. However, no attention has yet been paid to the possibility of local adaptation that might affect the establishment and sustainability of planted populations of these species, either on green roofs or in restored habitats. As a first step, I examined the chilling requirement for seed germination in *P. parviflorus* populations from different latitudes. Seed germination is a critical life-history stage; if the requirements for germination are not met in the target environment, a re-introduction or horticultural planting is unlikely to succeed.

Overview of *P. parviflorus*, a widespread autogamous species

Phemeranthus parviflorus (sunbright) is a widespread succulent perennial wildflower that occurs in dry, open, rocky or sandy habitats from northern Mexico to the Dakotas (Fig. 3.1). The closely related species *P. confertiflorus* (Greene) Hershkovitz is morphologically similar, and the two species have been treated as a single, variable taxon by Kiger (2003). Holzinger (1900) also noted geographically correlated variability among specimens assigned to *P. parviflorus* sens. lat. and suggested that the taxon might actually encompass two or three species. While the center of diversity of *Phemeranthus* is in the southwestern United States and northern Mexico, this *P. parviflorus* species complex is among the seven to nine *Phemeranthus* species distributed in the midwestern and southeastern United States. It is the most widespread species in the genus in terms of both geographic and ecological space, broadly overlapping the ranges of several other species that represent most major clades within *Phemeranthus*. Populations are often large, but they are scattered on isolated habitat patches.

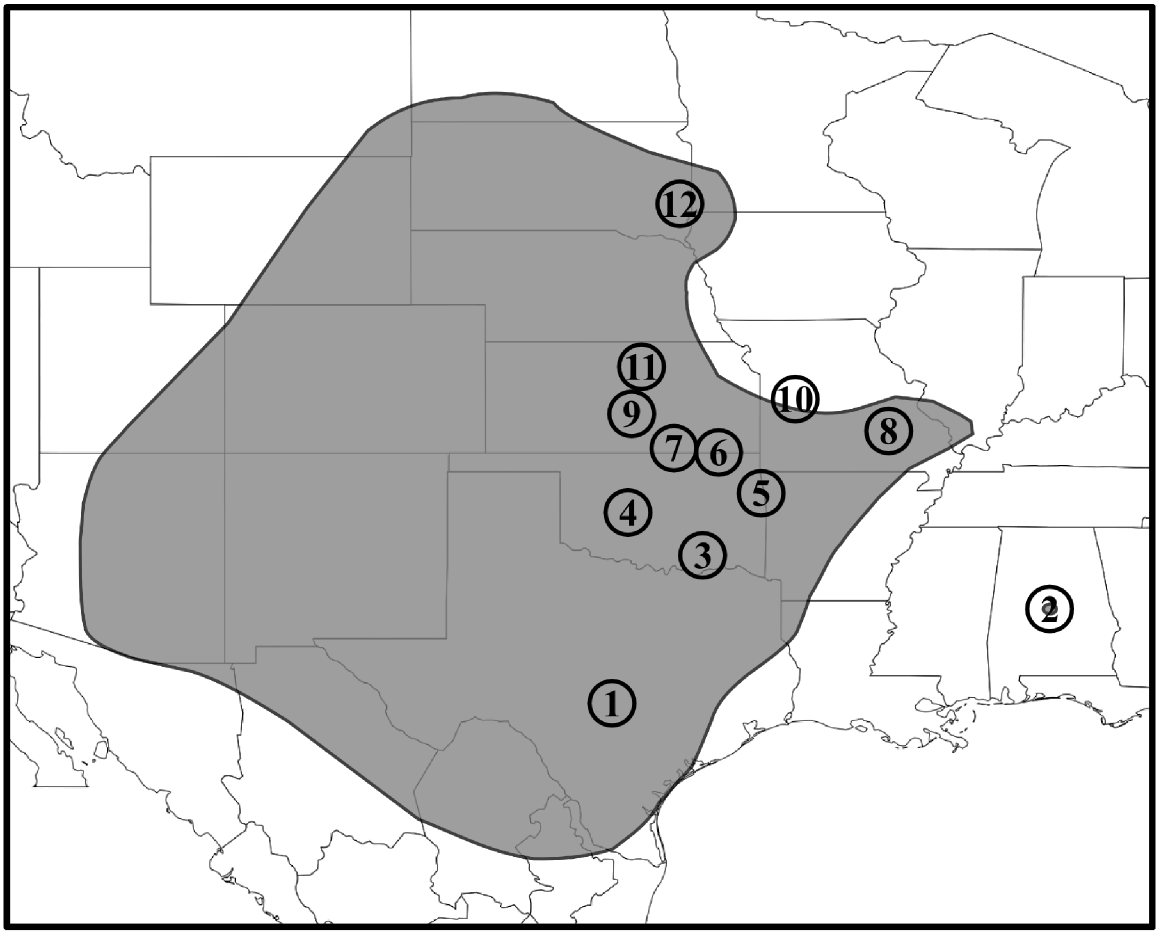

FIGURE 3.1. Approximate geographical range of *P. parviflorus* sens. lat. (including *P. confertiflorus*, which occupies the southwestern portion of the range). Note the outlying population area in central Alabama. Numbered circles indicate the locations of populations sampled in this study.

Sunbright is widespread between the Rocky Mountains and the Mississippi River, extending just across the river into southern Illinois. Additionally, a widely disjunct population is found in central Alabama (Fig. 3.1). The Alabama population is confined to an area with a radius of about one mile on gneiss bluffs along the Coosa River. These plants were first reported by R.M. Harper in 1937 and were named *Talinum appalachianum* W. Wolf (Wolf 1939). Carter and Murdy (1985) compared *T.*

appalachianum to *Talinum parviflorum* Nutt. (=*P. parviflorus*) and concluded that the former was synonymous with the latter, overlapping in all measured traits. Although the Alabama plants had slightly larger petals, they overlapped with Arkansas, Texas, and Kansas specimens in stamen number, style length, and ovule number, and anthesis occurred similarly late in the day. Furthermore, crosses between Alabama plants and other *P. parviflorus* yielded fruit-set and seed-set rates similar to those of intra-population controls, and the resulting offspring were fertile and able to self-pollinate, albeit with slightly reduced pollen fertility and seeds per capsule. Isozyme data also reinforced the conclusion that *T. appalachianum* was merely a disjunct population of *P. parviflorus*; the average genetic identity between populations of these taxa was higher than that between populations of *P. calycinus* or *P. mengesii* (W. Wolf) Kiger (Murdy and Carter 1985). The Alabama population of *P. parviflorus* may represent a remnant of a formerly more extensive distribution east of the Mississippi.

The presence of *P. parviflorus* in the southeastern United States, far east of its current main distribution, is particularly interesting because of its probable role in the origin of *P. teretifolius* (Pursh) Raf., the type species of *Phemeranthus*. This taxon is an allotetraploid distributed throughout the Piedmont region and Appalachian shale and serpentine barrens from Georgia north to Pennsylvania. Morphological (Murdy 1968), cytological (Black and Murdy 1972), and allozyme data (Murdy and Carter 1985) and artificial hybridization experiments (Carter and Murdy 1985) support the hypothesis that this species originated from a hybridization event between *P. parviflorus* and *P. mengesii* in the southeastern United States. Murdy and Carter (1985) scored 23 allozyme loci from 9 enzyme systems for 384 individuals of 21 populations of *P. teretifolius, P. mengesii, P.*

parviflorus, and *P. calycinus*. They found that *P. teretifolius* populations were genetically uniform and that their alleles were a combination of alleles found in the putative parents. Chloroplast sequence data (Chapter II) suggest that *P. parviflorus* is the maternal parent of *P. teretifolius*.

Furthermore, *P. parviflorus* may have been involved in additional hybridization events of evolutionary significance in the midwestern United States. For example, a morphologically atypical *P. calycinus* population in Arkansas shares its chloroplast haplotype with *P. parviflorus,* as do all sampled populations of the prairie fameflower *P. rugospermus* (Holz.) Kiger, which is morphologically intermediate between and broadly co-distributed with *P. parviflorus* and *P. calycinus*. Thus, the widespread *P. parviflorus* appears to have played a crucial role in the evolutionary history of the genus in the midwestern and southeastern United States.

The aerial stems of sunbright plants typically die back to the ground each winter and regenerate in the spring from resting buds borne on a usually underground caudex with a tuberous taproot. The plants grow rapidly under appropriate conditions, and the flowering period extends throughout the summer, with more or less continuous production of flowers and fruits from late spring to early fall. Seed production is generally high both in the field and in the greenhouse (pers. obs.). When raised under greenhouse conditions, plants of this species usually reach reproductive maturity in their first season of growth from seed; however, they may not consistently do so in their natural environments.

Like all *Phemeranthus* species, *P. parviflorus* has ephemeral flowers, which last for only a single afternoon. Sunbright flowers typically open late in the afternoon or even in the early evening and remain open for only one to three hours (pers. obs.) Although some *Phemeranthus* species show pronounced herkogamy, which promotes outcrossing, the small-flowered *P. parviflorus* has stigmas equal to the five stamens, enabling the flowers to self-pollinate upon closing in the evening. In some cases, the flowers may self-pollinate before opening or without ever opening completely. In the greenhouse, nearly 100% of flowers set fruit without the benefit of pollinators (pers. obs.). Consistent with these observations of autogamy, Murdy and Carter (1985) found low polymorphism in *P. parviflorus* in their isozyme survey.

Although it can be found on a variety of geological substrates, *P. parviflorus* is absent from calcareous soils, occurring on siliceous rocks in the Interior Highlands region (Ozark and Ouachita mountains) and on siliceous and igneous outcrops and in sandy prairie soils elsewhere. Reinhard and Ware (1989) examined the substrate adaptation of *Phemeranthus* species from the Interior Highlands region. They grew seeds and plants from multiple populations of *P. calycinus* and *P. parviflorus* in soil collected from their native outcrops and from outcrops of different geological types under controlled conditions. Sunbright accessions from sandstone outcrops grew well on either shale or sandstone soils but poorly on soils from calcareous outcrops, showing abnormal pigmentation, poor growth, and high mortality. Similarly, mortality of *P. parviflorus* seedlings was high on limestone soils but low on sandstone. In contrast, *P. calycinus* occasionally occurs on calcareous outcrops, and accessions from limestone outperformed those from other substrates when grown on calcareous soils under controlled conditions (Reinhard and Ware 1989). These results indicate some degree of substrate specificity and the possibility of local edaphic adaptation in sunbright and its relatives.

Clinal variation and phenotypic plasticity

Temporal environmental variation (e.g., seasonal patterns of temperature and precipitation) and the predictability of environmental change are important determinants of population dynamics and community structure (Angert et al. 2010). Natural selection can lead to differential local adaptation along environmental clines. Phenological variation along latitudinal clines has been observed in many species and communities (e.g., McMillan 1957, 1965, 1967, 1973). Individual plants can respond to environmental variation and change through adaptive phenotypic plasticity, which can be viewed as “habitat-selecting behavior” (Donohue 2003). By responding differently to varying environmental cues, plants can modify the environment they experience, a process known as niche construction (Donohue 2005; Donohue et al. 2005a, 2005d). Thus, the same genotype may be able to achieve similar fitness in different geographical locations and under differing seasonal conditions. However, mismatches between the environmental cues to which plants respond and actual environmental conditions can lead to reproductive failure. Such mismatches may increase with climate change.

Seed germination, a critical life-history stage

Seed germination and seedling establishment are important filters in community assembly, contributing to the association between environmental conditions and species’ functional traits by determining which genotypes can persist (Ackerly 2003). Because the timing of germination determines the environmental conditions that a plant will encounter as it begins its growth and establishment, this phenological trait is likely to be under strong natural selection (Donohue et al. 2005c; Bentsink et al. 2010). Germination timing also affects adult life-history traits and natural selection thereon (Donohue 2002; Donohue et al. 2005d). Various seed-dormancy mechanisms have evolved to help assure appropriate matching between environmental conditions during growth and species' functional traits.

Seed germination requirements vary among natural populations of many plant species (e.g., Schmitt et al. 1992; Donohue et al. 2005c; Veatch-Blohm and Koutavas 2011). This variation is best known in *Arabidopsis thaliana*, whose ecotypes differ in cold-stratification and other requirements for germination. In a field experiment with *Arabidopsis* ecotypes, Donohue and colleagues found that natural selection on germination timing is highly efficient in determining the persistence or failure of different genotypes at some locations (Donohue et al. 2005d; Donohue et al. 2005b). However, the efficiency of this selection varies with geography and with other life-history traits. Some environments might favor a "bet-hedging" strategy with variable germination requirements so as to promote germination at different times, while other environments might not. The rate at which germination timing and other phenological cuing can evolve in natural populations may affect the rate of range expansion (Donohue et al. 2005c) and thus species' ability to respond to climate change.

Genes associated with regulation of germination

The genetic basis of seed dormancy has been studied most extensively in *Arabidopsis*, where several interacting additive genetic and molecular pathways are apparently involved in controlling seed dormancy (Bentsink et al. 2010). Phytochromes mediate the responses of germination to multiple seasonal cues, including cold stratification, both during seed maturation and after dispersal (Donohue et al. 2007; Donohue et al. 2008; Heschel et al. 2008). A major flowering-time gene, *FLC* (Flowering Locus C), also regulates seed germination in *Arabidopsis* (Chiang et al. 2009). This gene regulates flowering responses to seasonal environmental factors and also natural variation in temperature-dependent germination. The resulting pleiotropy between seed germination and flowering time may be important in adaptive evolution. Additional genes in the flowering pathway, the abscissic acid catabolic pathway, and the giberrellin biosynthesis pathway are also involved, and the effect is largely maternally controlled (Chiang et al. 2009).

Seed germination requirements in *Phemeranthus*

Seed germination requirements have been studied in *P. mengesii*, *P. teretifolius*, and *P. calcaricus* (S. Ware) Kiger, three species that are closely related to *P. parviflorus* (Ware and Quarterman 1969; Ware and Pinion 1990). The germination requirements of these species appear to be selectively advantageous in their native glade and rock-outcrop habitats. In laboratory experiments, freshly harvested seeds failed to germinate under any tested conditions, suggesting that the seeds possess physiological dormancy. In *P. calcaricus*, moist cold treatment, light, and alternating temperatures were required for effective germination, and after-ripening (dry storage) increased germination rates but did not affect the need for moist cold treatment. Seeds of *P. mengesii* also required cold treatment and light for germination but were not affected by alternating vs. constant temperatures during the germination period (Ware and Quarterman 1969). *Phemeranthus calcaricus* required a shorter duration of cold treatment than *P. mengesii*, but for both species, just six weeks of moist cold treatment resulted in 90% or higher germination rates (Ware and Quarterman 1969; Ware and Pinion 1990). Six weeks of chilling were also sufficient for three populations of *P. teretifolius* from Georgia and Virginia, but eight weeks of cold treatment were necessary to achieve a similarly high germination rate in a northern Maryland population of *P. teretifolius* (Ware and Pinion 1990). All species germinated poorly in the dark; however, the requirement for light was less critical if the seeds had been aged in *P. mengesii*. A brief exposure to light did not trigger germination, but an eight-hour photoperiod was sufficient; thus, photoperiod does not control germination in the field (day length is never less than eight hours at the latitudes where these species are found) (Ware and Quarterman 1969).

In these *Phemeranthus* species, it takes about 20 days for seeds to mature following flower opening (Ware and Quarterman 1969). The plants flower from May to September, so they produce seeds continuously throughout the summer. The seeds then germinate the following spring, from late March to early May. Germination during the summer would likely result in seedling death due to desiccation, while seedlings germinating in the fall would be challenged by competition from abundant winter annuals, and *Phemeranthus* is a poor competitor (Ware and Quarterman 1969; Ware 1991). Growing *Phemeranthus* is also damaged by cold temperatures. Thus, spring is the best time for their germination, after the winter annuals have completed their life cycles and before temperatures become too hot and water too scarce for seedling establishment. The requirement for moist cold treatment ensures that seeds do not germinate in the fall and may limit the southward extent of the species, although winter conditions were sufficient to promote germination at a location 300 miles south of the southernmost populations of *P. calcaricus* (Ware 1968; Ware and Quarterman 1969). If only six to eight weeks of chilling are needed, then the requirement will generally be met well before spring arrives, and seed dormancy must subsequently be enforced by continuing cold.

Materials and Methods

Seed sources

Seed germination requirements and phenological traits were examined in twelve populations from across the broad latitudinal range of this species, including the outlying Alabama population formerly known as *Talinum appalachianum*. The southernmost population was located in the Edwards Plateau region of Texas, while the northernmost was in southeastern South Dakota (Table 1). Seeds were collected from natural populations during multiple field trips in 2005–2009. The primary purpose of these collections was to obtain plant tissue for DNA extraction; seeds were gathered so that plants could be raised in the greenhouse for morphological observation and to provide fresh tissue for DNA extraction as necessary. Thus, the number of maternal plants varied among populations and was not recorded. The seed germination experiment was designed later to use the existing resource of the seed collections. In a second experiment, seeds collected from plants grown in the greenhouse under common conditions were used.

TABLE 3.1. Localities of *Phemeranthus parviflorus* populations used as seed sources

Pop. #	Locality	Latitude	Longitude	Year*	Day*	Winter length†
1	Llano Co., TX	30.5	-98.8	2007	138	127 d
2	Coosa Co., AL	32.8	-86.4	2006	191	134 d
3	Johnston Co., OK	34.3	-96.4	2009	164	144 d
4	Cleveland Co., OK	35.2	-97.3	2009	162	159 d
5	Delaware Co., OK	36.2	-94.7	2009	161	157 d
6	Chautauqua Co., KS	37.0	-96.0	2008	204	169 d
7	Chautauqua Co., KS	37.2	-96.1	2008	204	169 d
8	Washington Co., MO	37.9	-91.0	2005	230	195 d
9	Reno Co., KS	37.9	-98.2	2008	203	171 d
10	St. Clair Co., MO	38.1	-93.7	2008	198	183 d
11	Ellsworth Co., KS	38.7	-98.0	2008	202	188 d
12	Minnehaha Co., SD	43.8	-96.7	2009	267	217 d

* Year and Day indicate the ordinal date when the seed was collected in the field.
†Winter length is the number of days between the average first date of frost in the fall and the average last date of frost in the spring.

Chilling treatments & greenhouse germination

In the first experiment, using field-collected seeds, seeds from each population were subjected to seven durations of moist chilling: zero, two, four, six, eight, ten, and twelve weeks. In the second experiment, using greenhouse-grown seeds, the ten-week treatment was eliminated and a sixteen-week treatment was added. For each chilling treatment, a 36-cell planting tray was prepared. The cells were filled with a mixture of three parts Turface®, one part sand, and one part standard commercial potting soil, which was covered with a 1/8-inch layer of fine-grained seedling mix potting soil. The trays were then thoroughly wetted and allowed to drain before the seeds were scattered on the surface of the planting medium. Each tray was divided into three 12-cell sections, and each population was randomly assigned to one cell within each section (three cells per tray). Cell assignment was fully randomized across each section and tray. Due to the limited number of field-collected seeds available, 10 seeds were planted in each cell for a total of 30 seeds per population per treatment in the first experiment. In the second experiment, 50 greenhouse-grown seeds were planted in each cell for a total of 150 seeds per population per treatment.

Prepared trays were placed in a cold room at 4ºC for chilling. In the first experiment, all trays were prepared at the same time, and each tray was sequentially brought into the greenhouse for germination after its designated chilling time had elapsed. In the second experiment, trays were prepared and placed in the cold room on a staggered timetable so that they were all brought into the greenhouse for germination at the same time.

In the greenhouse, all seeds encountered controlled conditions of 65% relative humidity, a 10/14-hour day/night schedule with alternating day and night temperatures of 25ºC and 18.3ºC, and 750 µmol light during the day. The trays were kept covered with clear plastic and the soil was kept moist by daily misting for two weeks, when germination was mostly complete. After two weeks, the covers were removed, and the soil was allowed to dry between watering as the plants grew. The trays were rotated daily to minimize any differences in conditions across positions on the greenhouse bench. The number of seedlings in each cell was recorded daily, and the plants were maintained for several months to observe their reproductive phenology. In the second experiment, seedlings in each cell were thinned to 10 after four weeks to reduce crowding.

Statistical analyses

Two response variables were considered: the probability of germination and the number of days to germination (from the time the trays were brought into the greenhouse). From the daily seedling counts, the final germination percentages and average days to germination were determined for each population in each treatment. Overall values were also calculated for each population across all treatments and for each treatment across populations.

Natural cubic spline functions were used to evaluate the response of seed germination to chilling duration. This method is an effective way to deal with data that show substantial non-linearities. First, the results for germination probability at a given latitude were compared between the first and second experiments. Because the two experiments appeared to differ (see Results), they were analyzed separately.

Each experiment was analyzed in terms of seed germination probability using a natural cubic spline with three degrees of freedom. The curves for each population were compared and *p*-values calculated to evaluate how the effect of chilling duration on germination probability changes with latitude. The same procedure was followed to evaluate the effect of chilling duration on the number of days to germination.

Results

In the first experiment, 1,105 seeds germinated out of a total of 2,520, for an overall germination percentage of 43.8%. The average number of days to germination was 7.94. In the second experiment, 7,878 seeds germinated out of a total of 12,600, for an overall germination percentage of 62.5%. The average number of days to germination was 6.68. Tables 3.2 and 3.3 show the germination percentages and average number of days to germination for each population across all treatments and for each treatment across all populations, respectively, in each experiment. Tables 3.4 and 3.5 show the germination percentages and average number of days to germination for each population in each treatment in the first and second experiments, respectively.

The germination percentage curves for most populations were significantly different between the first and second experiments (Table 3.6). Only for the three southernmost populations was the difference between experiments non-significant (populations 2 and 3) or marginally significant (population 1). However, the curves for days to germination did not differ between experiments (Table 3.6).

In the first experiment, the curves relating germination probability to chilling time clearly differed among populations from different latitudes (Fig. 3.2). Pairwise *p*-values comparing the curves for each population (Table 3.7, top) indicate significant differences among most populations. However, some populations have statistically indistinguishable curves. For example, the *p*-value comparing population 2 (Coosa Co., AL) to population 3 (Johnston Co., OK) is 0.194, suggesting that the two populations have the same curve. Populations 6, 7, and 11 might also exhibit a common response. Visual inspection shows that the corresponding germination probability curves for the second experiment (Fig. 3.3) are quite different from those of the first experiment. Here, populations 3 and 12 have similar curves (*p*-value = 0.48) (Table 3.7, bottom).

TABLE 3.2. Germination percentages and average number of days to germination for each population across all treatments

	Experiment 1		Experiment 2	
Pop.	**No. / %Germ. (*n*=210)**	**Days to Germ.**	**No. / %Germ. (*n*=1050)**	**Days to Germ.**
1	174 / 82.9%	5.9	793 / 75.5%	5.9
2	141 / 67.1%	6.2	737 / 70.2%	6.0
3	147 / 70.0%	9.2	661 / 63.0%	6.7
4	110 / 52.4%	8.4	679 / 64.7%	6.5
5	131 / 62.4%	7.3	759 / 72.3%	8.2
6	72 / 34.3%	8.8	538 / 51.2%	7.0
7	72 / 34.3%	9.4	576 / 54.9%	7.2
8	47 / 22.4%	11.8	709 / 67.5%	6.8
9	38 / 18.1%	8.1	394 / 37.5%	7.1
10	101 / 48.1%	8.4	604 / 57.5%	6.8
11	72 / 34.3%	8.5	782 / 74.5%	6.0
12	0 / 0.0%	N/A	646 / 61.5%	6.6

TABLE 3.3. Germination percentages and average number of days to germination for each treatment across all populations

	Experiment 1		Experiment 2	
Chilling Treatment	**%Germ. (*n*=360)**	**Days to Germ.**	**%Germ. (*n*=1800)**	**Days to Germ.**
0 weeks	26 / 7.2%	10.2	150 / 8.3%	14.3
2 weeks	99 / 27.5%	6.4	598 / 33.2%	9.3
4 weeks	129 / 35.8%	7.8	1178 / 65.4%	7.1
6 weeks	168 / 46.7%	10.5	1464 / 81.3%	5.7
8 weeks	208 / 57.8%	6.8	1448 / 80.4%	5.8
10 weeks	254 / 70.6%	6.7	N/A	N/A
12 weeks	221 / 61.4%	9.0	1516 / 84.2%	6.1
16 weeks	N/A	N/A	1524 / 84.7%	6.9

TABLE 3.4. Germination percentages and average number of days to germination for each population in each treatment in the first experiment

Chilling Treatment	**0 weeks**	**2 weeks**	**4 weeks**	**6 weeks**	**8 weeks**	**10 weeks**	**12 weeks**
Pop.	**number germinated (out of 30) / germination percentage**						
	average days to germination						
1	12 / 40.0	29 / 96.7	25 / 83.3	26 / 86.7	26 / 86.7	29 / 96.7	27 / 90.0
	7.7	4.7	5.2	11.2	5.2	3.5	5.4
2	4 / 13.3	16 / 53.3	22 / 73.3	22 / 73.3	25 / 83.3	27 / 90.0	25 / 83.3
	13.8	6.9	6.3	8.8	5.1	5.2	4.5
3	0 / 0.0	16 / 53.3	24 / 80.0	25 / 83.3	29 / 96.7	27 / 90.0	26 / 86.7
	N/A	9.4	9.0	9.9	7.7	7.2	12.3
4	0 / 0.0	5 / 16.7	16 / 53.3	18 / 60.0	22 / 73.3	27 / 90.0	22 / 73.3
	N/A	7.6	7.9	10.7	6.3	7.9	9.6
5	10 / 33.3	26 / 86.7	20 / 66.7	22 / 73.3	21 / 70.0	17 / 56.7	15 / 50.0
	11.7	5.8	8.4	8.0	6.0	5.4	8.9
6	0 / 0.0	1 / 3.3	2 / 6.7	12 / 40.0	13 / 43.3	24 / 80.0	20 / 66.7
	N/A	5.0	7.0	9.2	6.5	8.1	11.3
7	0 / 0.0	0 / 0.0	3 / 10.0	10 / 33.3	14 / 46.7	25 / 83.3	20 / 66.7
	N/A	N/A	17.7	16.3	7.3	4.5	12.2
8	0 / 0.0	1 / 3.3	8 / 26.7	10 / 33.3	10 / 33.3	9 / 30.0	9 / 30.0
	N/A	6.0	12.1	13.9	10.2	8.2	15.3
9	0 / 0.0	0 / 0.0	0 / 0.0	0 / 0.0	2 / 6.7	18 / 60.0	18 / 60.0
	N/A	N/A	N/A	N/A	16.5	8.1	7.2
10	0 / 0.0	5 / 16.7	3 / 10.0	16 / 53.3	26 / 86.7	26 / 86.7	25 / 83.3
	N/A	7.6	7.0	10.7	8.1	8.7	7.2
11	0 / 0.0	0 / 0.0	6 / 20.0	7 / 23.3	20 / 66.7	25 / 83.3	14 / 46.7
	N/A	N/A	8.2	11.1	6.8	8.0	10.7
12	0 / 0.0	0 / 0.0	0 / 0.0	0 / 0.0	0 / 0.0	0 / 0.0	0 / 0.0
	N/A	N/A	N/A	N/A	N/A	N/A	N/A

TABLE 3.5. Germination percentages and average number of days to germination for each population in each treatment in the second experiment

Chilling Treatment	**0 weeks**	**2 weeks**	**4 weeks**	**6 weeks**	**8 weeks**	**12 weeks**	**16 weeks**
Pop.	**number germinated (out of 150) / germination percentage**						
	average days to germination						
1	37 / 24.7	113 / 75.3	131 / 87.3	128 / 85.3	130 / 86.7	126 / 84.0	128 / 85.3
	8.9	6.5	5.8	4.8	5.5	5.3	6.5
2	20 / 13.3	94 / 62.7	125 / 83.3	130 / 86.7	110 / 73.3	127 / 84.7	131 / 87.3
	15.1	10.0	5.1	4.2	4.3	5.3	6.3
3	1 / 0.7	55 / 36.7	97 / 64.7	119 / 79.3	124 / 82.7	140 / 93.3	125 / 83.3
	14.0	11.7	8.0	5.7	5.8	5.4	6.7
4	0 / 0.0	18 / 12.0	131 / 87.3	141 / 94.0	143 / 95.3	124 / 82.7	122 / 81.3
	N/A	7.1	6.7	6.3	6.6	6.5	6.2
5	72 / 48.0	101 / 67.3	108 / 72.0	114 / 76.0	108 / 72.0	133 / 88.7	123 / 82.0
	16.2	10.6	7.9	6.8	6.0	6.9	6.4
6	0 / 0.0	13 / 8.7	71 / 47.3	107 / 71.3	109 / 72.7	114 / 76.0	124 / 82.7
	N/A	10.8	8.5	6.2	5.7	6.9	7.8
7	0 / 0.0	21 / 14.0	74 / 49.3	111 / 74.0	117 / 78.0	134 / 89.3	119 / 79.3
	N/A	9.5	9.7	5.8	6.7	6.9	7.1
8	0 / 0.0	47 / 31.3	131 / 87.3	143 / 95.3	138 / 92.0	126 / 84.0	124 / 82.7
	N/A	9.8	6.2	5.5	5.5	5.4	10.5
9	0 / 0.0	0 / 0.0	7 / 4.7	71 / 47.3	66 / 44.0	112 / 74.7	138 / 92.0
	N/A	N/A	11.4	7.8	8.0	6.4	6.6
10	0 / 0.0	8 / 5.3	71 / 47.3	136 / 90.7	135 / 90.0	129 / 86.0	125 / 83.3
	N/A	9.3	9.0	6.9	5.8	6.2	6.7
11	11 / 7.3	79 / 52.7	139 / 92.7	148 / 98.7	148 / 98.7	118 / 78.7	139 / 92.7
	17.1	8.5	6.1	4.7	4.7	5.8	6.3
12	9 / 6.0	49 / 32.7	93 / 62.0	116 / 77.3	120 / 80.0	133 / 88.7	126 / 84.0
	17.1	10.5	7.6	5.4	5.7	6.0	5.9

TABLE 3.6. *p*-values comparing the germination percentage (%Germ.) and number of days to germination (Days to Germ.) curves for each population between the first and second experiments

Pop.	**%Germ.**	**Days to Germ.**
1	0.042	1.000
2	0.335	1.000
3	0.072	1.000
4	0.000	1.000
5	0.000	1.000
6	0.000	1.000
7	0.000	1.000
8	0.000	1.000
9	0.000	1.000
10	0.000	1.000
11	0.000	1.000
12	0.000	no data

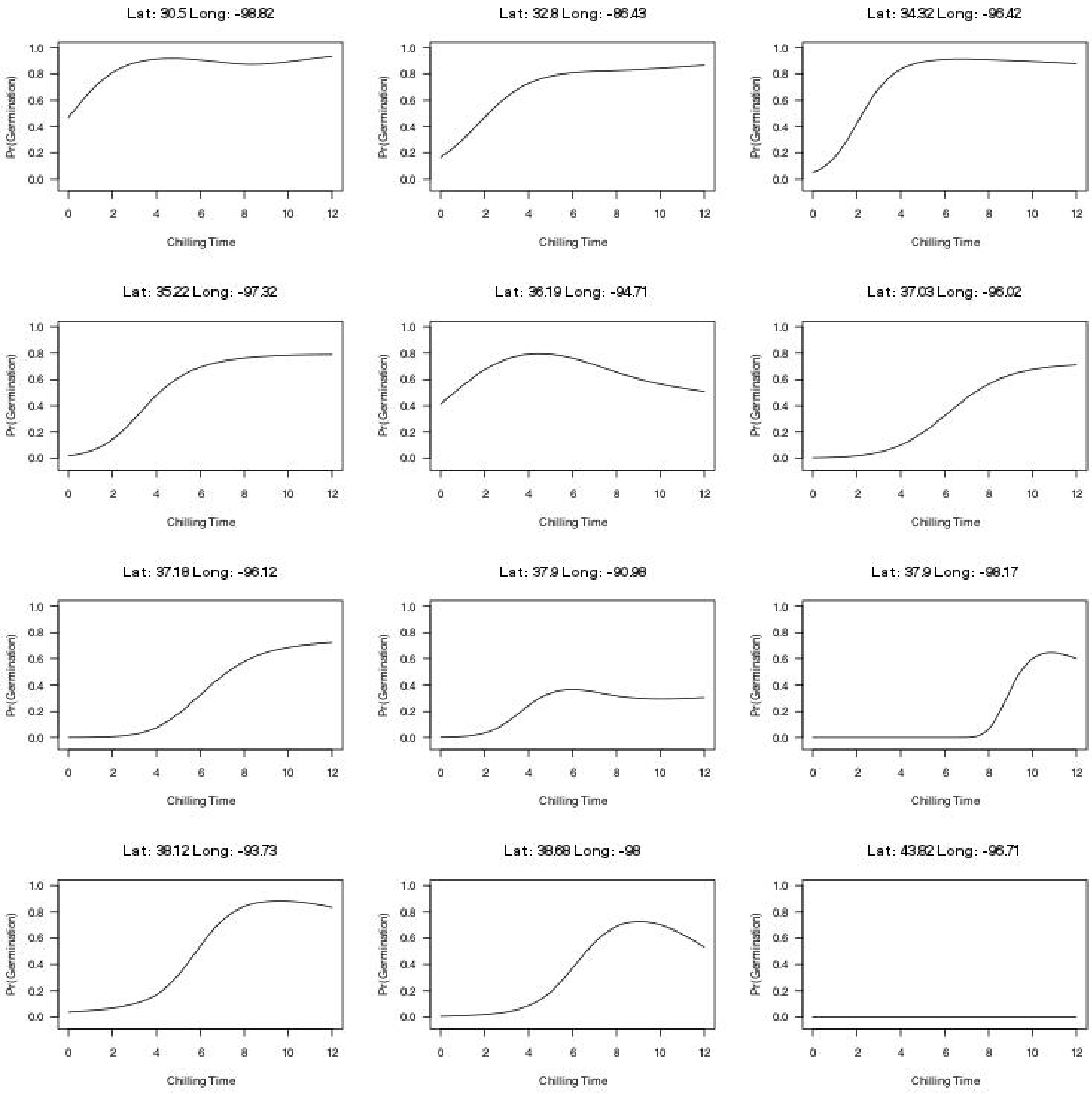

FIGURE 3.2. Natural cubic spline curves for germination probability versus chilling duration in the first experiment. Populations are designated by their latitude and longitude above each plot and are arranged from south to north from top left to bottom right.

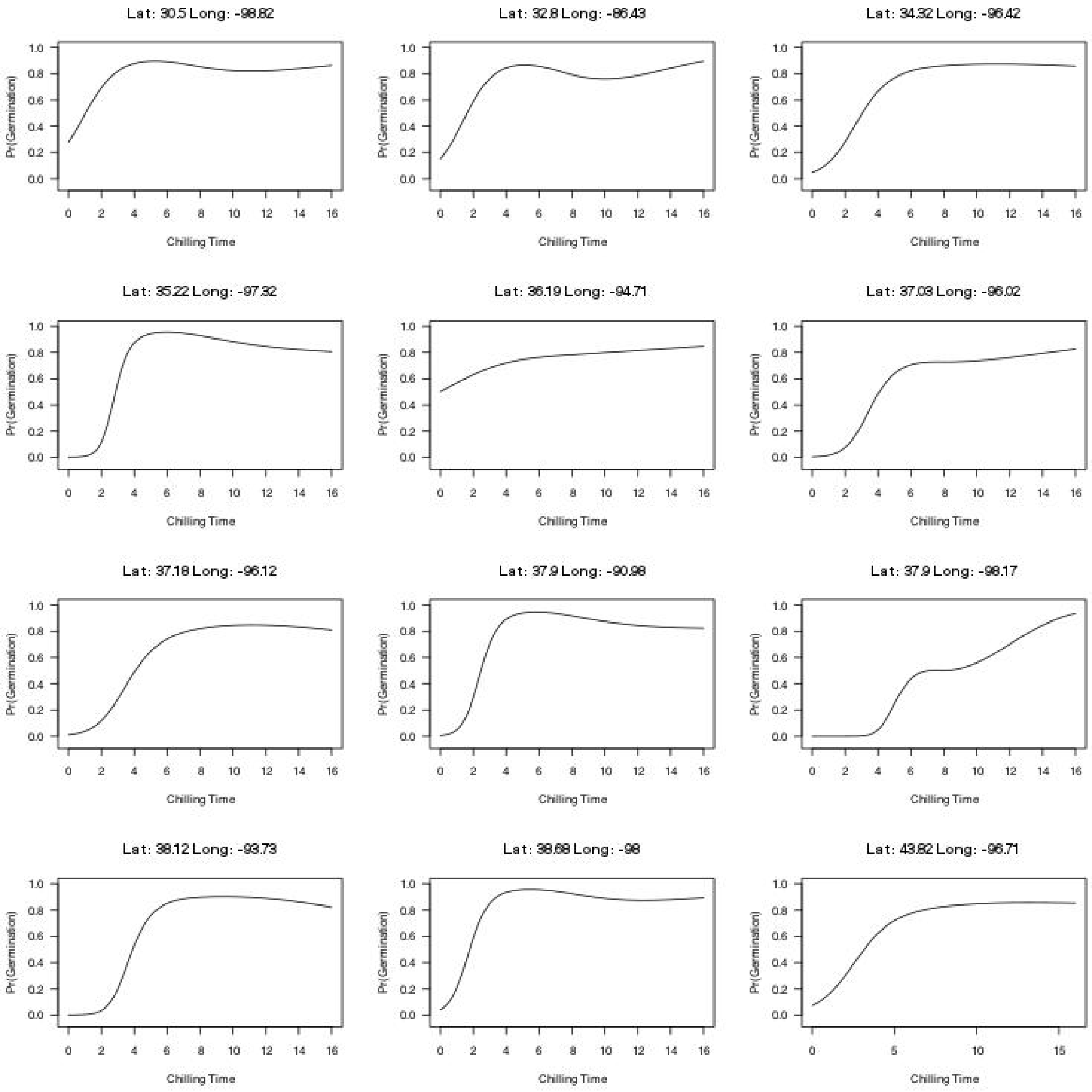

FIGURE 3.3. Natural cubic spline curves for germination probability versus chilling duration in the second experiment. Populations are designated by their latitude and longitude above each plot and are arranged from south to north from top left to bottom right.

TABLE 3.7. *p*-values comparing the germination percentage curves in each population for the first experiment (above the diagonal) and the second experiment (below the diagonal).

Pop.	1	2	3	4	5	6	7	8	9	10	11	12
1	**1**	0	0	0	0	0	0	0	0	0	0	0
2	0.004	**1**	0.194	0.001	0	0	0	0	0	0	0	0
3	0	0	**1**	0	0	0	0	0	0	0	0	0
4	0	0	0	**1**	0	0	0	0	0	0.025	0	0
5	0	0	0	0	**1**	0	0	0	0	0	0	0
6	0	0	0	0	0	**1**	0.98	0	0	0.003	0.505	0
7	0	0	0	0	0	0.037	**1**	0	0	0.002	0.437	0
8	0	0	0	0	0	0	0	**1**	0	0	0	0
9	0	0	0	0	0	0	0	0	**1**	0	0	0
10	0	0	0	0	0	0	0	0	0	**1**	0.003	0
11	0	0	0	0	0	0	0	0	0	0	**1**	0
12	0	0	0.485	0	0	0	0	0	0	0	0	**1**

For the number of days to germination, the *p*-values comparing the curves for each population in the first and second experiment indicate no difference between the two experiments (Table 3.6). Figures 3.4 and 3.5 show the response curves for days to germination in the first and second experiments, respectively. Most of these curves are flat or nearly so, suggesting that chilling duration does not have much effect on days to germination. For both experiments, the pairwise *p*-values comparing the curves across populations are all 1.0 (not shown), suggesting that latitude does not affect days to germination.

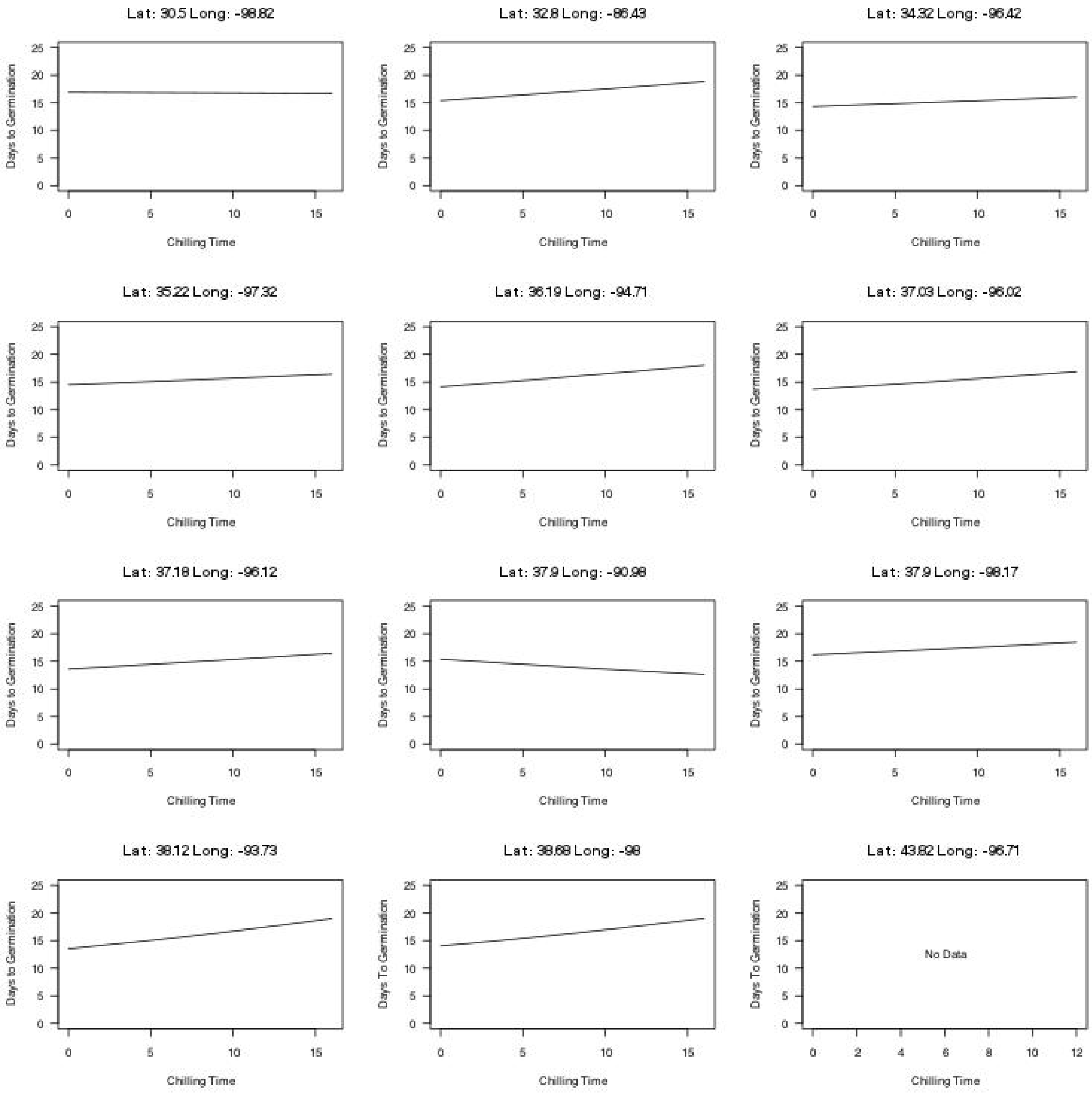

FIGURE 3.4. Natural cubic spline curves for days to germination versus chilling duration in the first experiment. Populations are designated by their latitude and longitude above each plot and are arranged from south to north from top left to bottom right.

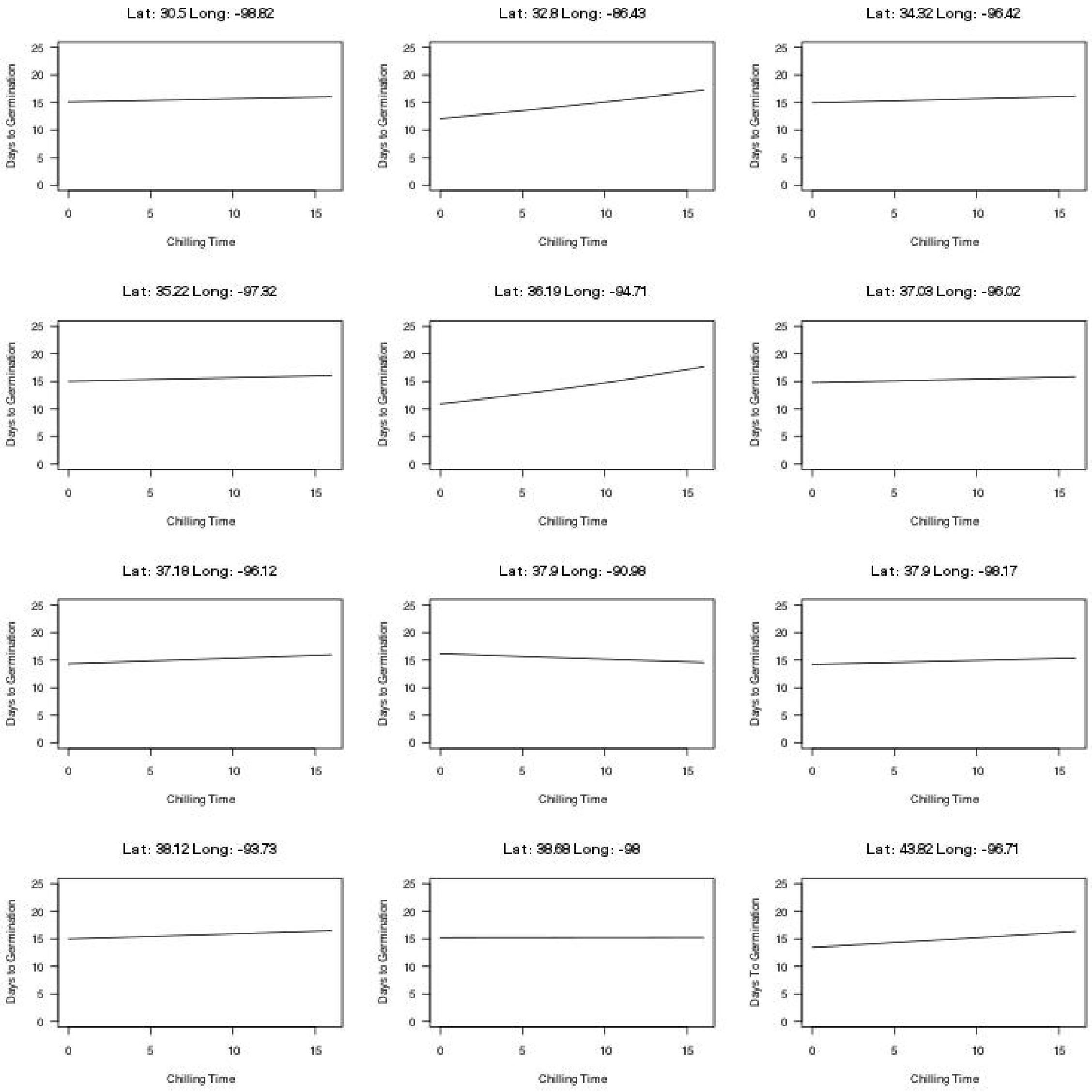

FIGURE 3.5. Natural cubic spline curves for days to germination versus chilling duration in the second experiment. Populations are designated by their latitude and longitude above each plot and are arranged from south to north from top left to bottom right.

Discussion

In the first experiment, using field-collected seeds, all populations germinated best with at least some chilling. However, the effect of chilling duration on germination probability varied strongly with latitude. Seeds from the southernmost populations (1, 2, and 5) were capable of germinating with no chilling and reached their peak germination rates at shorter durations of chilling (4–6 weeks). Seeds from the northernmost populations failed to germinate with no or brief chilling and required longer chilling periods (8–12 weeks) to achieve high germination rates. The duration of the experiment was apparently insufficient to break dormancy in the northernmost population. Separately, large numbers of seedlings appeared in the pots alongside adult plants from the northernmost population that had been potted up with some of their own soil and chilled for several months.

In the second experiment, using greenhouse-grown seeds, most populations again required at least some chilling to germinate. Populations 1, 2, and 5 were capable of germinating with no chilling. However, populations from all latitudes, even the northernmost, reached their peak germination rates (80-90% for most populations) at four to six weeks of chilling. Only in population 9 did germination continue to increase substantially with increasing chilling duration.

Chilling time had no apparent effect on days to germination for any latitude in either experiment. Thus, moist chilling helps to break seed dormancy but does not affect the speed of germination, and whatever differences existed between the first and second experiments also affected whether seeds germinated but not how long it took.

Cold stratification of the seeds appeared to affect the adult life history of the plants, and this effect varied with latitude. Seeds from the southernmost population could germinate without chilling, and the resulting plants flowered abundantly in their first season of growth. Seeds from populations 2 and 5 could also germinate without chilling, but the resulting plants remained vegetative and did not flower before entering dormancy a few months later. All of these plants did flower after they had been placed in the cold room for four months, then returned to the greenhouse for a second season of growth.

The latitudinal pattern in the response of seed germination to chilling duration suggests the presence of local adaptation in *P. parviflorus*. The average length of winter generally increases with increasing latitude (Table 3.1). For the northernmost populations, seed dormancy may be critical to fitness because any seed that germinated prematurely would likely be killed by frost. For the southernmost population, where the growing season is long and winters are relatively mild, seed dormancy may be less critical because seeds that germinate in the fall may be able to establish themselves and survive the winter.

However, several confounding variables are present in the first experiment, making its interpretation more complex. First, the seeds were collected over several years (2005–2009); some populations were represented by much older seed than others (Table 3.1). If seed viability declines with extended storage, then populations that were collected earlier would show lower overall germination and possibly different response curves. Indeed, the population collected in 2005, population 8, had the lowest germination percentage at 10 and 12 weeks and the lowest peak germination percentage (other than population 12, which did not germinate at all in the first experiment) (Table 3.4).

Nevertheless, population 1, which was collected in 2007, had the highest germination rate at 10 and 12 weeks and overall; and population 2, which was collected in 2006, was also among the highest germinating populations.

The ordinal date (i.e., time of year) when the seeds were collected may be even more important as a confounding variable. Seasonal environmental variation during seed formation could influence their dormancy requirements through maternal effects, which may vary over a long reproductive period. Because *P. parviflorus* can produce seed over several months, such effects are likely to differ in seeds collected early in the growing season versus seeds collected late in the growing season. Unfortunately, by coincidence, the southernmost populations were collected relatively early in the year, while the northernmost were collected relatively late in the year (Table 3.1). By the time the seeds were collected from population 12, in South Dakota, the mature plants in the population had already begun to enter dormancy. Thus, the possible effect of ordinal date of collection is anti-conservative with respect to the hypothesis that the required duration of chilling increases with latitude due to local adaptation. The southernmost population happened to be collected early in the season, when dormancy might not be essential because seeds germinating immediately might still have time to establish themselves that summer and survive to reproduce. The northernmost happened to be collected very late in the season, when any seeds that germinated immediately would definitely not survive, so the seeds must be kept from germinating until the next spring. Therefore, if maternal effects were present, they would enhance the latitudinal pattern or possibly even generate a false pattern.

The purpose of the second experiment was to minimize maternal effects present in field-collected seeds by using seeds grown under common, controlled conditions. The fact that the germination probability curves in this experiment differed strongly from those in the first experiment and that the latitudinal pattern mostly disappeared suggest that the observed effects were, indeed, due to maternal effects linked to seasonal environmental conditions during seed germination. Though field-collected seeds from population 12 did not germinate at all, greenhouse-grown seeds germinated at high rates after 8–16 weeks of chilling, and a few even germinated without chilling (Table 3.5).

Maternal effects have been defined as “the causal influence of the maternal genotype or phenotype on the offspring phenotype” (Wolf and Wade 2009). Significant maternal effects on seed germination have been reported for several plant species, including members of Primulaceae, Boraginaceae, Asteraceae, Lamiaceae, and Plantaginaceae (Schmitt et al. 1992; Bischoff and Müller-Schärer 2010; Kagaya et al. 2010). Ecotypic variation in germination timing is largely maternally controlled in *Arabidopsis thaliana* (Munir et al. 2001; Boyd et al. 2007). Maternal effects on germination can have major consequences for life-history traits, generation time and population growth rates, natural selection on germination, the expression of genetic variation for germination traits, and the very genes involved in regulating germination (Donohue 2009). Maternal environmental effects can be an important part of population differentiation and may be adaptive; in restoration or re-vegetation plantings, they may strongly affect seedling recruitment and the success of population establishment at the target site (Bischoff and Müller-Schärer 2010).

Although suggestive, the results of this study are preliminary and not conclusive. They raise several intriguing questions for further study. The nature and role of maternal effects on seed germination in *P. parviflorus* are particularly interesting. To better understand these effects, seeds could be collected from each population at designated times across the growing season. The response of seed germination to chilling duration could then be compared among seeds produced at different points in the growing season and seeds raised under common greenhouse conditions. Common-garden growth experiments at northern, middle, and southern latitudes (or in growth chambers programmed to mimic corresponding environmental conditions) would also be instructive in evaluating the adaptive role of maternal effects. For example, would plants from Texas produce seeds with a long chilling requirement in the late-season South Dakota environment, or do they lack the ability to enforce such dormancy?

Further studies should add populations to fill the latitudinal gaps between the southernmost and northernmost extremes and the remaining populations. Genetic surveys using highly variable markers, such as AFLPs or microsatellites, would help to determine whether population differentiation in seed germination requirements is linked to population genetic differentiation. Populations linked by gene flow would be expected to show similar response patterns. Genetic variation in genes linked to seed germination timing, such as the phytochrome gene family, may be linked to the observed latitudinal variation.

As a highly selfing species, *P. parviflorus* exhibits little genetic variation within populations. Its co-distributed congener *P. calycinus* is mostly outcrossing, while *P. rugospermus* is intermediate. Both of these species also have wide latitudinal ranges, especially *P. rugospermus,* which has disjunct populations ranging from east Texas to central Wisconsin. Do *P. calycinus* and *P. rugospermus* exhibit patterns of local adaptation and/or maternal effects in seed germination response to chilling duration similar to those seen in *P. parviflorus*? How does the variation in breeding system affect the distribution of within- and between-population variation in these traits?

Many other phenological traits in addition to seed germination can exhibit local adaptation to latitudinal variation in environmental conditions and environmentally induced maternal effects. Further studies could examine such life-history traits as the timing of flowering and fruiting, the duration of the growth period, and the onset of vegetative growth following winter dormancy. Tolerance of extreme cold and heat and light requirements for germination and flowering would also be of interest.

Finally, as observed by Ware and Quarterman (1969), the duration of cold treatment required for seed germination is far shorter than the length of winter, even at the southernmost site. Llano County, Texas, the location of population 1 in the present study, experiences only 127 days between the average first and last frost dates. Yet, just twelve weeks (84 days) of chilling was more than enough to promote maximum germination in all but the northernmost population. How is dormancy enforced after the chilling requirement is met? Presumably, light and temperature are involved, but specific requirements may vary among populations and may have adaptive significance.

Acknowledgements

I thank the federal, state, and local land managers and private land owners who gave permission to collect *Phemeranthus* on their land. I also extend special thanks to the greenhouse staff at Duke University (M. Barnes, J. Mays, and J. Gordon) and to M. Heaton for help with statistical analyses.

Literature Cited

Ackerly, D. D. 2003. Community assembly, niche conservatism, and adaptive evolution in changing environments. *International Journal of Plant Sciences* 164: 165-184.

Angert, A. L., J. L. Horst, T. E. Huxman, and D. L. Venable. 2010. Phenotypic plasticity and precipitation response in Sonoran Desert winter annuals. *American Journal of Botany* 97: 405-411.

Bentsink, L., J. Hanson, C. J. Hanhart, H. Blankestijn-De Vries, C. Coltrane, P. Keizer, M. El-Lithy, C. Alonso-Blanco, M. T. De Andres, M. Reymond, F. Van Eeuwijk, S. Smeekens, and M. Koornneef. 2010. Natural variation for seed dormancy in *Arabidopsis* is regulated by additive genetic and molecular pathways. *Proceedings of the National Academy of Sciences, USA* 107: 4264-4269.

Bischoff, A. and H. Müller-Schärer. 2010. Testing population differentiation in plant species—how important are environmental maternal effects. *Oikos* 119: 445-454.

Black, C. and W. H. Murdy. 1972. The evolutionary origin of *Talinum teretifolium* Pursh. *Botanical Gazette* 133: 405-410.

Boyd, E. W., L. A. Dorn, C. Weinig, and J. Schmitt. 2007. Maternal effects and germination timing mediate the expression of winter and spring annual life histories in *Arabidopsis thaliana*. *International Journal of Plant Sciences* 168: 205-214.

Carter, M. E. B. and W. H. Murdy. 1985. Systematics of *Talinum parviflorum* Nutt. and the origin of *T. teretifolium* Pursh (Portulacaceae). *Rhodora* 87: 121-130.

Chiang, G. C. K., D. Barua, E. M. Kramer, R. M. Amasino, and K. Donohue. 2009. Major flowering time gene, FLOWERING LOCUS C, regulates seed germination in *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences, USA* 106: 11661-11666.

Donohue, K. 2002. Germination timing influences natural selection on life-history characters in *Arabidopsis thaliana*. *Ecology* 83: 1006-1016.

Donohue, K. 2003. Setting the stage: Phenotypic plasticity as habitat selection. *International Journal of Plant Sciences* 164: S79-S92.

Donohue, K. 2005. Niche construction through phenological plasticity: life history dynamics and ecological consequences. *New Phytologist* 166: 83-92.

Donohue, K. 2009. Completing the cycle: maternal effects as the missing link in plant life histories. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* 364: 1059-1074.

Donohue, K., C. Polisetty, and N. Wender. 2005a. Genetic basis and consequences of niche construction: Plasticity-induced genetic constraints on the evolution of seed dispersal in *Arabidopsis thaliana*. *American Naturalist* 165: 537-550.

Donohue, K., M. S. Heschel, G. C. K. Chiang, C. M. Butler, and D. Barua. 2007. Phytochrome mediates germination responses to multiple seasonal cues. *Plant, Cell & Environment* 30: 202-212.

Donohue, K., L. A. Dorn, C. Griffith, E. Kim, A. Aguilera, C. R. Polisetty, and J. Schmitt. 2005b. Environmental and genetic influences on the germination of *Arabidopsis thaliana* in the field. *Evolution* 59: 740-757.

Donohue, K., L. Dorn, C. Griffith, E. Kim, A. Aguilera, C. Polisetty, and J. Schmitt. 2005c. The evolutionary ecology of seed germination of *Arabidopsis thaliana*: Variable natural selection on germination timing. *Evolution* 59: 758-770.

Donohue, K., L. Dorn, C. Griffith, E. Kim, A. Aguilera, C. R. Polisetty, and J. Schmitt. 2005d. Niche construction through germination cueing: Life-history responses to timing of germination in *Arabidopsis thaliana*. *Evolution* 59: 771-785.

Donohue, K., M. S. Heschel, C. M. Butler, D. Barua, R. A. Sharrock, G. C. Whitelam, and G. C. K. Chiang. 2008. Diversification of phytochrome contributions to germination as a function of seed-maturation environment. *New Phytologist* 177: 367-379.

Dvorak, B. 2010. Rooftop membrane temperature reductions with green roof technology in south-central Texas. 17th Symposium for Improving Building Systems in Hot and Humid Climates, Austin, Texas, ESL-HH-10-08-23: 1-7.

Getter, K. L. and D. B. Rowe. 2008. *Selecting Plants for Extensive Green Roofs in the United States*, ed. Michigan State University Extension. East Lansing, MI: Michigan State University Extension.

Getter, K. L., D. B. Rowe, and B. M. Cregg. 2009. Solar radiation intensity influences extensive green roof plant communities. *Urban Forestry & Urban Greening* 8: 269-281.

Heschel, M. S., C. M. Butler, D. Barua, G. C. K. Chiang, A. Wheeler, R. A. Sharrock, G. C. Whitelam, and K. Donohue. 2008. New roles of phytochromes during seed germination. *International Journal of Plant Sciences* 169: 531-540.

Holzinger, J. M. 1900. The geographical distribution of the *Teretifolium* group of *Talinum*. *The Asa Gray Bulletin* 8: 36-39.

Kagaya, M., T. Tani, and N. Kachi. 2010. Maternal and paternal effects on the germination time of non-dormant seeds of a monocarpic perennial species, *Aster kantoensis* (Compositae). *Plant Species Biology* 26: 66-72.

Kiger, R. W. 2003. *Phemeranthus*. Pp. 488-495 in *Flora of North America North of Mexico* vol. 4, ed. Flora of North America Editorial Committee. New York, NY and Oxford, UK: Oxford University Press.

McMillan, C. 1957. Nature of the plant community. IV. Phenological variation within five woodland communities under controlled temperatures. *American Journal of Botany* 44: 154-163.

McMillan, C. 1965. Ecotypic differentiation within four North American prairie grasses. II. Behavioral variation within transplanted community fractions. *American Journal of Botany* 52: 55-65.

McMillan, C. 1967. Phenological variation within seven transplanted grassland community fractions from Texas and New Mexico. *Ecology* 48: 807-813.

McMillan, C. 1973. Photoperiodic adaptation in desert populations of *Xanthium strumarium*. *American Journal of Botany* 60: 397-405.

Munir, J., L. Dorn, K. Donohue, and J. Schmitt. 2001. The effect of maternal photoperiod on seasonal dormancy in *Arabidopsis thaliana* (Brassicaceae). *American Journal of Botany* 88: 1240-1249.

Murdy, W. H. 1968. Plant speciation associated with granite outcrop communities of the southeastern Piedmont. *Rhodora* 70: 394-407.

Murdy, W. H. and M. E. B. Carter. 1985. Electrophoretic study of the allopolyploidal origin of *Talinum teretifolium* and the specific status of *T. appalachianum* (Portulacaceae). *American Journal of Botany* 72: 1590-1597.

Reinhard, R. and S. Ware. 1989. Adaptation to substrate in rock outcrop plants: interior highlands *Talinum* (Portulacaceae). *Botanical Gazette* 150: 449-453.

Schmitt, J., J. Niles, and R. D. Wulff. 1992. Norms of reaction of seed traits to maternal environments in *Plantago lanceolata*. *American Naturalist* 139: 451-466.

Templeton, A. R. 1997. Coadaptation, Local Adaptation, and Outbreeding Depression. Pp. 171-172 in *Principles of Conservation Biology*, second edition, ed. Gary K. Meffe and C. Ronald Carroll. Sunderland, MA: Sinauer Associates.

Veatch-Blohm, M. E. and E. Koutavas. 2011. The effect of stratification and after-ripening time on seed germination of three populations of *Arabidopsis lyrata* ssp. *lyrata* (Brassicaceae). *Castanea* 76: 199-209.

Ware, S. 1991. Influence of interspecific competition, light and moisture levels on growth of rock outcrop *Talinum* (Portulacaceae). *Bulletin of the Torrey Botanical Club* 118: 1-5.

Ware, S. and E. Quarterman. 1969. Seed germination in cedar glade *Talinum*. *Ecology* 50: 137-140.

Ware, S. and G. Pinion. 1990. Substrate adaptation in rock outcrop plants: eastern United States *Talinum* (Portulacaceae). *Bulletin of the Torrey Botanical Club* 117: 284-290.

Ware, S. A. 1968. *Responses and adaptations of a cedar glade endemic (*Talinum calcaricum, *Portulacaceae) to factors of its habitat*. Ph.D. thesis. Nashville, TN: Vanderbilt University.

Wolf, J. B. and M. J. Wade. 2009. What are maternal effects (and what are they not)? *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* 364: 1107-1115.

Wolf, W. 1939. The status of *Talinum* in Alabama. *American Midland Naturalist* 22: 315-332.

APPENDIX 1. VOUCHER INFORMATION

Localities, collection vouchers (with herbarium abbreviations), and sequences obtained (*ndhF*, *matK*, *PepC*, *PhyB1*, *PhyB2*, *PhyC*) for plant materials used in this study. Voucher information for sequences downloaded from GenBank and for certain other DNA and tissue samples can be found in the following references: (1) Applequist & Wallace, 2001 (*ndhF*); (2) Applequist et al., 2006 (*ndhF*–*Hectorella*); (3) Cuenoud et al., 2002 (*matK*); (4) Nyffeler, 2002 (*matK*); (5) Nyffeler, 2007 (*ndhF*, *matK*); and (6) Ogburn and Edwards, 2009 (tissue samples). Following *Phemeranthus*, genera and species within genera are arranged alphabetically. Missing sequences are denoted by —. For nuclear markers, numbers represent clones sequenced / putative alleles detected. D = direct sequence (not cloned); n.d. = not detected; cult. SRPN = live plants in cultivation obtained from Siskiyou Rare Plants Nursery, Talent, OR; cult. MG = live plants in cultivation grown from seed obtained from Mesa Garden, Belen, NM.

Family	**Genus**	**species**	**Locality or source**		**Voucher**	***ndhF***	***matK***	***PepC***	***PhyB1***	***PhyB2***	***PhyC***
Montiaceae	*Phemeranthus*	*brevicaulis*	USA: New Mexico: Bernalillo Co.	Chilili (originally D.J. Ferguson s.n.; cult. MG, grown at Washington Univ.)	T.M. Price s.n. (MO)	D	D	5 / 1	2 / 2?	n.d.	D
			USA: New Mexico: Sierra Co.	Quartzite Ridge SW of Lake Valley	T.M. Price 250 (MO)	D	D	2 / 1	3 / 1	n.d.	D
			USA: New Mexico: Torrance Co.	1.5 mi. NW of jct. US-54 and NM-42 at Corona	T.M. Price 319 (MO)	D	D	1 / 1	7 / 2?	1 / 1	8 / 2
			USA: Texas: El Paso Co.	Franklin Mts. State Park, ridge along Smugglers' Pass trail	T.M. Price 315 (MO)	D	D	2 / 2?	—	—	D

			below Mammoth's Trunk							
	brevifolius	USA: Arizona: Navajo Co.	5 mi. N of Woodruff, 6.5 mi. SE of Holbrook, along Old Woodruff road	T.M. Price 253 (MO)	D	D	D	2 / 2?	n.d.	5 / 2
		USA: Utah: Garfield Co.	Grand Staircase-Escalante National Monument, S of Burr Trail and W of Deer Creek, SE of Boulder	T.M. Price 293 (MO)	D	D	D	3 / 2?	n.d.	12 / 2
		USA: Utah: San Juan Co.	E side of S end Comb Reef ca. 6.5 mi. WSW of Bluff along US-163	T.M. Price 297 (MO)	D	D	8 / 2	6 / 2?	n.d.	7 / 2
		USA: cult. SRPN	Cultivated plant obtained from Siskiyou Rare Plants Nursery, Talent, OR	T.M. Price s.n. (MO)	D	D	4 / 1	7 / 1	n.d.	D
	calcaricus	USA: Tennessee: Davidson Co.	Couchville Cedar Glade Natural Area	T.M. Price 228 (MO)	D	D	8 / 2	1 / 1	n.d.	12 / 2
		USA: Alabama: Franklin Co.	Roadside E of Waco and W of CR-83 on AL-724	T.M. Price 239 (MO)	D	D	11 / 2	6 / 2?	1 / 1	4 / 2
	calycinus	USA: Missouri: Dade Co.	Bona Glade Natural Area	T.M. Price 269 (MO)	D	D	9 / 2	2 / 2?	1 / 1	—
		USA: Missouri: Montgomery Co.	Danville Conservation Area	T.M. Price 220 (MO)	D	D	7 / 2	1 / 1	n.d.	—
		USA: Missouri: St. Clair Co.	Dave Rock Natural Area	T.M. Price 256 (MO)	D	D	8 / 2	—	—	3 / 2
		USA: Missouri: Washington Co.	Hughes Mountain Natural Area	T.M. Price 202 (MO)	D	D	8 / 2	4 / 2?	2 / 1	7 / 2
		USA: Arkansas: Izard Co.	Along Hwy. 9 near Brandenburg	T.M. Price 285 (MO)	?	?	D	1 / 1	1 / 1	4 / 2
		USA: Arkansas: Izard Co.	Bluffs above White River, S side Calico Rock	T.M. Price 286 (MO)	D	D	D	—	—	D
		USA: Kansas: Lincoln Co.	Wilson Lake State Park	T.M. Price 259 (MO)	D	D	D	3 / 1	n.d.	4 / 2
		USA: Kansas: Ellsworth Co.	Kanapolis State Park, Buffalo Tracks trail to	T.M. Price 260 (MO)	D	D	D	3 / 1	n.d.	D

			Horsethief Canyon							
	cf. calycinus	USA: Arkansas: Conway Co.	Petit Jean State Park, Turtle Rocks	T.M. Price 282 (MO)	D	D	6 / 2	4 / 2?	n.d.	D
	confertiflorus	USA: Arizona: Cochise Co.	Coronado National Forest, just above the Reef waterfall	T.M. Price 248 (MO)	D	D	7 / 2	2 / 1	1 / 1	7 / 2
		USA: Arizona: Gila Co.	Tonto National Forest, E side Parker Creek Chasm	T.M. Price 247 (MO)	?	?	11 / 2	3 / 2	n.d.	8 / 2
		USA: Arizona: Yavapai Co.	Kaibab National Forest, jct. Round Mtn. Bike Loop (FR-138) with FR-105	T.M. Price 254 (MO)	D	D	8 / 2	—	—	10 / 2
		USA: Utah: Wayne Co.	Dixie National Forest, S of Grover on UT-12 btw. mile marker 115 and 114	T.M. Price 292 (MO)	D	D	8 / 3?	3 / 2?	3 / 2	2 / 2
		USA: Utah: Garfield Co.	N side of Panguitch Lake E of Ipson Creek	T.M. Price 301 (MO)	D	D	12 / 2	2 / 2	n.d.	5 / 2
		USA: New Mexico: Guadalupe Co.	Santa Rosa Lake State Park, Rocky Point campground	T.M. Price 320 (MO)	D	D	8 / 2	6 / 2	n.d.	10 / 2
		USA: Texas: El Paso Co.	Franklin Mountains State Park, trail to North Franklin Peak from Mundy's Gap	T.M. Price 317 (MO)	D	D	D	5 / 2?	1 / 1	—
	cf. confertiflorus	USA: Arizona: Mohave Co.	Arizona Strip District, above Hack Reservoir on road 109	T.M. Price 302 (MO)	D	D	3 / 1	1 / 1	n.d.	8 / 2
		USA: New Mexico: Grant Co.	Gila National Forest, Cherry Creek area N of Pinos Altos	T.M. Price 251 (MO)	D	D	8 / 1	3 / 1	1 / 1	8 / 2?
	humilis	Mexico: Queretaro: mpio. Amealco	km 7 de la carretera Amealco-San Ildefonso	Ocampo 1475 (RSA)	D	D	5 / 1	2 / 1	2 / 1	4 / 2
		USA: New Mexico: Grant Co.	Gila National Forest, Cherry Creek area N of Pinos Altos	T.M. Price 252 (MO)	D	D	D	3 / 2?	4 / 2?	5 / 1
	longipes	USA: Texas: El Paso Co.	Franklin Mountains State Park, ridge on Smugglers' Pass Trail to Mammoth Peak	T.M. Price 314 (MO)	D	D	D	1 / 1	n.d.	—
		USA: New	Power Dam Janes-	T.M. Price	D	D	D	5 / 3?	n.d.	6 / 1?

		Mexico: Guadalupe Co.	Wallace Memorial Park, 0.1 mi. S of Santa Rosa city limit on NM-19	321 (MO)						
	mengesii	USA: Tennessee: Marion Co.	Foster Falls TVA recreation site, between Foster Falls and Fiery Gizzard Overlooks	T.M. Price 230 (MO)	D	D	D	5 / 4?	n.d.	—
		(1)	DNA sample ex W. Applequist	(1)	AF194861	D	—	3 / 1	n.d.	D
		USA: Alabama: Blount Co.	jct. Chandler Road and Graves Creek, south of Blountsville	T.M. Price 232 (MO)	D	D	D	7 / 1	1 / 1	D
		USA: Alabama: Winston Co.	Bankhead National Forest, along CR-63 near Houston	T.M. Price 238 (MO)	D	D	D	8 / 1	n.d.	D
		USA: Alabama: Randolph Co.	along AL-77 ca. 3 mi. W of Wadley	T.M. Price 235 (MO)	D	D	D	5 / 1	n.d.	D
	multiflorus	Mexico: Queretaro: mpio. El Marques	ca. 3.5 km de La Laborcilla sobre el camino a Rancho La Yerbabuena	Ocampo & Morales 1484 (RSA)	D	D	4 / 1	2 / 1	3 / 1	4 / 1
		Mexico: Chihuahua: mpio. Basaseachic	Cascada de Basaseachi area on main trail leading to top of falls	D.O. Burge 1254 (DUKE)	D	D	6 / 1	5 / 1	1 / 1	4 / 1
	napiformis		leaf sample ex M. Ogburn	M. Ogburn 266 (MO)	D	D	5 / 1	3 / 2?	4 / 2?	5 / 2?
	parviflorus	USA: Illinois: Johnson Co.	Shawnee National Forest, Trigg Tower	T.M. Price 266 (MO)	D	D	D	6 / 2?	n.d.	D
		USA: Missouri: St. Clair Co.	Dave Rock Natural Area	T.M. Price 255 (MO)	D	D	7 / 1	8 / 1	n.d.	11 / 1
		USA: Missouri: Washington Co.	Mark Twain National Forest, Potosi Ranger District, Little Lost Creek	T.M. Price 217 (MO)	D	D	7 / 1	7 / 1	n.d.	7 / 1
		USA: Oklahoma: Cleveland Co.	S side Alameda Rd. W of 84th Ave. NE	T.M. Price 277 (MO)	?	?	D	2 / 1	n.d.	4 / 1
		USA: Oklahoma: Delaware Co.	Flint Ridge RV Park, SE bank Flint Creek, NE side US-59	T.M. Price 275 (MO)	?	?	8 / 1	11 / 2	n.d.	3 / 1

		USA: Oklahoma: Noble Co.	E side Lake Perry, 2 mi. S of US-77 along N-3180	T.M. Price 278 (MO)	D	D	D	4 / 1	n.d.	D
		USA: Oklahoma: Johnston Co.	ca. 3.6 mi. N of Coleman on Hwy. 48	T.M. Price 280 (MO)	D	D	8 / 1	7 / 1	n.d.	8 / 1
		USA: Arkansas: Conway Co.	Petit Jean State Park, CCC Overlook on Red Bluffs Drive	T.M. Price 283 (MO)	D	D	D	7 / 1	n.d.	D
		USA: Alabama: Coosa Co.	Bluffs above river SE of Mitchell Dam and N of AL-22	T.M. Price 234 (MO)	D	D	D	7 / 1	n.d.	1 / 1
		USA: South Dakota: Minnehaha Co.	Dells of the Sioux Recreation Area, ca. 0.5 mi. S of Dell Rapids	T.M. Price 264 (MO)	D	D	5 / 1	6 / 2?	1 / 1	2 / 1
		USA: South Dakota: Minnehaha Co.	Palisades State Park, bluffs along Split Rock Creek	T.M. Price 333 (MO)	?	?	5 / 1	6 / 1	n.d.	4 / 1
		USA: Kansas: Chautauqua Co.	5.4 air miles NE of Sedan at head of deep ravine	T.M. Price 267 (MO)	?	?	8 / 1	6 / 1	n.d.	1 / 1
		USA: Kansas: Chautauqua Co.	Ca. 2.5 mi. SW of Niotaze, SW corner jct. Dalton Rd. and Road 29	T.M. Price 266 (MO)	?	?	8 / 1	5 / 1	n.d.	2 / 1
		USA: Kansas: Ellsworth Co.	Kanapolis State Park, Buffalo Tracks trail to Horsethief Canyon	T.M. Price 261 (MO)	?	?	8 / 1	7 / 1	n.d.	5 / 1
		USA: Kansas: Reno Co.	Arlington Cemetery, NE edge of Arlington along KS-61	T.M. Price 264 (MO)	D	D	D	5 / 1	n.d.	8 / 1
		USA: Texas: Lee Co.	Lake Somerville State Park, Nails Creek Div.	T.M. Price 304 (MO)	?	?	D	6 / 1	n.d.	D
		USA: Texas: Llano Co.	Enchanted Rock State Natural Area	T.M. Price 243 (MO)	D	D	7 / 1	4 / 1	n.d.	6 / 1
		USA: Texas: Newton Co.	Toledo Village, along Hwy. R255	T.M. Price 325 (MO)	D	D	D	6 / 1	n.d.	D
	parvulus	USA: Arizona: Cochise Co.	Coronado National Forest, Huachuca Mtns., above Ramsey Canyon via Brown Canyon Trail	T.M. Price 249 (MO)	D	D	4 / 1	3 / 1	8 / 3?	7 / 2
		cult. MG	grown at Duke Univ. from seed obtained	T.M. Price s.n. (MO)	D	D	4 / 1	2 / 2?	4 / 2?	6 / 1

			from Mesa Garden, Belen, NM							
	piedmontanus	USA: North Carolina: Granville Co.	Butner Glade	A. Weakley 2010 (NCU)	D	D	8 / 2	—	—	6 / 2
	punae	Argentina: Jujuy	Yavi	Múlgura 4236 (MO)	D	D	8 / 2	—	—	8 / 2
	rugospermus	USA: Nebraska: Buffalo Co.	S side NE-2, 1.1 mi. W of Hall Co. line	T.M. Price 258 (MO)	D	D	4 / 1	3 / 1	4 / 2?	8 / 1
		USA: Kansas: Harvey Co.	Sand Hills Nature Preserve, Harvey County West Park	T.M. Price 262 (MO)	D	D	8 / 2	—	—	—
		USA: Kansas: Reno Co.	Sand Hills State Park, along Dune Trail	T.M. Price 263 (MO)	?	?	4 / 1	5 / 1	3 / 1	6 / 2?
		USA: Oklahoma: Atoka Co.	Boehler Seeps & Sandhills Preserve (TNC)	T.M. Price 279 (MO)	D	D	4 / 1	1 / 1	3 / 1	—
		USA: Texas: Limestone Co.	NW of Personville and SE of Mexia along Hwy. 39	T.M. Price 327 (MO)	D	D	4 / 1	3 / 2?	6 / 2?	D
		USA: Wisconsin: Grant Co.	Blue River Sand Barrens State Natural Area	T.M. Price 240 (MO)	D	D	4 / 1	1 / 1	6 / 2	2 / 2
		USA: Wisconsin: Sauk Co.	Spring Green Preserve State Natural Area	T.M. Price 241 (MO)	D	D	D	1 / 1	1 / 1	D
	cf. rugospermus	USA: Texas: Leon Co.	SE corner of jct. FR-1469 and FR-1146, 6.1 mi. W of Newby	T.M. Price 328 (MO)	D	D	D - 2	—	—	D
	sediformis	USA: Washington: Ferry Co.	Colville National Forest, Republic Ranger District, along Rattlesnake Road FSR-5320	T.M. Price 271 (MO)	D	D	D	6 / 3?	n.d.	8 / 2
		USA: cult. SRPN	Cultivated plant obtained from Siskiyou Rare Plants Nursery, Talent, OR	T.M. Price s.n. (MO)	D	D	2 / 1	10 / 1	n.d.	D
	spinescens	USA: Washington: Lincoln Co.	3.5 road mi. SSE of Swanson Lake Wildlife Area entrance along Seven Springs Dairy Rd.	T.M. Price 270 (MO)	D	D	7 / 4?	5 / 3?	n.d.	7 / 3?

		USA: Washington: Lincoln Co.	3.5 road mi. SSE of Swanson Lake Wildlife Area entrance along Seven Springs Dairy Rd.	T.M. Price 270B (MO)	?	?	8 / 3	5 / 2?	2 / 1	7 / 2
		cult. SRPN	Cultivated plant obtained from Siskiyou Rare Plants Nursery, Talent, OR	T.M. Price s.n. (MO)	D	D	13 / 1	5 / 2?	n.d.	D
	teretifolius	USA: Georgia: Johnson Co.	Rock Springs Rd. (CR-140) 3 mi. E of Wrightsville	M. Ogburn 4 (MO)	D	D	12 / 4	1 / 1	n.d.	9 / 2
		USA: North Carolina: Wake Co.	E side Little River on SW side Zebulon Rd. (NC-96)	T.M. Price 272 (MO)	D	D	12 / 2	2 / 2	1 / 1	8 / 2
		USA: North Carolina: Granville Co.	Butner Glade	A. Weakley 2010 (NCU)	D	D	13 / 4	3 / 3?	3 / 2	6 / 3
	thompsonii	USA: Utah: Emery Co.	Cedar Mountain	T.M. Price 288 (MO)	D	D	5 / 2	4 / 3?	n.d.	4 / 2
	validulus	USA: Arizona: Coconino Co.	Kaibab National Forest, Williams Ranger District, S of jct. FR-105 and 354	T.M. Price 303 (MO)	D	D	1 / 1	4 / 2	n.d.	6 / 2
Calandrinia	*ciliata*			(1)	AF194835	—				
	compressa			(1)	AF194836	—				
Calyptridium	*umbellatum*			(1)	AF194840	—				
Cistanthe	*grandiflora*			(1, 3)	AF194842	AY042568				
	guadalupensis	cult. MG	grown at Duke Univ. from seed obtained from Mesa Garden, Belen, NM	T.M. Price s.n. (MO)	D	D		3 / 3	1 / 1	8 / 2
	mucronulata			(1)	AF194843	—				
Claytonia	*perfoliata*	USA: California: Santa Clara Co.	Stanford University Arboretum	T.M. Price 336 (MO)	D	—		#2 / 1	#n.d.	
	virginica	USA: Missouri: St. Louis City	Forest Park	T.M. Price 223 (MO)	D	D				
	virginica	USA: North Carolina: Durham Co.	Duke Forest	T.M. Price 337 (MO)	D	D		#5 / 4	#n.d.	
Hectorella	*caespitosa*			(2)	DQ093963	DQ267197				
Lewisia	*pygmaea*	USA: Utah:	along ridge between	T.M. Price	D	—		#3 / 2	#n.d.	3 / 2

			Salt Lake Co.	AF Twin Peaks	300 (MO)		
	Montia	*diffusa*			(1)	AF194848	—
		parvifolia			(1)	AF194851	—
	Montiopsis	*cumingii*			(1)	AF194850	—
		umbellata			(1)	AF194837	—
Talinaceae	*Talinum*	*aurantiacum*	USA: Texas: Val Verde Co.	5 mi. N of Juno at jct. TX-163 and ranch road 189	T.M. Price 307 (MO)	D	D
			USA: Texas: El Paso Co.	Franklin Mountains State Park, trail to North Franklin Peak from Mundy's Gap	T.M. Price 318 (MO)	D	D
			USA: New Mexico: Guadalupe Co.	Power Dam Janes-Wallace Memorial Park, 0.1 mi. S of Santa Rosa city limit on NM-19	T.M. Price 322 (MO)	D	D
		angustissimum		DNA sample ex W. Applequist	(1)	AF194866	D
		polygaloides			(5)	DQ855867	DQ855845
		caffrum			(1, 3)	AF194859	AY042662
		fruticosum			(5)	DQ855865	DQ855844
		portulacifolium			(5)	DQ855869	DQ855847
		paniculatum			(1)	AF194830	—
		paniculatum (as T. patens)			(1)	AF194864	—
	Talinella	*pachypoda*		leaf sample ex M. Ogburn	(6)	D	D
Portulacaceae	*Portulaca*	*bicolor*			(5)	DQ855870	DQ855848
		grandiflora			(1)	AF194853	—
		molokiniensis			(1)	AF194854	—
		mundula			(1)	AF194855	—
		oleracea	USA: Missouri: St. Louis City	Washington Univ. Danforth Campus	T.M. Price 224 (MO)	D	D
		pilosa	USA: Texas: Val Verde Co.	along Hwy. 163 ca. 31.5 mi. S of Ozona	T.M. Price 306	D	D
Cactaceae	*Maihuenia*	*patagonica*			(4)	AY015281	—
	Pereskia	*aculeata*			(1, 2)	AF194852	AY042626
	Quiabentia	*verticillata*			(1, 2)	AF194858	AY042641
Anacampserotaceae	*Grahamia*	*bracteata*			(1, 4)	AF194846	AY015273

Didiereaceae	*Calyptrotheca*	*somalensis*	(1, 3)	AF194839	AY042563
	Ceraria	*fruticulosa*	(1)	AF194841	—
	Decarya	*madagascariensis*	(1, 3)	AF194844	AY042574
	Portulacaria	*afra*	(1, 3)	AF194857	AY042637
Basellaceae	*Basella*	*alba*	(1, 3)	AF194834	AY042553
	Ullucus	*tuberosus*	(1)	AF194865	—

References—

Applequist, W. L. and R. S. Wallace. 2001. Phylogeny of the portulacaceous cohort based on *ndhF* sequence data. *Systematic Botany* 26: 406-419.

Applequist, W. L., W. Wagner, E. A. Zimmer, and M. Nepokroeff. 2006. Molecular evidence resolving the systematic position of *Hectorella* (Portulacaceae). *Systematic Botany* 31: 310-319.

Cuenoud, P., V. Savolainen, L. W. Chatrou, M. Powell, R. Grayer, and M. Chase. 2002. Molecular phylogenetics of Caryophyllales based on nuclear 18S rDNA and plastid *rbcL*, *atpB*, and *matK* DNA sequences. *American Journal of Botany* 89: 132-144.

Nyffeler, R. 2002. Phylogenetic relationships in the cactus family (Cactaceae) based on evidence from *trnK/matK* and *trnL-trnF* sequences. *American Journal of Botany* 89: 312-326.

Nyffeler, R. 2007. The closest relatives of cacti: insights from phylogenetic analyses of chloroplast and mitochondrial sequences with special emphasis on relationships in the tribe Anacampseroteae. *American Journal of Botany* 94: 89-101.

Ogburn, R. M. and E. J. Edwards. 2009. Anatomical variation in Cactaceae and relatives: Trait lability and evolutionary innovation. *American Journal of Botany* 96: 391-408.

<u>APPENDIX 2. PRELIMINARY TAXONOMIC TREATMENT</u>

Abstract—The genus *Phemeranthus* Raf. (Montiaceae) is summarized, and a preliminary taxonomic treatment of infrageneric taxa and species is presented. *Phemeranthus* has traditionally been included in the genus *Talinum* Adans. as *Talinum* sect. *Phemeranthus*, but morphological and molecular evidence indicate that the two groups are not closely related. Herein, two sections are recognized within *Phemeranthus*: sect. *Phemeranthus* and sect. *Eutmon*. Synonymies and brief descriptions are provided for each species, with notes on putative undescribed species. An identification key is also included. New nomenclatural combinations and species names included herein are not to be considered as published but may be included in a later formal revision.

***Taxonomic Overview of* Phemeranthus**—The genus *Phemeranthus* Raf. has recently been resurrected to accommodate the terete- to subterete-leaved species of Talinum Adans. (Portulacaceae sens. lat.) (Hershkovitz and Zimmer 1997; Kiger 2001; Ocampo 2002, 2003). *Phemeranthus* species, which are primarily found in temperate North America, differ in numerous morphological features from the flat-leaved *Talinum* sens. str., which are primarily from semi-arid subtropical and tropical regions of North and South America and southern Africa. Morphological and molecular data clearly show that *Phemeranthus* is not closely related to *Talinum* sens. str. (Carolin 1987; Hershkovitz 1993; Hershkovitz and Zimmer 1997, 2000; Applequist and Wallace 2001; Nyffeler and Eggli 2010). Most terete-leaved *Talinum* species distributed in the United States and Mexico, as well as a disjunct species from northern Argentina, have now been transferred to *Phemeranthus* (Hershkovitz and Zimmer 1997; Kiger 2001; Ocampo 2002, 2003; Nyffeler and Eggli 2010; Price and Ferguson In Press).

The traditional Portulacaceae is paraphyletic with respect to Cactaceae and possibly Didiereaceae, Basellaceae, and Halophytaceae. To address this paraphyly, multiple well-supported clades within Portulacaceae sens. lat. and allied families (i.e., suborder Portulacineae) have now been recognized at the family level (APG III 2009; Nyffeler and Eggli 2010; Ocampo and Columbus 2010). Phylogenetic analyses using nuclear (ITS) and chloroplast (*ndhF*, *matK*) DNA sequence data have shown that *Talinum* sens. str. is more closely related to *Portulaca* and Cactaceae than to *Phemeranthus*, which falls within a clade of predominantly western North American taxa (Hershkovitz and Zimmer 1997, 2000; Applequist and Wallace 2001; Applequist et al. 2006) that has been elevated to family level as Montiaceae (APG III 2009; Nyffeler and Eggli 2010). *Talinum*, *Talinella* Baill., and the monotypic taxon *Amphipetalum* Bacigalupo constitute the small family Talinaceae (Nyffeler and Eggli 2010), and Portulacaceae sens. str. now comprises only the single genus *Portulaca* L. (APG III 2009; Nyffeler and Eggli 2010).

The type species of *Phemeranthus* was first validly described by Frederick Pursh in 1814 as *Talinum teretifolium* Pursh. Constantine Rafinesque had published the name *Phemeranthus teretifolius* in 1808, but the name was invalid (nomen nudum) because no type was specified. Believing the new species to be sufficiently distinct from *Talinum* as to merit its own genus, Rafinesque validated the generic name *Phemeranthus* when he published the combination *P. teretifolius* (Pursh) Raf. in 1814. In 1828, Augustin Pyramus de Candolle described *Talinum napiforme* DC., establishing *Talinum* sect.

Phemeranthus to accommodate it and *T. teretifolium*. Believing that *T. napiforme* also warranted its own generic ranking, Rafinesque published the combination *Eutmon napiforme* (DC.) Raf. in 1833. Like much of Rafinesque's work, the generic names *Phemeranthus* and *Eutmon* were generally ignored by subsequent workers. Although most authors followed De Candolle in treating the terete-leaves species as *Talinum* sect. *Phemeranthus*, von Poellnitz (1934) did not recognize any basis for maintaining this sectional division in his monograph, the most recent for *Talinum*. Numerous additional terete-leaved species have been described since 1828; the most recent is *Phemeranthus piedmontanus* Ware, published in 2011.

***Characteristics of* Phemeranthus *and* Talinum—**

Overall, *Phemeranthus* is characterized by terete to subterete leaves; a slender, wiry, scape-like peduncle (reduced in some species); and pantocolpate pollen. Each of these traits may be found in other Portulacaceous genera, but they are rarely combined in one genus. *Phemeranthus* also possesses a trait that is unique among Portulacineae, a funicular aril or pellicle (a thin, chartaceous membrane) covering the seed.

The flowers open at a particular time of day (which varies among species and populations but is usually in the afternoon) and remain open for only one or a few hours on a single day. These ephemeral flowers are probably the basis of the name *Phemeranthus* and of some species' vernacular names, such as "fameflower". The Greek "phimi" (φημη) + "anthos" (ανθος) literally means "fameflower". Rafinesque may have meant to combine "anthos" with the Greek "ephimeros" (εφημερος), which is equivalent to the English "ephemeral". "Fameflower" is often mistakenly transformed into “flameflower” in horticultural literature. Other vernacular names for *Phemeranthus* species include “rockpink”, “rockrose”, “sandpink”, and “sunbright”.

Phemeranthus and *Talinum* share several traits that can be considered typical of Portulacineae in general. They are primarily succulent, herbaceous perennials (sometimes suffrutescent, becoming woody with age) with fleshy, tuberous taproots. Their inflorescences are cymose, and each flower is subtended by a pedicel, usually with a pair of reduced bracts at the base. The flowers have two foliaceous or scarious sepals (actually sepaloid bracts), which may be deciduous or persistent in fruit, and usually five petals (tepals). The number of stamens ranges from equal to the petals up to 60 or more. The slender style is topped by three short, spreading to capitate stigmas. The fruits are unilocular, three-valved capsules that dehisce longitudinally and often circumscissilely at the base. The seeds are reniform with coiled embryos and borne on free-central placentae.

Despite these shared traits, *Talinum* and *Phemeranthus* are highly distinct. In *Phemeranthus*, the palisade mesophyll extends all the way around the leaf (see Ocampo and Columbus 2010, Fig. 5H), and the midvein is not externally visible. The leaves are sometimes slightly dorso-ventrally compressed, and young leaves that have been appressed in winter buds may be nearly planar adaxially with angular edges (D-shaped in cross-section). However, there is no defined lateral margin. *Talinum* species possess flattened leaves with palisade mesophyll only on the adaxial side. Although the margins may be revolute, particularly under drought conditions, at least the midvein is prominently visible.

Phemeranthus capsules are usually held erect or nearly so (rarely pendent) and dehisce basipetally. The valves persist briefly after dehiscence in some species and disintegrate upon maturity in others. The endocarp and exocarp are not differentiated. The seeds are enclosed by a chartaceous membrane of funicular origin (“pellicle”). *Talinum* capsules are pendent to horizontal on curved pedicels and dehisce acropetally. The exocarp and endocarp are differentiated and sometimes separate at maturity. The seeds are strophiolate but lack an investing pellicle.

Phemeranthus species are found primarily in North America, with a center of diversity in the southwestern United States and northern Mexico. East of the Rocky Mountains, the range of the genus extends across the Great Plains to the Mississippi River and north to the Dakotas. Across the Mississippi Embayment, *Phemeranthus* species are found in the Central Basin of Tennessee; in the Piedmont of Alabama, Georgia, and the Carolinas; and in Appalachian shale and serpentine barrens north to Pennsylvania. Two species are located in the inland Northwest, on the Columbia Plateau and in the Okanagan region extending into British Columbia, Canada. The genus’ range in Mexico extends south to the Isthmus of Tehuantepec. One species is disjunct in the southern Andes, in the Puna region of northern Argentina and southern Bolivia.

Fameflowers typically grow on shallow substrates over exposed rock on flatrocks, glades, ledges, hilltops, and cliffs. These habitats are characterized by full sun, mineral-based soils with little organic matter, and reduced competition from surrounding vegetation. The genus is unknown from coastal regions, except for sandy hills along part of the Texas Gulf Coast around Galveston Island. The plants are active during warm weather, usually dying back to a shallowly subterranean tuber, rhizome, or caudex during the winter and resuming growth after spring rains (in the midwestern and southeastern

United States) or after summer rains (in desert climates). They are highly drought-resistant and may remain dormant in particularly dry years.

Although they are among the most charismatic summer-flowering plants of their patchy, xeric rock-outcrop and sand-barren habitats, *Phemeranthus* species have long been taxonomically confusing and commonly misidentified in herbaria. This difficulty is due in part to the poor preservation of many herbarium specimens; the succulent leaves and stems, ephemeral flowers, and stout, tuberous roots or rhizomes tend to dry poorly, and few sheets preserve the necessary combination of vegetative, floral, fruit, and seed characters for confident identification. Leaves in pressed herbarium specimens often appear to have translucent lateral margins, and some species have been mistakenly described as having flat, marginate leaves. Indeed, Greene (1912) published the name *Talinum marginatum* (= *Phemeranthus parvulus*; see below) based upon such an error.

Several fameflower species are quite attractive and have long been grown by succulent-plant fanciers and rock gardeners. Today, some *Phemeranthus* species are increasingly popular in native-species-based, water-conservative gardening and green-roof plantings (e.g., Getter et al. 2009; Dvorak 2010). Therefore, it is critical to resolve the confusion surrounding the taxonomy of and species identification within this genus.

***Infrageneric Classification of* Phemeranthus—**

Phemeranthus can be divided into two well-defined sections (Clades 1 and 2 in CHAPTER II), sect. *Phemeranthus* and sect. *Eutmon*. These sections are morphologically and geographically distinct. Members of sect. *Phemeranthus* are found predominantly in the United States, extending into northern Chihuahua, Coahuila, and Sonora, Mexico, and southern British Columbia, Canada. The plants are distinctly caulescent, usually with visible internodes. They may have long, tapering, tuberous taproots; narrowly napiform or branching tuberous rootstocks; thickened, branching rhizomes, or amorphous, often shallowly subterranean, perennial caudices. The flowers range from white through pink to magenta. In most species, the fruit valves persist for some time after dehiscence. The seed testa is nearly smooth in most species, with a pattern of low convexities, although the pellicle may be wrinkled.

Members of sect. *Eutmon* are found predominantly in northern and central Mexico, extending into Arizona and New Mexico, U.S.A., and with a disjunct species in northern Argentina. The plants appear acaulescent, with the leaves forming a basal rosette. The rootstock is always tuberous, sometimes napiform, but often globose. The flowers are typically yellow, though some species have white flowers. The fruits normally disintegrate at maturity. The seed testa exhibits a series of raised concentric ridges, although these may be obscured by the pellicle.

Synonymy and Descriptions of Infrageneric Taxa and Species—

***Phemeranthus* Raf.** TYPE: *Phemeranthus teretifolius* (Pursh) Raf., Specchio delle Scienze 1: 86, 1814.

Phemeranthus Raf., nom. nud., Medical Repository 5: 350, 1808.

Litanum Nieuwl. TYPE: *Litanum parviflorum* (Nutt.) Nieuwl., American Midland Naturalist 4: 90, 1915.

Talinum sect. *Phemeranthus* (Raf.) DC., Prodromus Systematis Naturalis Regni Vegetabilis 3: 357, 1828.

Eutmon Raf. TYPE: *Eutmon napiforme* (DC.) Raf., Atlantic Journal 177, 1833.

***Phemeranthus* sect. *Phemeranthus*, stat. nov.**

Perennial stems generally short and subterranean (aboveground and suffrutescent in *P. spinescens* and *P. sediformis*), borne atop a thickened rootstock. Annual stems erect or prostrate, usually with visible internodes (compressed internodes concealed by leaves in *P. brevifolius* and *P. sediformis*). Leaves terete (or somewhat dorso-ventrally flattened), generally crowded on lower stems, spreading to ascending, glabrous and often glaucous. Inflorescences cymose, appearing terminal or axillary, generally with wiry, scape-like peduncles (subsessile in *P. brevifolius*); many-flowered dichasia or single- to few-flowered reduced cymes, erect or sprawling and usually well exceeding the height or spread of the leafy stems. Stamens 5 (4–8) to 60+. Distributed from northern Mexico to southern British Columbia and from the Rocky Mountains to the Carolina Piedmont.

***Phemeranthus brevicaulis* (S. Watson) Kiger**, Novon 11(3): 319, 2001.

Talinum brevicaule S. Watson, Proceedings of the American Academy of Arts and Sciences 21(2): 446, 1886. TYPE: Mexico, Chihuahua, Santa Eulalia Mountains, 20 May 1885, *C. G. Pringle 26* (holotype, GH not seen; isotype, US).

Talinum pulchellum Wooton & Standl., Contributions from the United States National Herbarium 16(4): 121, 1913. TYPE: U.S.A., New Mexico, Queen, 2 Aug 1909, *E. O. Wooton s.n.* (holotype, US).

Talinum eximium A. Nelson, American Journal of Botany 18(6): 431, 1931. TYPE: U.S.A., New Mexico, Carlsbad Caverns, *G. Convis 56* (holotype, RM).

Talinum youngiae C. H. Mull., Torreya 33(6): 148–149, 1933 [as "*Youngae*"]. TYPE: U.S.A., Texas, Cat Tail Cañon, Chisos Mtns., 6 July 1932, *C. K. Muller 8571* (holotype, NY ex TEX; isotype, F not seen).

SHOWY FAMEFLOWER

Plants spreading to ascending; stems stout, branched, sometimes woody. Roots often highly branched, fusiform, fleshy, woody. Leaves 10–30 mm long, upturned, acute; lower leaves often awl-shaped. Inflorescences 1- to several-flowered, cymose, on short (5–15 mm) peduncles. Sepals broadly lanceolate, acuminate, often reflexed at tips, persistent in fruit, exceeding the capsules. Petals large, showy (10–16 mm), light pink to magenta. Stamens ca. 20, usually shorter than style. Stigma subcapitate. Capsules football-shaped, 5–7 mm long. Seeds smooth, ca. 1 mm wide. $2n = 24$ (Ward and Spellenberg 1986). Chihuahuan desert, grassland, and open woodland, ca. 1500-3000 m, on limestone and igneous substrates; New Mexico, trans-Pecos Texas, northern Coahuila and Chihuahua.

***Phemeranthus brevifolius* (Torr.) Hershkovitz**, Taxon 46(2): 222, 1997

Talinum brevifolium Torr., in Sitgreaves, Report of an Expedition down to the Zuni and Colorado Rivers 156, 1853. TYPE: U.S.A., Arizona, Camp No. 6 on the Little Colorado [River], 29 Sep 1851, *S.W. Woodhouse s.n.* (Holotype, NY).

Talinum brachypodum S. Watson, Proceedings of the American Academy of Arts and Sciences 20: 355, 1885. TYPE: U.S.A., New Mexico, Laguna Pueblo, July 1884, *Mr. & Mrs. J.G. Lemmon s.n.* (Holotype, ?)

Claytonia brevifolia (Torr.) Kuntze, Revisio Generum Plantarum 1: 57, 1891.

CANYONLANDS FAMEFLOWER, PYGMY FAMEFLOWER

Plants spreading, often mat-forming; stems branched, sometimes woody. Roots elongate, often highly branched, woody. Leaves subterete, usually somewhat flattened, blunt, crowded along stems, upturned and concealing internodes, usually glaucous and reflective. Inflorescences 1- or occasionally 2–3-flowered, appearing subsessile. Sepals orbicular to ovate, deciduous. Petals obovate, 8–12 mm, rose pink to magenta, sometimes smaller and creamy white. Stamens ca. 20–25, usually much shorter than style. Stigma 3-lobed, the lobes spreading. Capsules globose to ellipsoid, 3–4 mm long. Seeds smooth, usually appearing gray, ca. 1 mm wide. Colorado Plateau, ca. 1500-2200 m, in shallow deposits of fine sand overlying sandstone slopes and ledges; southeastern Utah, northeastern Arizona, and northwestern New Mexico.

Plants from calcareous substrates in central New Mexico are larger in vegetative and floral proportions and have been described as *T. brachypodum* S. Watson. With further study, this entity may merit specific recognition, which would necessitate publication of the combination *Phemeranthus brachypodus*. A population from shallow clay soil over conglomerate rock north of Reserve, Catron Co., New Mexico is reported to have exceptionally long, slender rhizomes and shiny black seeds and may also deserve recognition as a new species (D. J. Ferguson, pers. comm.).

***Phemeranthus calcaricus* (S. Ware) Kiger**, Novon 11(3): 320, 2001.

Talinum calcaricum S. Ware, Rhodora 69(780): 466–474, 1967. TYPE: U.S.A., Tennessee, Davidson Co., Mountain View School, 21 Aug 1966, *S. Ware 215* (Holotype, US; isotypes, C not seen, SMS, UT not seen, VDB).

LIMESTONE FAMEFLOWER

Plants tall (to 25 cm), erect; stems stout, sparingly branched, arising from amorphous, tuberous rhizomes at soil surface. Vegetative propagules produced on lower stems in fall. Leaves terete, to 5 cm long. Inflorescences many-flowered, dichasial or polychasial, sometimes appearing monochasial distally, on erect, wiry, straw-colored, scape-like peduncles. Sepals ovate, persistent in fruit. Petals about 1/2 as wide as long, 8–10 mm, purplish pink. Stamens 25–45, ca. 3/4 length of style. Stigma 3-lobed, the lobes nearly erect. Capsules ovoid, 4–6 mm long. Seeds smooth, appearing gray, ca. 1.2 mm wide. $2n = 48$. Central Basin of Tennessee, ca. 100-400 m, shallow soil on limestone cedar glades; central Tennessee, northern Alabama, extreme southern Kentucky.

This species is similar to *P. calycinus* from eastern Missouri, and molecular and cytological evidence indicates that it is derived from that species by autotetraploidy (Murdy and Carter 2001).

***Phemeranthus calycinus* (Engelm.) Kiger**, Novon 11(3): 320, 2001.

Talinum calycinum Engelm., in F.A. Wislizenus, Memoir of a Tour to Northern Mexico: connected with Col. Doniphan's Expedition in 1846 and 1847: 88, 1848. TYPE: U.S.A., [Kansas or Oklahoma], in sandy soil on the Cimarron [River], June 1846, *F.A. Wislizenus s.n.* (holotype, MO).

Claytonia calycina (Engelm.) Kuntze, Revisio Generum Plantarum 1: 57, 1891.

LARGE-FLOWERED FAMEFLOWER, OZARK FAMEFLOWER, ROCKPINK

Plants usually tall (to 40 cm), erect; stems stout, sparingly or densely branched, arising from amorphous, shallowly subterranean tuberous rhizomes; horizontally branching rhizomes near the soil surface; or deeply buried fusiform tuberous taproots. Leaves terete, to 7 cm long. Inflorescences many-flowered, dichasial or polychasial, sometimes appearing monochasial distally, on erect, wiry, straw-colored, scape-like peduncles. Sepals ovate to sub-triangular, persistent in fruit. Petals 10-15 mm long, bright pink to dark magenta. Stamens 25–45, from about 1/2 to nearly equal the length of the style. Stigma 3-lobed, the lobes variously spreading or subcapitate. Capsules ovoid to globose, 4–7 mm long. Seeds smooth, appearing gray or black, ca. 1 mm wide. $2n = 24$, 48. Great Plains and Interior Highlands, ca. 100-1200 m, sandhills or shallow soil on usually non-calcareous rock outcrops and glades; Colorado south to Texas and east to the Mississippi River (with isolated occurrences in western Illinois).

Most populations are diploid, while some are tetraploid. Autotetraploidy in eastern *P. calycinus* probably gave rise to *P. calcaricus* (Murdy and Carter 2001), and certain populations in northern Arkansas closely resemble the latter species (Kiger 2003).

Populations on limestone and dolomite substrates in southwestern Missouri and eastern Kansas may have a similar origin (Reinhard and Ware 1989).

As presently recognized, this species is highly variable and taxonomically confusing. Plants from sandhill areas of the Great Plains in Colorado, New Mexico, Texas, Oklahoma, Kansas, and Nebraska possess thick, elongated, fusiform tuberous taproots and lack shallow rhizomes or caudices. They tend to have longer leaves, taller and thicker peduncles, and (often dramatically) larger flowers, which may be fragrant (D. J. Ferguson, pers. comm.). The sepals appear thickened and scarious in fruit. These plants correspond to the type specimen and could be considered *P. calycinus* sens. str.

Plants from the Ozark and Boston Mountains in northern Arkansas, southern Missouri, eastern Kansas, and northeastern Oklahoma are distinguished by highly branched stems borne on amorphous, shallowly subterranean rhizomes or caudices; secondary roots arising directly from the rhizome, without a tuberous taproot except in immature plants; and smaller, dark magenta flowers. Cultivated *P. calycinus,* which are popular with native-plant gardeners and are attracting attention as green-roof components, belong to this group. As a putative segregate species, these plants have been informally called *Phemeranthus ozarkensis,* but no name has yet been published.

Plants from the Ouachita Mountains of west-central Arkansas and adjacent Oklahoma resemble *P. mengesii* in having subcapitate to short-lobed (rather than distinctly 3-lobed) stigmas and sepals that tend to be deciduous. These plants are often shorter in stature than other *P. calycinus* but may form dense clumps with many annual stems arising from the thick, glossy, horizontal, branching rhizomes that lie at the soil surface. These populations may also merit recognition as a new species.

***Phemeranthus confertiflorus* (Greene) Hershkovitz**, Taxon 46(2): 222, 1997.

Talinum confertiflorum Greene, Bulletin of the Torrey Botanical Club 8(11): 121, 1881. TYPE: U.S.A., New Mexico, Pinos Altos Mountains, 13 Sep 1880, *E.L. Greene s.n.*; lectotype (first-step), Wooton & Standley, Contr. U.S. Natl. Herb. 19: 233, 1915; (second-step), Holmgren, Brittonia 62: 266, 2010 (lectotype, NDG not seen; isolectotype, NY).

Talinum gracile J. N. Rose & Standl., nom. illeg. hom. [non Colla, 1833], Contributions from the United States National Herbarium 13(8): 285, 1911. TYPE: Mexico, Chihuahua, "thin soil of granitic ledges; La Bufa Mt. above Cusihuiriachic", 31 Aug 1887, *C.G. Pringle 1197* (holotype, US; isotypes, MO, NY).

Talinum rosei P. Wilson, North American Flora 21(4): 287, 1932. nom. nov. for *Talinum gracile* J. N. Rose & Standl.

Talinum gooddingii P. Wilson, North American Flora 21(4): 287, 1932 [as "*Gooddingii*"]. TYPE: USA, Arizona, Greenlee Co., Boyle's, San Francisco River, 5 Aug 1912, *L.N. Goodding 1282* (holotype, NY)

Talinum fallax Poelln., Berichte der Deutschen Botanischen Gesellschaft 51(2): 113, 1933. SYNTYPES: USA, New Mexico, Sierra Co., Rab's [Robs] Canyon, s. end of Black Range, 6500 ft., 20 Aug 1904, *O.B. Metcalfe 1238* (NY); USA, Arkansas, *H.K. Beyrich s.n.* (not seen)

ROCKY MOUNTAIN FAMEFLOWER, SUNBRIGHT

Plants 5–25 cm tall, rarely taller, erect; stems short, slender, sparingly branched, arising from an elongated, fleshy taproot. Leaves usually tightly clustered, sometimes flattened adaxially, 1–5 cm long. Inflorescences many-flowered, congested, on erect, wiry, straw-colored, scape-like peduncles; pedicels stout, usually green. Sepals broadly ovate, acute to acuminate-cornate, usually dark purplish apically and slightly reflexed, often persistent in fruit. Petals 3.5–7 mm long, white to pale pink. Stamens (4–)5(–10), equal the length of the style. Stigma capitate or minutely 3-lobed. Capsules ovoid to oblong, often obtusely triquetrous, usually persisting for a short time after dehiscence, 3–5 mm long. Seeds smooth, appearing dark gray, ca. 0.7–1 mm wide. $2n = 48$ (Ward and Spellenberg 1986). Western Great Plains and southwestern grasslands to mountain woodlands, ca. 1500-2700 m, shallow, sandy or rocky soils over usually non-calcareous rock; southwestern South Dakota, eastern Wyoming, Colorado, central and southern Utah, Arizona, New Mexico, trans-Pecos Texas, to central Chihuahua and northeastern Sonora, Mexico.

This species has generally been treated as a synonym of *P. parviflorus* (Nutt.) Kiger, to which it is closely related. It is distinguished by its more congested inflorescences; pointed, often purple-tipped and reflexed sepals; grayish seeds; and ploidy level [although tetraploid *P. parviflorus* has been reported from Arkansas (Steiner 1944)]. *P. confertiflorus* often grows sympatrically with *P. brevicaulis*, *P. brevifolius*, *P. calycinus*, and *P. validulus* and has been observed to hybridize with *P. validulus* in northern Arizona and central Utah. It also grows sympatrically with species of sect. *Eutmon* in southern Arizona and New Mexico and northern Mexico.

Plants of northern Mexico identified as *Talinum gracile* or *Talinum rosei* are distinguished by their massively thickened, highly branched, tangled, woody roots and strongly reflexed, dark-striped sepals. Recognition as a separate species would necessitate publication of the combination *Phemeranthus rosei*.

***Phemeranthus longipes* (Wooton & Standl.) Kiger**, Novon 11(3): 320, 2001.

Talinum longipes Wooton & Standl., Contributions from the United States National Herbarium 16(4): 120–121, 1913. TYPE: U.S.A., New Mexico, Tortugas Mountain, 27 Aug 1894, *E.O. Wooton s.n.* (holotype, US)

TORTUGAS FAMEFLOWER

Plants 5–15 cm tall, erect; stems gracile, sparingly branched, grayish, often clothed with stiff, spiny persistent leaf bases; arising from an elongate, fusiform, woody, sometimes branching taproot. Leaves 1–2.5 cm long, glaucous. Inflorescences several-flowered, cymose, on erect, scape-like peduncles. Sepals broadly orbicular, often pinkish in color, deciduous. Petals pale pink, obovate, 4–5 mm long. Stamens 5 or 10, equal the length of the style, the filaments bright pink, contrasting with the lighter petals. Stigma 3-lobed. Capsules subglobose, 2.5–4 mm long, often persisting after dehiscence. Seeds appearing gray with pellicle intact, with strongly raised concentric ridges on the testa, ca. 1 mm wide. Chihuahuan Desert region, rocky limestone soils on slopes and ridges, ca. 1600-2000 m; north-central New Mexico and trans-Pecos Texas south to northern Coahuila, Chihuahua, and Tamaulipas, Mexico.

P. longipes specimens are often misidentified as depauperate individuals of *P. parviflorus* or *P. confertiflorus*. However, living plants are easily distinguishable in flower or fruit by their sepal and petal shape, stamen color, fruit shape, and ridged seeds.

***Phemeranthus mengesii* (W. Wolf) Kiger**, Novon 11(3): 320, 2001.

Talinum mengesii W. Wolf, American Midland Naturalist 6(8): 153–155, 1920 [as "*Mengesii*"]. TYPE: U.S.A., Alabama, Cullman Co., cliff banks, Little River, no date, *W. Wolf 1668* (holotype, SB transferred to AUA not seen).

MENGES' FAMEFLOWER OR ROCKPINK

Plants tall (to 40 cm), erect to spreading; stems stout, fleshy, branching above with usually multiple branches from a single point, arising from amorphous, fleshy to woody rhizomes near the soil surface. Leaves to 8 cm long. Inflorescences open, many-flowered dichasia or polychasia, often appearing monochasial distally late in the season, on wiry, straw-colored, scape-like peduncles. Leaf clusters sometimes present at nodes of inflorescence; vegetative propagules produced within the inflorescence in some populations (Carter and Murdy 1986). Sepals ovate, 3–4 mm, deciduous in fruit. Petals 9–15 mm long, about 1/2 as wide as long, rose pink. Stamens (35–)45-60(–90), spreading to erect. Stigma subcapitate, somewhat exceeding the stamens. Capsules subglobose, 3–4 mm long, disintegrating at maturity. Seeds black, ca. 0.8 mm wide. $2n = 24$ (rarely 48). Southern Appalachia and Piedmont, sandstone and igneous outcrops, glades, ledges, and flatrocks; ca. 100–1000 m; northern and central Alabama and adjacent Tennessee, Georgia, and Kentucky.

This species sometimes grows in sympatry with *P. teretifolius*, an allotetraploid species derived from hybridization between *P. mengesii* and *P. parviflorus* (Black and Murdy 1972; Carter and Murdy 1985; Murdy and Carter 1985, 2001). Where the two species are found together, the predominantly outcrossing *P. mengesii* exhibits reproductive character displacement (Murdy et al. 1970; Carter and Murdy 1986).

***Phemeranthus parviflorus* (Nutt.) Kiger**, Novon 11(3): 320, 2001.

Talinum parviflorum Nutt., in J. Torrey and A. Gray, A Flora of North America 1(2): 197, 1838. TYPE: U.S.A., Arkansas, on rocks, no date, *T. Nuttall s.n.* (possible isotypes or syntypes, K, image seen).

Claytonia nuttalliana Kuntze, Revisio Generum Plantarum 1: 57, 1891. nom. nov. meant to replace *T. parviflorum* Nutt. [as “*T. parvifolium* Nutt.”, sic] under *Claytonia*. The nom. nov. was meant to avoid homonymy with *Claytonia parvifolia* Moçiño, although *Claytonia parviflora* would actually have been a homonym of *Claytonia parviflora* Douglas ex Hook., 1832.

Litanum parviflorum (Nutt.) Nieuwl., American Midland Naturalist 4: 90, 1915.

Talinum appalachianum W. Wolf, American Midland Naturalist 22(2): 319–320, 1939.

SUNBRIGHT, SMALL-FLOWERED FAMEFLOWER, PRAIRIE FAMEFLOWER

Plants 5-20 cm tall, rarely taller, erect; stems slender, simple or branching, arising from an elongate, fusiform, fleshy taproot. Leaves 2–7 cm long. Inflorescences many-flowered dichasia or polychasia on wiry, straw-colored, scape-like peduncles; pedicels generally slender and straw-colored. Sepals ovate, blunt to acute, usually early deciduous.

Petals 4–7 mm long, light to dark pink. Stamens (4–)5(–12), equal the length of the style. Stigma capitate or 3-lobed, the lobes triangular. Capsules ellipsoid or ovoid to oblong, disintegrating promptly at maturity, 3–5 mm long. Seeds smooth, appearing dark brown to black, ca. 0.6–0.9 mm wide. $2n = 24$ [rarely 48 (Steiner 1944)]. Eastern Great Plains and Interior Highlands west of the Mississippi, and southern Appalachia in central Alabama, ca. 0–1500 m; sandy barrens or rocky soils over non-calcareous rock in dry grasslands, rock outcrops, glades, and ledges; central Texas north to southeastern North Dakota west to the Mississippi River, with populations also in southern Illinois and in a small area of Central Alabama.

Across its wide range, *P. parviflorus* often grows sympatrically with *P. calycinus* sens. lat. and in close proximity to *P. rugospermus* and *P. mengesii*. It is one of the diploid parents of the allotetraploid *P. teretifolius*, along with *P. mengesii* (Black and Murdy 1972; Carter and Murdy 1985; Murdy and Carter 1985, 2001), and it likely has also hybridized with *P. calycinus* in some areas.

***Phemeranthus piedmontanus* S. Ware**, Journal of the Botanical Research Institute of Texas 5(1): 1-7, 2011. TYPE: U.S.A., Virginia, Franklin Co., Bald Knob, Rocky Mount, 1 Aug 2007, *C. Ludwig 5051* (holotype, UNC).

PIEDMONT FAMEFLOWER

Plants tall, erect; stems usually several, stout, fleshy, branching above, arising from rhizomes near the soil surface; mature rhizomes usually multi-branched from a central point, each branch giving rise to one or two stems in spring. Vegetative propagules apparently not produced. Leaves to 4 cm long. Inflorescences many-flowered, cymose, on wiry, scape-like peduncles. Sepals deciduous in fruit. Petals 6–10 mm long, more than 1/2 as wide as long, purplish pink. Stamens 20–35(–42), 2/3 to 3/4 length of style, mostly erect. Pollen orange. Stigma subcapitate. Capsules ovoid to obovoid, 3–5 mm long. Seeds smooth, black, ca. 0.6 mm wide. Piedmont of southern Virginia and northern North Carolina, shallow soil on mafic and ultramafic rock outcrops or glades.

P. piedmontanus and *P. teretifolius* co-occur at one site in North Carolina.

***Phemeranthus rugospermus* (Holz.) Kiger**, Novon 11(3): 320, 2001.

Talinum rugospermum Holz., Asa Gray Bulletin 7(6): 117, 1899. TYPE: U.S.A., Wisconsin, Trempealeau Prairie, July 1888, *J.M. Holzinger s.n.* (holotype, WINO transferred to MIN not seen); TOPOTYPES: U.S.A., Wisconsin, Trempealeau Prairie, July 1897, Aug 1899, *J.M. Holzinger s.n.* (MO)

ROUGH-SEEDED FAMEFLOWER, SAND-PRAIRIE FAMEFLOWER, SANDPINK

Plants tall (up to 30 cm), mostly erect; stems stout, fleshy, simple or branching, arising from long, fleshy, tapering taproots. Leaves to 6 cm long. Inflorescences many-flowered, cymose, on stout, wiry, scape-like peduncles. Sepals broad, ovate and usually tapering apically, deciduous or sometimes persistent in fruit. Petals 6–8 mm long, often acute or mucronulate, pale to bright pink, usually mottled light pink. Stamens 12–28, equal to length of style. Stigma strongly 3-lobed, the lobes linear and widely spreading. Capsules globose, 4–5 mm long. Seed testa smooth but seeds appearing bluish-gray and corrugate-rugulose due to wrinkled pellicle, ca. 1.2 mm wide. Usually found on aeolian sand barrens or sandy pockets derived from sandstone outcrops, but also on thin soils over igneous and metamorphic outcrops at the northern limits of its range (Cochrane

1993); Driftless Area of Wisconsin, Minnesota, Illinois, and northern Indiana; sandy prairies in central Nebraska, central Kansas, south-central Oklahoma, eastern Texas, and western Louisiana.

This species has a wide but patchy distribution, with its largest area of concentration in the Upper Midwest. It has apparently been extirpated at numerous former localities in Indiana and Illinois but was only recently discovered in Oklahoma and may also be present in Missouri and/or Arkansas. Older specimens in herbaria are often identified as *P. teretifolius* or *P. parviflorus,* but the former species can be ruled out by distribution alone, and *P. rugospermus* is easily distinguished from *P. parviflorus* if seeds or well-preserved flowers are present.

***Phemeranthus sediformis* (Poelln.) Kiger**, Novon 11(3): 320, 2001.

Talinum sediforme Poelln., Berichte der Deutschen Botanischen Gesellschaft 51(2): 113–114, 1933. TYPE: Canada, British Columbia, Seme-ke-mele [Similkameen] River, 49ºN, 15 July 1851, *J. Jeffrey 177* (Holotype, B?; isotype, K image seen).

Talinum okanoganense English, Proceedings of the Biological Society of Washington 47(35): 191–192, 1934. TYPE: U.S.A., Washington, Okanogan Co., Fir Mountain, 28 May 1933, *C.S. English 1733* (Holotype, ?)

Talinum wayae Eastw., Leaflets of Western Botany 1(12): 139, 1934 [as "*Wayae*"]. TYPE: Canada, British Columbia, Mount Baldy near Kamloops, *Mrs. A. E. Way s.n.* (Holotype, CAS not seen).

OKANAGAN FAMEFLOWER

Plants low, caespitose, mat-forming; stems spreading, highly branched, suffrutescent, bearing persistent, dense, bristlelike remnants of old leaves, arising from elongate, branching, woody roots. Leaves grayish-green, subterete, blunt apically, usually less than 1 cm long, attenuate at the base, crowded along stems and concealing the internodes. Inflorescences multi-flowered, cymose, on slender, sprawling, scape-like peduncles. Sepals ovate, early deciduous, 2-4 mm long. Petals 6–8 mm long, creamy white, sometimes light pink. Stamens 15, yellow, shorter than the style. Stigma subcapitate. Capsules globose, often trigonous, 3–4 mm long. Seeds smooth, ca. 1 mm wide. Barren, rocky slopes and ledges, 1000–2000 m; Okanagan region of north-central Washington and southern British Columbia, Canada.

P. sediformis is a highly attractive plant and is well established in the commercial rock-garden trade. A cultivar known as “Zoe”, of unknown origin, may be a hybrid of *P. sediformis* × *P. spinescens.* It differs from typical *P. sediformis* in having darker purplish-pink flowers, longer and more erect peduncles, and longer and darker green leaves that are more pointed apically.

***Phemeranthus spinescens* (Torr.) Hershkovitz**, Taxon 46(2): 222, 1997.

Talinum spinescens Torr., in C. Wilkes et al., United States Exploring Expedition 17(2): 250, 1874. **T. L.**: Oregon & Washington.

Claytonia spinescens (Torr.) Kuntze, Revisio Generum Plantarum 1: 57, 1891.

COLUMBIA FAMEFLOWER, SPINY FAMEFLOWER

Plants succulent, long-lived subshrubs; stems highly branched, suffrutescent, bearing persistent, spinelike remnants of old leaves, arising from elongate, branching, woody roots. Leaves dark green or often red when stressed, acute apically, up to 2.5 cm long, attenuate at the base. Inflorescences many-flowered, cymose, on tall (to 20 cm), stout, erect, scape-like peduncles. Sepals ovate, deciduous or persistent in fruit, ca. 3 mm long. Petals 8–10 mm long, pale pink to magenta. Stamens 20–30, ca. 1/2 to 2/3 length of the style. Stigma subcapitate. Capsules ovoid to globose, ca. 5 mm long. Seeds smooth, ca. 1.2 mm wide. Columbia Plateau; fine, shallow soils on basaltic cliffs, ledges, and rock pans, ca. 700–1100 m; east-central Washington and adjacent northern Oregon.

Phemeranthus teretifolius **(Pursh) Raf.**, Specchio delle Scienze 1: 86, 1814.

Talinum teretifolium Pursh, Flora Americae Septentrionalis 2: 365, 1814. TYPE: USA, Delaware and Virginia, on sunny rocks, July, *? s.n.* (Holotype?)

Phemeranthus teretifolius Raf., nom. nud., Medical Repository 5: 350, 1808.

Talinum trichotomum Desf., Tableau de l'École de Botanique 166, 1804.

Talinum ciliatum Lindley, nom. illeg., Edwards's Botanical Register 29: pl. 1, 1843.

Claytonia teretifolia Kuntze, Revisio Generum Plantarum 1: 57, 1891.

FAMEFLOWER, ROCKPINK, FLOWER-OF-AN-HOUR

Plants tall (up to 50 cm), erect; stems stout, fleshy, simple or branching, arising from amorphous, tuberous rhizomes at the soil surface. Vegetative propagules produced on lower stems in fall. Leaves to 6 cm long. Inflorescences many-flowered, cymose, on stout, wiry, scape-like peduncles. Sepals elliptic to ovate, early deciduous, 3–4 mm long.

Petals 5–7 mm long, about 1/2 as wide as long, magenta. Stamens 12–20, as long as style, erect. Stigma 3-lobed, the lobes often indistinct. Capsules subglobose, 4–5 mm long. Seeds smooth, black, ca. 0.8 mm wide. $2n = 48$. Piedmont and Appalachians; thin soil overlying sandstone, granitic, shale, and serpentine outcrops, ca. 200–1000 m; eastern Alabama, Tennessee, and Kentucky; Georgia, North and South Carolina, Virginia, West Virginia, Maryland, Pennsylvania (also reported from Connecticut and Delaware).

This species overlaps with *P. mengesii* in Georgia and eastern Alabama, and the two species occasionally occur together. *P. teretifolius* is an allotetraploid hybrid species derived from *P. mengesii* and *P. parviflorus*, both of which it has apparently displaced in southern Appalachia (Murdy et al. 1970; Black and Murdy 1972; Carter and Murdy 1985; Murdy and Carter 1985, 2001).

***Phemeranthus validulus* (Greene) Kiger**, Novon 11(3): 321, 2001.

Talinum validulum Greene, Leaflets of Botanical Observation and Criticism 2(12): 270, 1912. TYPE: U.S.A., Arizona, Tusayan Forest Reservation, 11 Aug [type], 11 July [protologue] 1912, *R.R. Hill s.n.* (Lectotype, US).

Talinum thompsonii N.D. Atwood & S.L. Welsh, Great Basin Naturalist 45(3): 485–487, 1985. TYPE: U.S.A., Utah, Emery Co., Cedar Mountain, 19 July 1981, *N.D. Atwood & R. Thompson 8056* (Holotype, BRY; Isotypes, NY, RSA not seen, US).

Phemeranthus thompsonii (N.D. Atwood & S.L. Welsh) Kiger, Novon 11(3): 321, 2001.

TUSAYAN FAMEFLOWER, CEDAR MOUNTAIN FAMEFLOWER

Plants spreading to ascending; stems stout, branching, sometimes decumbent basally, arising from elongate, branched, woody tuberous roots. Leaves 10–40 mm long, upturned, acute; lower leaves often awl-shaped. Inflorescences multi-flowered, cymose, on wiry, scape-like peduncles (these sometimes reduced), slightly to substantially exceeding the leaves. Sepals broadly lanceolate, acuminate, often reflexed at tips, persistent in fruit, exceeding the capsules. Petals 7–9 mm long, white to light pink, usually paler abaxially. Stamens (6–)10–15(–20), shorter than style. Stigma subcapitate or 3-lobed. Capsules football-shaped, trigonous, 5–7 mm long. Seeds smooth, 1–1.2 mm wide. Thin, rocky clay soil derived from chert, basalt, cinders, or conglomerate in coniferous woodland openings and xeric shrub communities, ca. 1800-2500 m; central Utah (Cedar Mountain) and northern Arizona.

This species is similar to *P. brevicaulis*, differing in its smaller, lighter-colored flowers, fewer stamens, and allopatric (more northern and western) distribution. It often grows sympatrically with *P. confertiflorus*, and the two species are known to hybridize.

Phemeranthus **sect. *Eutmon* (Raf.) D.J. Ferguson, stat. nov.** BASIONYM: *Eutmon* Raf., Atlantic Journal 177, 1833. TYPE: *Phemeranthus napiformis* (DC.) G. Ocampo, Acta Botanica Mexicana 59: 79, 2002.

Perennial stems mostly highly reduced, subterranean; plants appearing acaulescent (stems well developed and plants caulescent in *P. mexicanus* and *P. oligospermus*). Taproots tuberous, broadly napiform to globose, sometimes branching below. Leaves terete, clustered in basal rosettes (clustered at stem apices in *P. mexicanus* and *P. oligospermus*). Inflorescences cymose, borne on wiry, scape-like peduncles, erect or sprawling, sometimes well exceeding the leaves, sometimes borne among the leaves. Flowers white to yellow; sepals deciduous; petals 5; stamens 5–10. Capsules often trigonous, usually disintegrating at maturity. Seed testa with raised concentric ridges. Distributed from southern Arizona and New Mexico south to Oaxaca and Puebla, Mexico.

Phemeranthus humilis **(Greene) Kiger**, Novon 11(3): 320, 2001.

Talinum humile Greene, Botanical Gazette 6(3): 183, 1881. TYPE: U.S.A., New Mexico, Grant Co., Pinos Altos Mountains, 11 Aug 1880, *E.L. Greene 217* (Holotype, NDG? not seen; isotypes, MO, GH image seen, K image seen).

Talinum greenmanii Harshb., Bulletin of the Torrey Botanical Club 24(4): 183–184, 1897 [as "*Greenmanii*"]. TYPE: Mexico, Mexico (state), Sierra de Ajusco, 31 Aug 1896, *C.G. Pringle 6472* (Holotype, ?; Isotypes, MO, US, NY).

PINOS ALTOS FAMEFLOWER

Plants succulent, subacaulescent; stems subterranean, short, erect, usually unbranched, arising from turbinate to globose, fleshy tuberous roots. Leaves yellowish green, thick, up to 8 cm long. Inflorescences few- to several-flowered, cymose, borne among the leaves and not exceeding them in height. Sepals ovate, deciduous, ca. 3 mm long. Petals ca. 4 mm long, yellow. Stamens 5–8. Stigma subcapitate. Capsules ellipsoid to globose, sometimes trigonous, 4–6 mm long. Seeds with strong concentric ridges, ca. 1 mm wide. Thin, rocky soil in open mid-elevation habitats, ca. 1600-1800 m; southwestern New Mexico and south-central Arizona south to central Chihuahua, Mexico.

According to D. J. Ferguson (pers. comm.), *Talinum greenmanii* is distinguished by occasionally having lobed leaf bases, fewer-flowered inflorescences, a smooth seed pellicle that partly obscures the ridged testa, and a napiform (vs. globose) taproot. It also occurs at higher elevation, in gravel scree on steep pine-forested slopes. Few specimens are available however. Recognition of this entity as a separate species would necessitate publication of the combination *Phemeranthus greenmanii*.

***Phemeranthus mexicanus* (Hemsl.) G. Ocampo**, Acta Botánica Mexicana 59: 77, 2002.

Talinum mexicanum Hemsl., Diagnoses plantarum novarum vel minus cognitarum Mexicanarum et Centrali-Americanarum 2: 23, 1879. TYPE: Mexico, "in regione San Luis Potosí", 1800-2400 m, 1878, *C. C. Perry & E. Palmer 69* (Holotype, K image seen; Isotype, MO)

Claytonia mexicana (Hemsl.) Kuntze, Revisio Generum Plantarum 1: 57, 1891.

MEXICAN FAMEFLOWER

Plants caulescent, 4–10 cm tall; stems slender, erect, branched, mostly 2–5 cm long, smooth grayish to brown and exfoliating slightly with age, clothed with stiff, needle-like remnants of old leaves. Proximal portion of roots elongated, slender, 2.5–7 cm long, simple or branched; distal portion of roots tuberous, globose or fusiform, clothed with thin, brown scales. Leaves clustered at the apex of each stem, 3–13 mm long, acute, glaucous. Inflorescences several from each stem, erect, cymose, few- to several-flowered, borne on slender peduncles up to 25 mm long. Sepals elliptic to orbicular, obtuse, 1.8–2.5 mm long, deciduous; petals obtuse, 2.5–4 mm long, about 1/2 as wide as long, yellow to orange-yellow. Stamens 5. Stigma capitate. Capsule globose to ovoid, 3–3.5 mm long, dehiscing basipetally with valve tips recurving slightly, persisting for some time if not disturbed. Seeds with concentric raised ridges, appearing rather smooth, the translucent pellicle not conforming to the ridges of the testa, ca. 0.6 mm wide. Shallow, rocky soils in grassland openings surrounded by oak woodland on rhyolite slopes, ca. 2300 m, San Luis Potosí and Queretaro, Mexico.

***Phemeranthus multiflorus* (J. N. Rose & Standl.) G. Ocampo**, Acta Botánica Mexicana 59: 79. 2002.

Talinum multiflorum J. N. Rose & Standl., Contributions from the United States National Herbarium 13(8): 285, 1911. TYPE: Mexico, Durango, Otinapa, 23 July–5 Aug 1906, *E. Palmer 434* (Holotype, US; isotype, NY).

MANY-FLOWERED FAMEFLOWER

Plants succulent, subacaulescent; stems subterranean, short, arising from fleshy, fusiform to globose tuberous roots. Leaves slender, usually under 3 cm long. Inflorescences many-flowered, congested cymes on scape-like peduncles, spreading beyond the leaves. Sepals deciduous, often with reddish coloration, ca. 2.5 mm long. Petals 5–6 mm long, yellow. Stamens 5. Stigma subcapitate. Capsules ellipsoid, strongly trigonous, ca. 4 mm long, with purplish coloration along the sutures. Seeds strongly ridged, the pellicle conforming to the testa. Sierras of Mexico; shallow, rocky soils overlying bedrock; Durango and Chihuahua, Mexico.

This species most closely resembles *P. punae* of Argentina. However, it is poorly known, and pressed specimens are often difficult to distinguish from *P. parvulus*. The relationships of these species require further study.

Phemeranthus napiformis **(DC.) G. Ocampo**, Acta Botánica Mexicana 59: 79, 2002.

Talinum napiforme DC., Prodromus Systematis Naturalis Regni Vegetabilis 3: 357, 1828. LECTOTYPE: sheet 6331.0468 of the Sessé & Mociño expedition, Mexico, 1787-1803 [designated by R. McVaugh, 2000. Botanical results of the Sessé & Mociño expedition (1787-1803). VII. A guide to relevant scientific names of plants. Hunt Institute for Botanical Documentation. Pittsburgh, p. 446 of 626].

Eutmon napiforme (DC.) Raf., Atlantic Journal 177, 1833.

Claytonia napiformis (DC.) Kuntze, Revisio Generum Plantarum 1: 57, 1891.

Claytonia tuberosa Sessé & Moc. ex DC., nom. nud., Prodromus Systematis Naturalis Regni Vegetabilis 3: 357, 1828.

Talinum palmeri J. N. Rose & Standl., Contributions from the United States National Herbarium 13(8): 284, 1911. TYPE: Mexico, Durango, Otinapa, 25 Jul–5 Aug 1906, *E. Palmer 436* (Holotype, US; Isotype, MO, NY).

NAPIFORM FAMEFLOWER

Plants succulent, subacaulescent, 8–15 cm or up to 40 cm tall; stems subterranean, short, erect, one or several arising from each rootstock; tuberous root stout, napiform, with smooth, reddish bark exfoliating in thin sheets. Leaves 4–9 cm long, stout, ascending. Inflorescences many-flowered, cymose, on tall, straw-colored, scape-like peduncles. Sepals broadly ovate to orbicular, obtuse to acute, ca. 3–4 mm long. Petals white, 7–10 mm long. Stamens 5. Capsule oblong, slightly triquetrous, ca. 5 mm long. Seeds gray, with raised concentric ridges. Madrean region; thin soil over surfacing bedrock in relatively level grasslands or open woodlands; Distrito Federal, Durango, Guanajuato, Jalisco, Queretaro, Mexico (state), San Luis Potosi, and Zacatecas, Mexico.

As described by Rose & Standley, *T. palmeri* differs from *P. napiformis* in having larger leaves, taller peduncles, and greater floral dimensions. However, Ocampo (Ocampo 2002) reports that *P. napiformis* tends to develop taller peduncles in the northern part of its range and that *P. napiformis* plants maintained in cultivation grow larger than those in the field, approaching the size of *T. palmeri* specimens. The description of *T. palmeri* was based on greenhouse-maintained plants. Thus, *T. palmeri* is considered synonymous with *P. napiformis*. However, D. J. Ferguson (pers. comm.) has cultivated typical *P. napiformis* alongside plants from the *T. palmeri* type locality, and reports that the overall difference in size is maintained under these conditions. Ferguson also observes that the larger white flowers of *T. palmeri* are nocturnal, a unique trait in the genus, while those of *P. napiformis* open in the afternoon. If *T. palmeri* is indeed a separate species, it would require publication of the combination *Phemeranthus palmeri*.

***Phemeranthus oligospermus* (Brandegee) G. Ocampo**, Acta Botánica Mexicana 63: 56, 2003.

Talinum oligospermum Brandegee, Zoë 5(11): 245, 1908. TYPE: Mexico, Puebla, Cerro de la Yerba, July 1907, *C.A. Purpus 2513* (Holotype, UC image seen; Isotypes, MO, NY, US).

PUEBLA FAMEFLOWER

Plants caulescent; stems numerous, slender, highly branched, whitish, clothed with persistent dried leaf bases, arising from subglobose fleshy tuberous roots. Leaves short, usually less than 1 cm. Inflorescences several, multi-flowered, cymose, on spreading, scape-like peduncles. Sepals oblong to ovate, purplish, ca. 2.5 mm. Petals 4–5 mm long, yellow. Stamens 5. Stigma subcapitate. Capsules obtusely triquetrous, purplish, ca. 3 mm long. Seeds with raised concentric ridges. Tehuacán-Cuicatlán Valley, locally abundant in oak forest and thorn scrub vegetation, 2000–2600 m; endemic to Oaxaca and Puebla, Mexico.

***Phemeranthus parvulus* (J. N. Rose & Standl.) D.J. Ferguson & T.M. Price**, Novon [in press], 2012.

Talinum parvulum J. N. Rose & Standl., Contributions from the United States National Herbarium 13(8): 283, 1911. TYPE: Mexico, Durango, Otinapa, July 25–Aug 5, 1906, *E. Palmer 451* (holotype, US; isotypes, GH not seen, K image seen, NY).

Talinum marginatum Greene, Leaflets of Botanical Observation and Criticism 2(12): 270–271, 1912. TYPE: Mexico, Nayarit, Sierra Madre near Santa Teresa, Tepic, 12 Aug 1897, *J.N. Rose 2221* (holotype, US).

Phemeranthus marginatus (Greene) Kiger, Novon 11(3): 320, 2001.

BOTTLE-LEAF FAMEFLOWER

Plants diminutive, succulent, subacaulescent; stems subterranean, short, erect, unbranched, arising from fleshy tuberous roots. Leaves strongly narrowed at or below mid-length, appearing petiolate, the apex rounded, 1–5 cm long. Inflorescences few- to several-flowered, cymose, on scape-like peduncles; at least the lowest flowers borne among the leaves but mature inflorescences exceeding the leaves. Sepals broadly lanceolate to ovate, deciduous, 2–3 mm long. Petals 3–5 mm long, yellow. Stamens 5. Stigma subcapitate. Capsules ellipsoid, sometimes trigonous, ca. 3 mm long. Seeds with raised concentric ridges, ca. 1 mm wide. Madrean region; thin, rocky soil on slopes and ridges, ca. 1900-2200 m; southeastern Arizona and Chihuahua, Durango, Hidalgo, Jalisco, Nayarit, Sonora, and Zacatecas, Mexico.

***Phemeranthus punae* (R.E. Fr.) Eggli & Nyffeler**, Taxon 59(1): 240, 2010.

Calandrinia punae R.E. Fr., Nova Acta Regiae Societatis Scientiarum Upsaliensis, ser. 4, 1(1): 149, 1905. TYPE: Argentina, Jujuy, Santa Catalina, date?, *? #* (Holotype ?not seen).

Talinum punae (R.E. Fr.) Carolin, Parodiana 3(2): 331, 1985.

PUNA FAMEFLOWER

Plants succulent, subacaulescent; stems subterranean, short, arising from fleshy, fusiform to globose tuberous roots. Leaves usually under 3 cm long. Inflorescences many-flowered, congested cymes on scape-like peduncles, sprawling beyond the leaves. Sepals deciduous, often with reddish coloration, ca. 3 mm long. Petals 3–4 mm long, yellow. Stamens 5. Stigma subcapitate. Capsules ellipsoid, trigonous, ca. 3-4 mm long. Seeds appearing smooth, testa ridges only slightly raised and obscured by pellicle. Puna region of southern Andes; shallow, gravelly soils and soil pockets overlying rock or in cracks of rocks along ridgetops or benches at high elevation (ca. 3500 m); northern Argentina (Catamarca, Jujuy, La Rioja, Salta, Tucuman) and southern Bolivia (Potosi and Tarija).

Key to Sections and Currently Recognized Species—

1a. Leaves not terete (though may be narrowly linear and/or revolute); seeds without investing pellicle— ***Talinum* (not included here)**

1b. Leaves terete; seeds enclosed by membranous pellicle (may be partly rubbed away)— ***Phemeranthus*** **(2)**

2a. Taproot fusiform to napiform, not globose, or absent and plants rhizomatous or with an amorphous subterranean caudex; plants strongly caulescent; flowers pink to magenta or white— **sect. *Phemeranthus*** **(3)**

2b. Taproot tuberous, napiform to globose, at least distally; plants usually appearing acaulescent; flowers yellow to orange or white— **sect. *Eutmon*** **(16)**

3a. Stems erect; leaves mostly over 2.5 cm long, not concealing internodes; inflorescences mostly over 5 cm long, usually appearing terminal, erect, many-flowered, with the lowest flowers usually above the leaves— **(4)**

3b. Stems prostrate to procumbent; leaves mostly under 2.5 cm long, crowded along stem, concealing the internodes, upturned; inflorescences mostly under 5 cm long, usually appearing axillary, mostly spreading laterally, one- to several-flowered, with at least the lowest flowers usually among the leaves— **(13)**

4a. Plants suffrutescent, with well-branched perennial, woody stems clothed in spiny, lignified leaf bases; Columbia Plateau— ***Phemeranthus spinescens***

4b. Plants usually dying back to ground level, sometimes with semi-woody perennial caudices or lower stems clothed in persistent leaf bases, but not developing into subshrubs; east of the Rocky Mountains and in the Southwest— **(5)**

5a. Flowers mostly under 12 mm across; stamens 5–10— **(6)**

5b. Flowers mostly over 12 mm across; stamens (12)15–60 or more— **(8)**

6a. Petals blunt, white to pale pink; filaments bright pink; seeds with strongly raised concentric ridges— ***Phemeranthus longipes***

6b. Petals generally acute, white to dark pink; filaments yellow; seeds smooth— **(7)**

7a. Petals white (rarely) to magenta; sepals early deciduous, obtuse; fruit globose to ovate or elliptical, nearly as wide as long; Great Plains, Ozarks, central Alabama— ***Phemeranthus parviflorus***

7b. Petals white to pale pink; sepals usually persistent, acute, sometimes acuminate-cornate and reflexed, often with dark purplish pigment apically; fruit usually pointed apically, narrower than long; desert and semi-desert southwestern states— ***Phemeranthus confertiflorus***

8a. Flowers (10–)15(–20) mm across; stamens usually less than 30— **(9)**

8b. Flowers over 15 mm (up to 30 mm) across; stamens usually more than 30— **(11)**

9a. Stamens 20–35(–42), 2/3–3/4 as long as style; stigma subcapitate; pollen orange or golden— ***Phemeranthus piedmontanus***

9b. Stamens 12–20(–25), equal to or slightly exceeding length of style; stigma 3-lobed; pollen yellow— **(10)**

10a. Petals light to medium pink; stigma lobes spreading, nearly as long as style; seeds large, with gray, wrinkled pellicle— ***Phemeranthus rugospermus***

10b. Petals magenta; stigma lobes short, not spreading; seeds small, appearing black and smooth, even with pellicle intact— ***Phemeranthus teretifolius***

11a. Sepals early deciduous; stamens (30–)45–60+; stigma subcapitate; southern Appalachia, Alabama and Georgia Piedmont— ***Phemeranthus mengesii***

11b. Sepals persistent in fruit; stamens 25–45; stigma subcapitate to short-lobed; Central Tennessee Basin, Interior Highlands, and Great Plains— **(12)**

12a. Flowers mostly under 20 mm across, stigma lobes short, nearly erect; limestone in Central Tennessee Basin and adjacent states— ***Phemeranthus calcaricus***

12b. Flowers usually over 20 mm across; stigma lobes short, spreading or subcapitate; Great Plains and Interior Highlands— ***Phemeranthus calycinus***

13a. Leaves usually under 15 mm, slightly dorso-ventrally compressed, apically rounded, blunt to apiculate, tightly crowded and concealing the internodes; inflorescence one- to few-flowered; sepals blunt; petals about as wide as long; capsules globose— **(14)**

13b. Leaves usually over 15 mm, apically pointed; inflorescence few- to several-flowered; sepals acute, sometimes reflexed, exceeding fruit, persistent; petals narrower than long; capsules football-shaped— **(15)**

14a. Plants mat-forming, with highly branched, spiny, suffrutescent above-ground stems; inflorescences pedunculate, multi-flowered; stamens 2/3–3/4 length of style; Washington and British Columbia— ***Phemeranthus sediformis***

14b. Plants spreading by rhizome-like underground stems; inflorescences single-flowered (rarely 2–3-flowered), subsessile; pistil up to twice as long as stamens; Colorado Plateau in Utah, Arizona, and New Mexico— ***Phemeranthus brevifolius***

15a. Flowers mostly under 18 mm across; petals white to pale pink; stamens 10–15; east-central Utah and northern Arizona— ***Phemeranthus validulus***

15b. Flowers mostly over 18 mm across; petals magenta (rarely lighter pink); stamens (15–)20–30(–45); New Mexico and western Texas, Chihuahua, and Coahuila— ***Phemeranthus brevicaulis***

16a. Plants caulescent, with slender, branching perennial stems clothed with persistent dried leaf bases— **(17)**

16b. Perennial stems short, subterranean; plants appearing acaulescent— **(18)**

17a. Root with a long, slender proximal portion and tuberous distal portion; sepals orbicular; petals ca. 3 mm long; capsule globose to ovoid, light green; San Luis Potosí and adjacent Guanajuato, Mexico— ***Phemeranthus mexicanus***

17b. Root subglobose; sepals oblong to ovate, purplish; petals 4–5 mm long; capsule obtusely triquetrous, purplish; Tehuacán-Cuicatlán Valley, Oaxaca and Puebla, Mexico— ***Phemeranthus oligospermus***

18a. Leaves appearing petiolate, strongly narrowed proximally; inflorescences few-flowered, somewhat exceeding leaves; capsules under 5 mm long— ***Phemeranthus parvulus***

18b. Leaves not appearing petiolate— **(19)**

19a. Flowers white; rootstock stout, napiform, with smooth, reddish bark exfoliating in thin sheets— ***Phemeranthus napiformis***

19b. Flowers yellow; tuberous root fusiform to globose— **(20)**

20a. Leaves usually over 3 cm long; flowers usually over 9 mm across; inflorescences few-flowered, not or only slightly exceeding leaves; capsules over 5 mm long— ***Phemeranthus humilis***

20b. Leaves usually under 3 cm long; flowers usually under 9 mm across; inflorescences many-flowered, sprawling, exceeding leaves; capsules under 5 mm long— **(21)**

21a. Seeds appearing smooth, testa ridges only slightly raised, obscured by pellicle; Puna region of northern Argentina and southern Bolivia—***Phemeranthus punae***

21b. Seeds strongly ridged, pellicle conforming to testa; Sierras of Mexico— ***Phemeranthus multiflorus***

Literature Cited—

Applequist, W. L. and R. S. Wallace. 2001. Phylogeny of the portulacaceous cohort based on *ndhF* sequence data. *Systematic Botany* 26: 406-419.

Applequist, W. L., W. Wagner, E. A. Zimmer, and M. Nepokroeff. 2006. Molecular evidence resolving the systematic position of *Hectorella* (Portulacaceae). *Systematic Botany* 31: 310-319.

Black, C. and W. H. Murdy. 1972. The evolutionary origin of *Talinum teretifolium* Pursh. *Botanical Gazette* 133: 405-410.

Carolin, R. 1987. A review of the family Portulacaceae. *Australian Journal of Botany* 35: 383-412.

Carter, M. E. B. and W. H. Murdy. 1985. Systematics of *Talinum parviflorum* Nutt. and the origin of *T. teretifolium* Pursh (Portulacaceae). *Rhodora* 87: 121-130.

Carter, M. E. B. and W. H. Murdy. 1986. Divergence for sexual and asexual reproductive characters in *Talinum mengesii* (Portulacaceae). *Bulletin of the Torrey Botanical Club* 113: 259-267.

Cochrane, T. S. 1993. Status and distribution of *Talinum rugospermum* Holz. (Portulacaceae). *Natural Areas Journal* 13: 33-41.

Dvorak, B. 2010. Rooftop membrane temperature reductions with green roof technology in south-central Texas. 17th Symposium for Improving Building Systems in Hot and Humid Climates, Austin, Texas, ESL-HH-10-08-23: 1-7.

Getter, K. L., D. B. Rowe, and B. M. Cregg. 2009. Solar radiation intensity influences extensive green roof plant communities. *Urban Forestry & Urban Greening* 8: 269-281.

Greene, E. L. 1912. Miscellaneous specific types—VI. *Leaflets of Botanical Observation and Criticism* 2: 270-272.

Hershkovitz, M. A. 1993. Revised circumscriptions and subgeneric taxonomies of *Calandrinia* and *Montiopsis* (Portulacaceae) with notes on phylogeny of the portulacaceous alliance. *Annals of the Missouri Botanical Garden* 80: 333-365.

Hershkovitz, M. A. and E. A. Zimmer. 1997. On the evolutionary origins of the cacti. *Taxon* 46: 217-232.

Hershkovitz, M. A. and E. A. Zimmer. 2000. Ribosomal DNA evidence and disjunctions of Western American Portulacaceae. *Molecular Phylogenetics and Evolution* 15: 419-439.

Kiger, R. W. 2001. New combinations in *Phemeranthus* Rafinesque (Portulacaceae). *Novon* 11: 319-321.

Kiger, R. W. 2003. *Phemeranthus*. Pp. 488-495 in *Flora of North America North of Mexico* vol. 4, ed. Flora of North America Editorial Committee. New York, NY and Oxford, UK: Oxford University Press.

Murdy, W. H. and M. E. B. Carter. 1985. Electrophoretic study of the allopolyploidal origin of *Talinum teretifolium* and the specific status of *T. appalachianum* (Portulacaceae). *American Journal of Botany* 72: 1590-1597.

Murdy, W. H. and M. E. B. Carter. 2001. Speciation in *Talinum* in the southeastern United States. *Castanea* 66: 145-153.

Murdy, W. H., T. Johnson, and V. Wright. 1970. Competitive replacement of *Talinum mengesii* by *T. teretifolium* in granite outcrop communities of Georgia. *Botanical Gazette* 131: 186-192.

Nyffeler, R. and U. Eggli. 2010. Disintegrating Portulacaceae: A new familial classification of the suborder Portulacineae (Caryophyllales) based on molecular and morphological data. *Taxon* 59: 227-240.

Ocampo, G. 2002. Transferencia de tres especies Mexicanas de *Talinum* Adans. a *Phemeranthus* Raf. (Portulacaceae). *Acta Botanica Mexicana* 59: 75-80.

Ocampo, G. 2003. Una combinación nueva en *Phemeranthus* (Portulacaceae). *Acta Botanica Mexicana* 63: 55-57.

Ocampo, G. and J. T. Columbus. 2010. Molecular phylogenetics of suborder Cactineae (Caryophyllales), including insights into photosynthetic diversification and historical biogeography. *American Journal of Botany* 97: 1827-1847.

Price, T. M. and D. J. Ferguson. 2012. A new combination in *Phemeranthus* (Montiaceae) and notes on the circumscription of *Phemeranthus* and *Talinum* (Talinaceae) from the southwestern United States and northern Mexico. *Novon* [scheduled for publication in 22(1)].

Reinhard, R. and S. Ware. 1989. Adaptation to substrate in rock outcrop plants: interior highlands *Talinum* (Portulacaceae). *Botanical Gazette* 150: 449-453.

Steiner, E. 1944. Cytogenetic studies on *Talinum* and *Portulaca*. *Botanical Gazette* 105: 374-379.

The Angiosperm Phylogeny Group. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society* 161: 105-121.

von Poellnitz, V. K. 1934. Monographie der Gattung *Talinum* Adans. *Repertorium Specierum Novarum Regni Vegetabilis* 35: 1-34.

Ward, D. E. and R. W. Spellenberg. 1986. Chromosome counts of angiosperms of western North America. *Phytologia* 61: 119-125.

Ware, S. 2011. A new *Phemeranthus* (Portulacaceae) from the Piedmont of Virginia and North Carolina. *Journal of the Botanical Research Institute of Texas* 5: 1-7.