

TAXONOMIC CHANGES IN NORTH AMERICAN CAMPANULOIDEAE (CAMPANULACEAE)

NANCY R. MORIN
Research Associate
UC/Jepson Herbaria
Berkeley, California
nancy.morin@nau.edu

ABSTRACT

Recent phylogenetic studies conclude that *Campanula* is polyphyletic and that all but one of the native North American species of Campanuloideae belong in the *Rapunculus* clade of *Campanula*; within the *Rapunculus* clade they fall into five different subclades, three of which also contain other genera. In preparing the treatment of Campanuloideae for Flora of North America, it has become apparent that these “*Campanula*” species should be reclassified, and it is preferable that their morphology, ecology, and distribution be taken into account for their reclassification. To that end, here six new genera are established, one is reinstated with a new name, and one is elevated from subsection rank, to accommodate the taxa in clades predominantly of other genera: **PROTOCOLODON** Morin, **gen. nov.**, containing *Protocodon robinsiae* (Small) Morin, **comb. nov.**; **PALUSTRICODON** Morin, **gen. nov.**, containing *Palustricodon aparinoides* (Pursh) Morin **comb. nov.**; **EASTWOODIELLA** Morin, **gen. nov.**, containing *Eastwoodiella californica* (Kellogg) Morin, **comb. nov.**; **RAVENELLA** Morin, **gen. nov.**, comprising four species, *Ravenella exigua* (Rattan) Morin, **comb. nov.**, *Ravenella angustiflora* (Eastw.) Morin, **comb. nov.**, *Ravenella griffinii* (Morin) Morin **comb. nov.**, and *Ravenella sharsmithiae* (Morin) Morin, **comb. nov.**; **SMITHIASTRUM** Morin, **gen. nov.**, comprising *Smithiastrum prenanthoides* (Durand) Morin, **comb. nov.**, and *Smithiastrum wilkinsiana* (Greene) Morin, **comb. nov.**; **POOLEA** Morin, **gen. nov.**, containing *Poolea reverchonii* (A. Gray) Morin, **comb. nov.**; and **ROTANTHELLA** Morin, **nom. nov.**, replacing *Rotantha* Small for the one species *Rotanthea floridana* (S. Wats. ex A. Gray) Morin, **comb. nov.** **MELANOCALYX** (Fed.) Morin, **stat. nov.**, is elevated to generic status and contains *Melanocalyx uniflora* (L.) Morin, **comb. nov.**

Campanuloideae Burnett (Campanulaceae Juss.) contains more than 1,000 species in some 50 genera worldwide, with most occurring in Africa, Asia, and Europe (Lammers 2007). *Campanula* L. is the largest genus in the subfamily, comprising 420 species (Lammers 2007) to 500 species (Contandriopoulos 1984). The treatment by Alphonse de Candolle (1830) is still the only worldwide monograph of Campanulaceae (he treated Campanulaceae and Lobeliaceae as separate families, as do many other authors), and there are few recent works that comprehensively treat even an entire genus throughout its range (e.g., *Codonopsis* and allied genera, Hong 2015). Campanuloideae has been the subject of a number of phylogenetic analyses (e.g., Eddie et al. 2003; Cosner et al. 2004; Borsch et al. 2009; Cellinese et al. 2009; Haberle et al. 2009; Roquet et al. 2009; Wendling et al. 2011; Mansion et al. 2012; Crowl et al. 2014; DeChaine et al. 2014; Crowl et al. 2016; Yoo et al. 2018). Some phylogenetic studies have focused on individual genera (e.g., *Phyteuma* L., Schneeweiss et al. 2013), species groups (e.g., isophyllous *Campanula*, Park et al. 2006), tribes or sections (e.g., Peracarpeae, Zhou et al. 2012; sect. *Quinqueloculares*, Eddie & Ingrouille 2008), biological characters (e.g. floral evolution, Crowl et al. 2016; stem anatomy, Schweingruber et al. 2014), or on geographical regions (e.g., Macaronesia, Menezes et al. 2018; Greece, Cellinese et al. 2009; Asia, Yoo et al. 2018). As the number of taxa sampled has increased, the phylogenies have been increasingly consistent, at least for the North American taxa. Mansion et al. (2012) characterized 17 clades within Campanuloideae that have continued to provide a backbone for subsequent work. These studies all agree that *Campanula*, as currently constituted, is polyphyletic.

McVaugh (1948), discussed the difficulties in defining genera within Campanulaceae. He noted that genera in Campanulaceae should be based on their coherence as biological units sharing combinations of characters not otherwise found in the family, emphasizing similarities and affinities among the members of the genus rather than differences from other genera. Lakušić et al. (2019) discussed this as a well-known taxonomic problem prevalent in Campanulaceae, noting “many of the genera cannot be diagnosed explicitly by single characters, but instead by a combination of them, or by overall appearance (*Gestalt*), often in combination with geographic distribution.” Liveri et al. (2019) concluded “*Campanula* is not a natural entity and its complex historical evolution is hard to reconstruct even with molecular tools.”

Historically, the North American taxa of Campanuloideae have been placed in four to eight genera, including *Campanula*. Shetler (1963) provided an overview of native and naturalized *Campanula* in North America. Rosatti (1986) gave a more in-depth discussion of the taxa in the southeastern USA. Most phylogenetic studies have included at least some North American taxa. Wendling et al. (2011) focused on taxa in western North America, including 21 North American species in their analysis; DeChaine et al. (2014) documented radiation of the seven arctic-alpine campanulas in western North America. Yoo et al. (2018), in their work on the origins of Asian Campanulaceae, included 24 North American species as well as more than half of the east Asian taxa.

Following Eddie et al. 2003, these molecular studies have consistently identified two major clades in Campanuleae Dumort. (Hong & Wang 2015): *Campanula* in the strict sense, and the Rapunculus clade. The monotypic Asian *Peracarpa* Hook f. & Thoms. is sister to the Rapunculus clade (Yoo et al. 2018).

All but one species (*Campanula chamissonis* Fed.) of North American Campanuleae are in the Rapunculus clade (Eddie 1997; Eddie et al. 2003). Wendling et al. (2011) distinguished two clades within the Rapunculus clade: Rapunculus 1 and Rapunculus 2. Yoo et al. (2018) and Wendling et al. (2011) sampled slightly different taxa — their combined results suggest that within the *Rapunculus* clade, North American taxa fall into two superclades:

1. Wendling et al.’s Rapunculus 1 contains species still considered *Campanula*. In Rapunculus 1A are the generally mountain-dwelling North American species *C. parryi* A. Gray, *C. scabrella* Engelm., *C. aurita* Greene, *C. divaricata* Michx., *C. lasiocarpa* Cham., and *C. piperi* Howell. Although *Campanula scouleri* Hook. ex A. DC. is shown as sister to *C. prenanthoides* in Rapunculus 2A of Wendling et al.’s cladogram, that is due to a misidentification. It is correctly placed in Rapunculus 1. *Campanula shetleri* Heckard would be expected to fall here. Yoo et al. 2018 showed these Cordilleran, high elevation western species nested within the *Campanula isophylla* Moretti clade. All are western species except the Appalachian *C. divaricata*. *Campanula rotundifolia* L., a circumboreal perennial, is in a distant subclade of taxa, Wendling et al.’s Rapunculus 1B, all of which are still in *Campanula* (Yoo et al. 2018).

2. Wendling et al.’s Rapunculus 2 has three subclades. *Rapunculus 2A* contains these North American taxa: *Campanula robinsiae* Small, *C. aparinoides* Pursh, *C. exigua* Rattan, *Githopsis* Nutt., *Heterocodon* Nutt., *Campanula wilkinsiana* Greene, and *C. prenanthoides* Durand. Mansion et al. 2012 placed *C. californica* (Kellogg) A. Heller and *C. angustiflora* Eastw. here. The second subclade (Wendling et al.’s Rapunculus 2B) contains *Campanulastrum* Small, *Campanula reverchonii* A. Gray, *Triodanis* Raf., and *Campanula floridana* S. Wats. ex A. Gray (together sister to the non-North American *Legousia*). Yoo et al. (2018) placed Eurasian *Campanula pterocaula* Hauskn., *C. stevenii* M. Bieb., and *C. persicifolia* L. as sister to this second subclade. A third subclade (Wendling’s *Rapunculus 2C*) contains North American *Campanula uniflora* L. associated with the non-North American genera *Petromarula* Vent. ex Hedwig fil., *Asyneuma* Griseb. & Schenk, *Physoplexis* (Endl.) Schur, and *Phyteuma* L.

In North America in particular, the most egregious problems in Campanuloideae are with the Rapunculus 2 clades, within which species still treated as *Campanula* are embedded. These “campanulas” are distinctive in their morphology, ecology, and geographic distribution, and maintaining them as *Campanula* within the other 400+ species obscures their relationships and history.

The Cordilleran, arctic-alpine *Campanula* species in Wendling et al.’s (2011) Rapunculus 1 clade (*Campanula lasiocarpa*, *C. scabrella*, *C. parryi*, *C. piperi*, *C. shetleri*, *C. aurita*, *C. scouleri*, and the Appalachian *C. divaricata*) and *Campanula rotundifolia* should also be placed in a different genus or different genera; because these species are embedded in a large clade of Eurasian species it seems better to wait until the entire group has been studied before making nomenclatural changes. Here I try to address the generic placement of taxa in Wendling et al.’s (2011) Rapunculus 2 clade.

MATERIALS AND METHODS

Herbarium specimens of all taxa were examined (see acknowledgements for list). All taxa in this paper have been seen in the field except *Campanula aparinoides*. Characters used are almost entirely qualitative and based on examination of herbarium specimens, photographic images, and plants in the field.

TAXONOMIC TREATMENT

Wendling’s Rapunculus 2A

This clade contains *Campanula robinsiae*, a Florida annual, *Campanula aparinoides*, an eastern and northcentral perennial, *C. californica* and *C. wilkinsiana*, two perennial California endemics, perennial *Campanula prenanthoides*, which is widespread in California and Oregon, the western annual genera *Githopsis* and *Heterocodon*, and the annual California campanulas. Most of these taxa differ radically from each other (Table 1), except perhaps *C. aparinoides*/*C. californica* and the species pair *C. prenanthoides*/*C. wilkinsiana*.

Campanula robinsiae and *Campanula aparinoides*

Shetler and Morin (1986) suggested that *C. aparinoides* and *C. robinsiae* were distinctive within *Campanula*, each species having unusual seed morphology. Zhou et al. (2012), first pointed out the relationship between *C. robinsiae* and the Asian species *Peracarpa carnos*a Hook. f. & Thomson based on nuclear and plastid DNA. The two species share a mesic to boggy habitat and have small flowers. Yoo et al. (2018) placed *C. aparinoides* and *C. robinsiae* as sister taxa on long branches at the base of the Rapunculus clade, showing them diverging from the rest of the clade and from each other more than 20 m.y.a.

Campanula robinsiae was placed in *Rotantha* (an illegitimate name) with *C. floridana* by Small (1933). It is annual, grows partially submerged in seasonally wet areas, and has terminal flowers that are cleistogamous on submerged branches and chasmogamous on emergent portions, all character states unknown or at least highly unusual in Campanulaceae. The leaves are cauline and linear or narrowly lanceolate, shallowly toothed, and there is no basal rosette (Figure 1). Flowers and capsules are erect, in those of cleistogamous flowers the sepals form a beak over the nearly round capsule (Figure 2), whereas in chasmogamous flowers the sepals remain erect over an oblong capsule that is 3-lobed in cross-section; both forms dehisce by basal pores. The seeds are triangular in cross section and bear conspicuous bulbous papillae on the angles, a state not known in any other Campanulaceae (Shetler and Morin 1986). See Table 1 for comparison of characters. *Peracarpa*, sometimes placed in Peracarpae Fed., is perennial, has a reduced rosette (Shulkina 1980; Shulkina et al. 2003) and broadly ovate cauline leaves, has terminal and axillary chasmogamous pendulous flowers, capsules dehiscent by irregular tears, and oblong or fusiform seeds (see Barnesky and Lammers 1997 for full description). At least some of the plants have nearly round capsules with small erect or inward-leaning sepals forming a beak (for example, Imperial University 1906, UVMVT158823), or more commonly elongate

elliptic capsules with erect sepals. It grows adjacent to streams or in woodlands. *Campanula robinsiae* is known from only four or five localities, all on the Brooksville Ridge in Hernando and Hillsborough counties (Kunzer et al. 2009) of west-central Florida. This area has diverse topography unusual in peninsular Florida and limestone outcrops unique on the peninsula. *Campanula robinsiae* is treated here as the monospecific genus *Protocodon*.



Figure 1. Holotype of *Protocodon robinsiae* (Small s.n., NY83302).



Figure 2. *Protocodon robinsiae* chasmogamous flower on the left, capsule of cleistogamous flower on the right. Photo: The Rare Plant Conservation Program, Bok Tower Gardens.

PROTOCOLODON Morin, **gen. nov.**

Type species *Protocodon robinsiae* (Small) Morin

Diagnosis: *Protocodon* is similar to *Peracarpa* in its round capsules; it differs from *Peracarpa* and all other Campanulaceae in the combination of annual habit, linear or narrowly lanceolate cauline leaves, cleistogamous flowers producing nearly round capsules, the sepals forming a beak in fruit, chasmogamous flowers producing straight-sided capsules with erect sepals, seeds triangular in cross-section bearing bulbous projections on the angles, and partially submerged habit.

Etymology: *Proto*, first, *codon*, bell, referring to the phylogenetic placement of this genus, which may have been related to the first Campanuloideae in North America, since it is basal to the rest of the superclade containing the other North American campanuloids.

Species 1, United States, Florida, Brooksville Ridge in Hernando and Highland counties (Figure 8).

Protocodon robinsiae (Small) Morin, **comb. nov.** *Campanula robinsiae* Small, *Torreyia* 26: 35–36. 1926. *Rotanthea robinsiae* (Small) Small, *nom. illeg.* *Man. S.E. Fl.* [Small] 1289. 1933. **Lectotype** (designated here): **Florida.** Packet labeled “Chinsegut Hill,” April 1924, *J.K. Small s.n.* (NY 83305!). This sheet has two transparent envelopes on it, one labeled from Chinsegut Hill, Fla., containing a slightly more complete plant, and one from Brooksville, both dated April 1924 in Small’s hand. There are multiple plants on the sheet and in a fragment packet. Small stated that the type was at NY. Other collections at NY by Small are from 1931.

Campanula aparinoides (Figs. 3, 4, 5, Table 1) is perennial and grows in seasonally wet areas, sometimes partially submerged. Like *C. californica* it clammers over adjacent vegetation and has retrorse hairs. It has elliptic to linear leaves distributed evenly along the stem. The hypanthium is turbinate, the capsule becoming globose or urceolate, the corolla is bowl-shaped with lobes distinct for about 75% of length, and the capsule is globose or urceolate with basal pores. The stamen filaments are unusual in being densely papillate on both surfaces of the dilated portion, a feature not reported for other Campanuloideae. *Campanula aparinoides* has seeds triangular in cross-section, although not as angular as *Protocodon robinsiae*. *Campanula aparinoides* seeds are unlike any *Campanula* reported to date, with an isodiametric surface pattern, the large surface cells separated by thin radial walls with small holes in them (Shetler & Morin 1986), although *C. olympica* Boiss. may be similar (Akcin 2009). *Campanula aparinoides* is widespread in eastern and north-central North America (Fig. 8); it also occurs in a few localities in Finland and Denmark, where it is introduced. *Campanula aparinoides* is placed here in a new genus, *Palustricodon*.

PALUSTRICODON Morin, **gen. nov.**

Type species, *Palustricodon aparinoides* (Pursh) Morin

Diagnosis: *Palustricodon* is similar to *Eastwoodiella* in habit and habitat and presence of retrorse hairs, but differs in being much-branched distally and in having open, bowl-shaped corollas with lobes distinct about 75% the length, capsules ovoid to nearly spherical; seeds generally triangular but without distinct angles in cross-section. It is similar to *Protocodon* in habit and habitat but differs in being perennial and having only chasmogamous flowers.

Etymology: *Palustris*, marsh, and *codon*, bell, alluding to the marsh habitat of this genus.

Species 1, central and eastern North America (Fig. 8).

Palustricodon aparinoides (Pursh) Morin, **comb. nov.** *Campanula aparinoides* Pursh, Fl. Amer. Sept. 1: 159. 1814 [1813]. **Lectotype** (designated here): Southern Expedition of 1806. *F. Pursh s.n.* (PH 908560, Herbarium of Benjamin Smith Barton, image seen). Barbara Cochran annotated this specimen as the lectotype in 1983 but did not publish the designation.

Palustricodon aparinoides var. grandiflorus (Holz.) Morin, **comb. nov.** *Campanula aparinoides* var. *grandiflora* Holz., Bull. Geol. Nat. Hist. Surv. 9: 566. 1896. **TYPE: USA. Minnesota.** Vermillion, 14 Jul 1891, *J. H. Sandberg 506* (holotype: US 68144, image seen).

Holzinger published identifications of collections housed at US made in Minnesota by Sandberg, according to Holzinger's introduction to the paper. Duplicates of Sandberg's herbarium were purchased and given to the Geological and Natural History Survey of Minnesota. There is no duplicate of *Sandberg 506* at MIN. The specimen at US seems to be the only specimen seen by Holzinger and is the holotype.

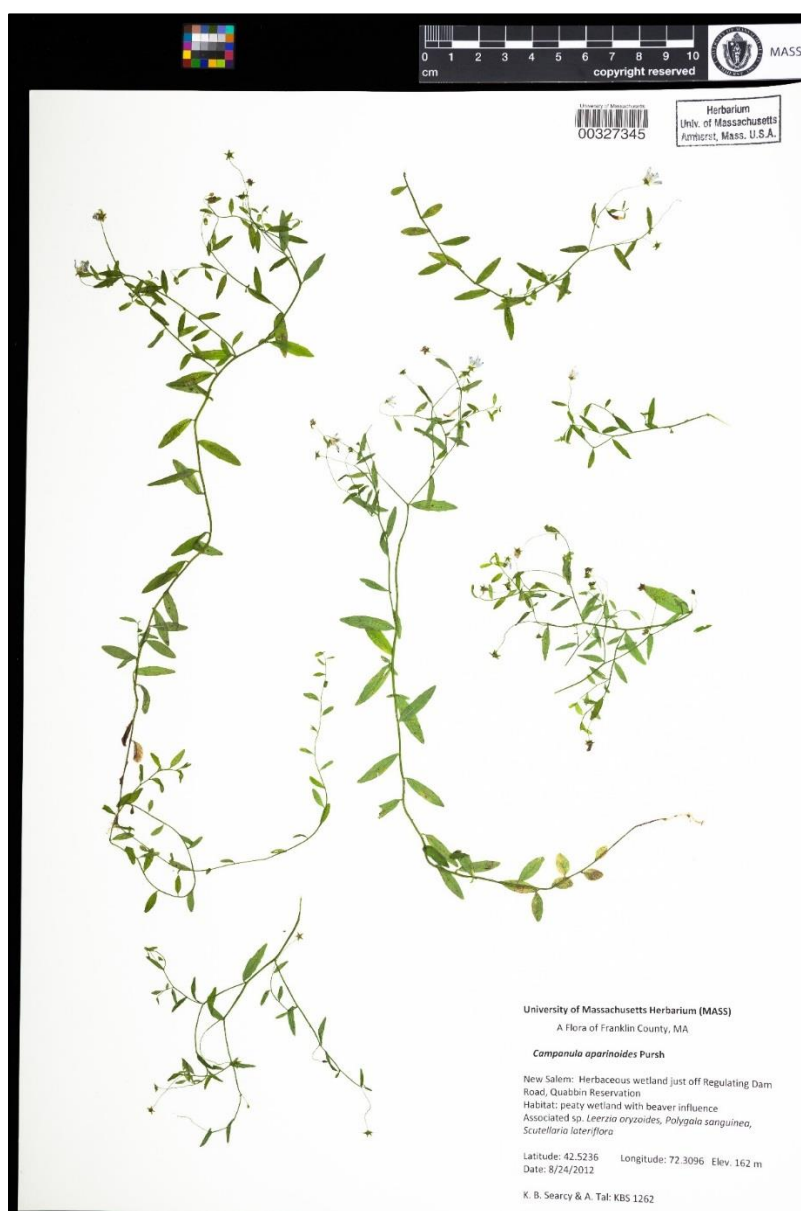


Figure 3. Representative specimen of *Palustricodon aparinoides*, Searcy & Tal KBS 1262 (MASS).



Figure 4. *Palustricodon aparinoides*. Photo K. Morse.



Figure 5. *Palustricodon aparinoides* capsule. Photo K. Morse.

Campanula californica

Neither Wendling et al. (2011) nor Yoo et al. (2018) included *Campanula californica* in their analysis, but Crowl (2016) placed *C. californica* (Figs. 6, 7) with the other western North American taxa in the equivalent of Wendling et al.'s Rapunculus 2A clade. *Campanula californica* is a perennial, weak-stemmed plant with elliptic leaves evenly distributed along the stems. The stems and leaves bear fine, retrorse, acicular hairs unusual in Campanuloideae and clamber over adjacent vegetation. *Campanula californica* has a turbinate hypanthium more rounded at base than *Palustricodon*. The corolla is campanulate with lobes that are distinct about half the length, the capsule is hemispheric with somewhat parallel sides, somewhat 3-lobed in cross section. *Campanula californica* grows in very wet areas or in standing water. Both *C. californica* and *P. aparinoides* have seeds with very deep, wide surface cells, perhaps making them buoyant (Shetler & Morin 1986). *Campanula californica* is endemic to coastal California from Santa Cruz County north to northern Mendocino County. Although *C. californica* and *P. aparinoides* are similar in habit and habitat, with buoyant seeds and retrorse hairs, they are not directly related phylogenetically according to molecular studies (Crowl et al. 2016), and their hypanthium and capsule shape and corolla shape are quite different. *Campanula californica* is placed in the monotypic genus *Eastwoodiella*.



Figure 6. *Eastwoodiella californica*, Mendocino County. Photo N. Morin.

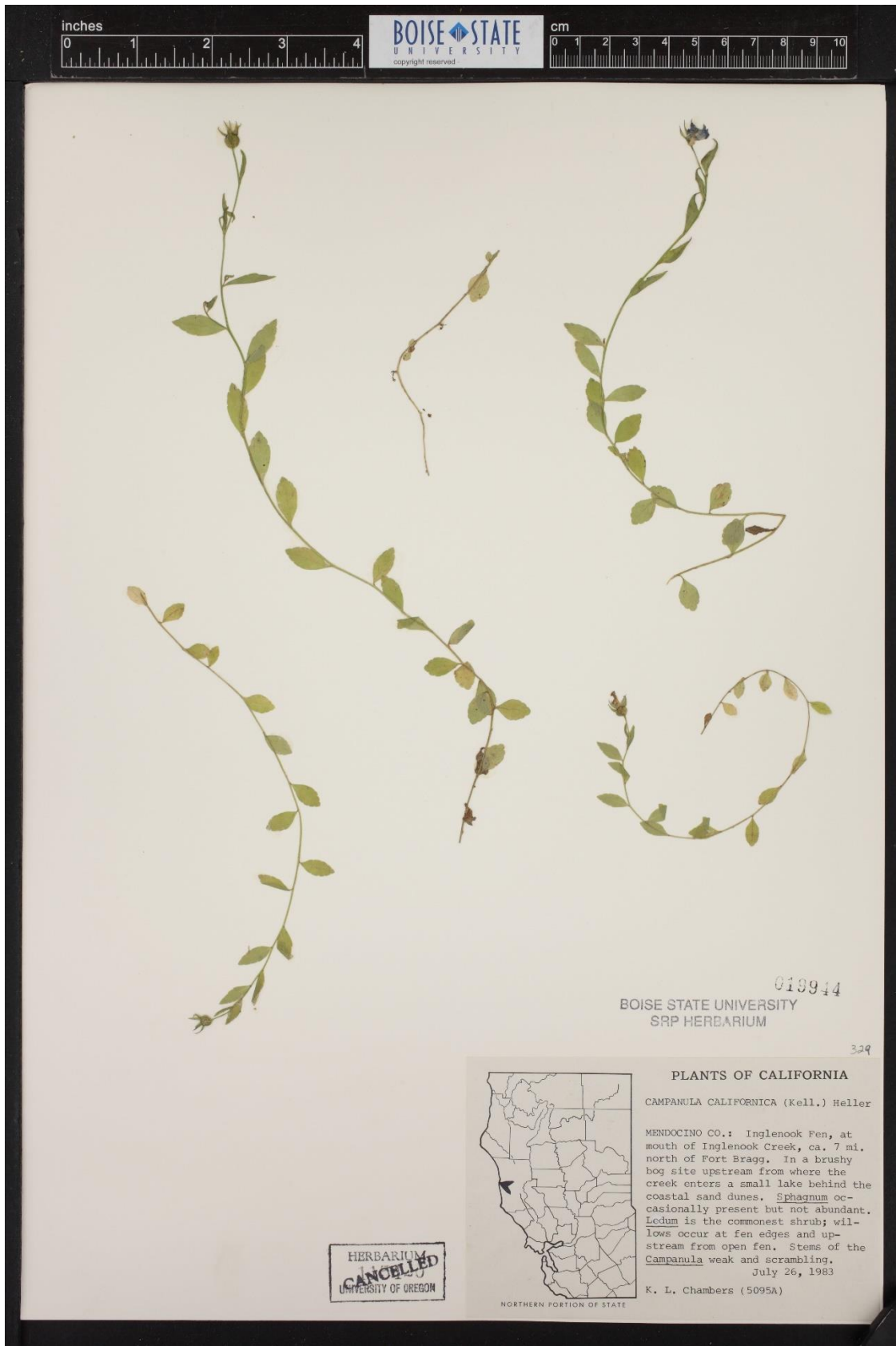


Figure 7. Representative specimen of *Eastwoodiella californica*, Chambers 5095A (SRP).

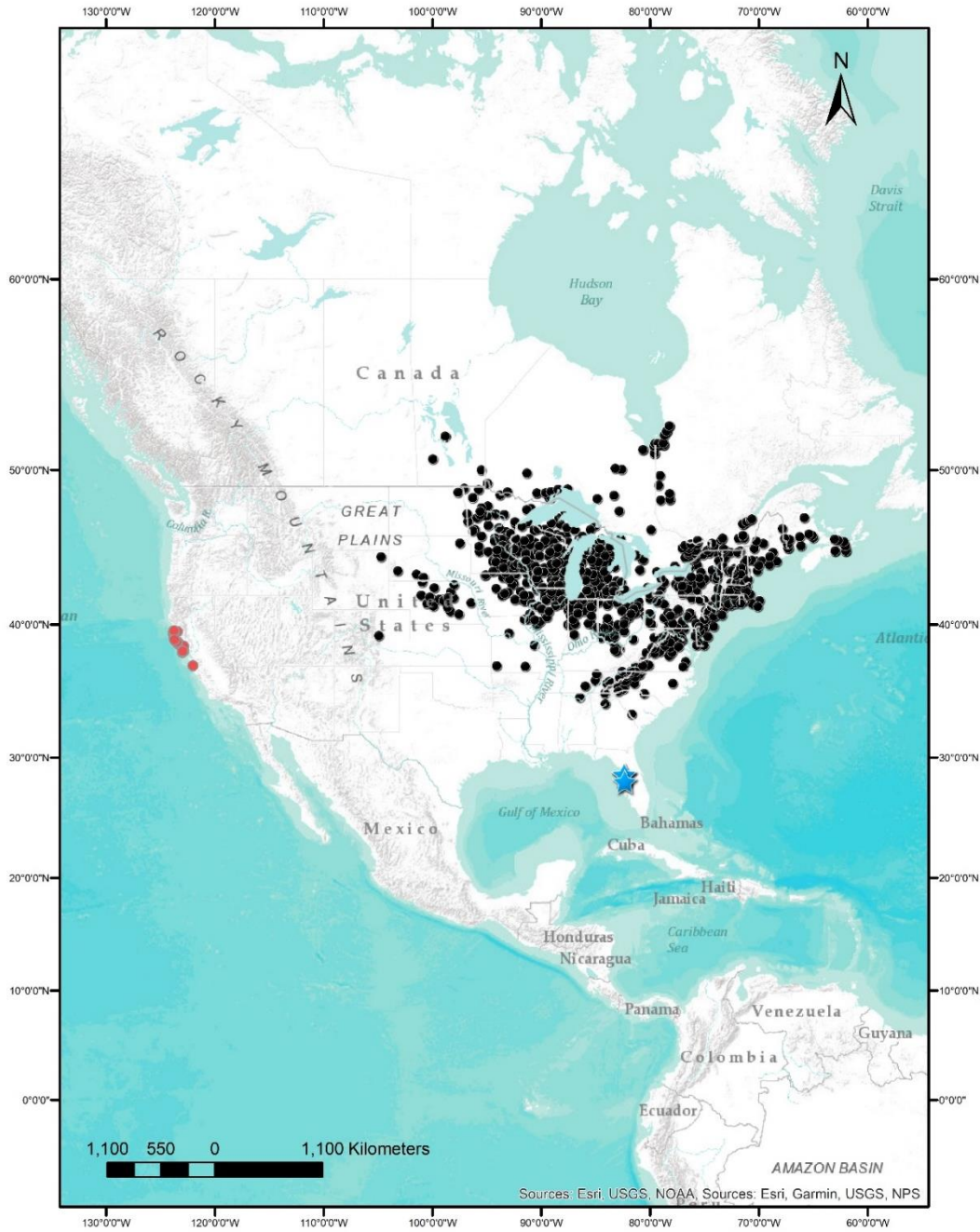


Figure 8. Distribution of *Palustricodon*, *Eastwoodiella*, and *Protocodon*. Blue stars, *Protocodon robinsiae*, locations based on herbarium specimens in USF. Black circles, *Palustricodon aparinoides*, U.S. distribution showing county presence based on records in Consortium of Northeast Herbaria 2020, Consortium of Pacific Northwest Herbaria 2020, SEINet 2020, and USDA, NRCS 2020; Canadian distribution based on records with coordinates from Consortium of Northeast Herbaria 2020 and Consortium of Pacific Northwest Herbaria 2020. Red circles, *Eastwoodiella californica* (Consortium of California Herbaria 2020).

EASTWOODIELLA Morin, **gen. nov.**

Type species, *Eastwoodiella californica* (Kellogg) Morin

Diagnosis: *Eastwoodiella* is similar to *Palustricodon* in habit and habitat and presence of retrorse hairs; it differs in having a campanulate corolla with lobes distinct about 50% the length, capsules rounded at base with parallel sides, and seeds terete in cross-section. It is similar to *Protocodon* in habit and habitat but differs in being perennial and having only chasmogamous flowers.

Etymology: The genus is named for Alice Eastwood, 1859–1953, revered botanist who was instrumental in developing the herbarium at the California Academy of Sciences and saving many of the type specimens from the 1906 earthquake and fire in San Francisco. She was one of the most prolific plant collectors in California and collected and studied many of the species of California Campanuloideae.

Eastwoodiella californica (Kellogg) Morin, **comb. nov.** *Wahlenbergia californica* Kellogg, Proc. Calif. Acad. Sci. 2:158. 1863. *Campanula californica* (Kellogg) A. Heller, Muhlenbergia 1(3): 46. 1904. **Lectotype** (designated here): Illustration: Fig. 49, based on “a plant brought from the coast range at some point north of San Francisco.” No specimen of this taxon collected in 1863 or earlier is extant at CAS. The material seen by Kellogg was presumably lost in the 1906 fire.

Campanula linnaeifolia A. Gray, Proc. Amer. Acad. Arts 7: 366. 1868. **TYPE: California.** Mendocino Co.: Swamps at Noyo, 1866, *Bolander 6571 bis*. (holotype: GH348401! isotypes: BM 901938; CAS 32399!; F 68734!; K 814513!; NY 232342!; PH 908326!; US 3222961!; YU 002081, YU 064154).

Campanula angustiflora*, *C. exigua*, *C. griffinii*, *C. sharsmithiae

Three of the four species of annual California *Campanula* are placed by Cowl et al. (2016) in the equivalent of Wendling et al.'s (2011) Rapunculus 2A clade, in a subclade sister to *Protocodon* and *Palustricodon*. This clade also includes the well-defined annual genera *Heterocodon* and *Githopsis* and perennial *Campanula prenanthoides* and *Campanula wilkinsiana* (the last two treated in the next section).

Fewer than 10% of the species of *Campanula* worldwide are annuals and most of these are in the Mediterranean region (Contandriopoulos 1984). All are in clades very distant from the California taxa (Cowl et al. 2014) and most have been placed in genera other than *Campanula*, e.g., *Annuae* Boiss. and *Roucela* Dumort. for twelve species in the *C. drabifolia* group; *Brachycodon* Fed. [= *Brachycodonia* Fed. ex Kolak.] for *Campanula fastigiata* Duf. ex A.DC, or as subgenera of *Campanula*, e.g., subg. *Megalocalyx* Damboldt, with twelve species in the *C. dichotoma* L. group, and subg. *Sicyocodon* (Feer) Damboldt.

The four annual California species have oblong, turbinate, or rhomboid hypanthia, the capsule dehiscing by medial pores (Morin 1980), setting them apart from the annual genera *Githopsis* (flowers chasmogamous, obconic capsule dehiscent by a hole left when the style falls off) and *Heterocodon* (flowers mostly cleistogamous, capsule broadly obconic or cylindric, dehiscing by basal pores), which also are in Wendling et al.'s (2011) Rapunculus 2A clade. See Table 1 for a comparison of characters.

The species of annual California campanulas are far more similar to each other than they are to any other Campanuloideae species, but they differ from each other in some significant ways. Most North American Campanuloideae have pollen that is 5- to 6-porate, the pores equatorial (Chapman 1966). *Campanula exigua*, *C. griffinii*, and *C. sharsmithiae* have pantoporate pollen (as do *Eastwoodiella californica* and *Campanulastrum americanum*), whereas most Campanuloideae pollen has 3–4 equatorial pores (Nowicke et al. 1992). *Campanula angustiflora* has 4–6 zonoporate pollen

(Nowicke et al. 1992). The chromosome number of $2n = 34$, found in *C. exigua*, *C. griffinii*, and *C. sharsmithiae* (Morin 1980), is the most common number in *Campanula* sensu lato, but it is unusual in annual campanulas, for which only $2n = 20, 24, 28, \text{ or } 32$ had been reported (Gadella 1964; Fedorov & Kovanda 1976; Contandriopoulos 1984). *Campanula angustiflora*, with $2n = 30$, is particularly unusual (Morin 1980) because this count has been reported only for *C. glomerata* L. (including *C. farinosa* (Roch.) Andr. Ex Bess.) and *C. michauxioides* Boiss. (Gadella 1964), neither of which have any relationship with the California species. *Peracarpa* also has $2n = 30$ as well as $2n = 28$ (Barnesky & Lammers 1997).

Campanula exigua (Fig. 9, 10), *C. griffinii* (Fig. 11), *C. sharsmithiae* (Fig. 12) and *C. angustiflora* (Fig. 13) are placed here in the new genus *Ravenella*.

RAVENELLA Morin, **gen. nov.**

Type species, *Ravenella exigua* (Rattan) Morin.

Diagnosis: *Ravenella* is similar to *Githopsis* in being annual, having divaricately sympodial branching, and occupying xeric habitats. It differs from *Githopsis* and other Campanuloideae having the combination of an oblong, turbinate, or rhomboid hypanthium with dark ribs and pale inter-rib areas, dehiscent by medial pores, and having pantoporate or irregularly 4–6 zonoporate pollen.

Etymology: The genus is named in honor of Peter H. Raven, in recognition of his contributions to our knowledge of the flora of California and his unstinting advocacy for plants of the world and their study.

Species 4, endemic to the California floristic province (Fig. 14).

***Ravenella exigua* (Rattan) Morin, comb. nov.** *Campanula exigua* Rattan, Bot. Gaz. (Crawfordsville) 11: 339. 1886. **LECTOTYPE** (designated here): **California**. Contra Costa Co.: Summit of Mt. Diablo, 14 Jun 1886, V. Rattan *s.n.* (JEPS 2508! Fig. 9; isolectotypes: F 372593!, GH 33006!, K 814510!).

Morin (1986) discussed reasoning for considering this JEPS specimen as the type but did not specifically designate it as the lectotype. An additional sheet at JEPS, *Rattan s.n.* June 1886, is probably also part of the type collection. Rattan mentioned two collections, his own from summit of Monte Diablo, 14 June 1886, and a collection by Mrs. Curran, 3 July, on Tamalpais “in full fruit and a larger and coarser form.” The Curran specimen is *Ravenella angustiflora*, which accounts for Rattan’s reference to the “calyx-lobes ... connivent after flowering.” Eastwood (1898) in her publication of *Campanula angustiflora* mentioned a collection as *C. angustiflora* by Mrs. Brandege (= M.K. Curran) made 5 July 1886 from Mt. Tamalpais (see below).

***Ravenella angustiflora* (Eastw.) Morin, comb. nov.** *Campanula angustiflora* Eastw., Proc. Calif. Acad. Sci. ser. 3, 1: 132–133. 1898. **LECTOTYPE** (designated here): **California**. Marin Co.: Mt. Tamalpais, 5 Jul 1886, M.K. Curran *s.n.* (CAS131! [image CAS32395!], labeled “holotype” in an unknown hand with an explanatory label by N. F. Bracelin, 1935; isolectotype: US 342449).

CAS 54678! (image CAS32396), annotated as holotype by me in 1980, contains two plants thought to have been remounted from the original CAS131 based on a label hand-written by J.T. Howell that suggested these had been rescued from the 1906 San Francisco fire. The specimen bears two collection labels, one with “*Campanula exigua* Rattan” over which is written “*brandegei* Eastwood sp. nov.” collected Summit of Tamalpais 5 July 1886, M.K.C. The second bearing “*Campanula angustiflora* Eastw. Mt. Tamalpais, Marin Co. Calif. Coll. Mrs. K. Curran, July 5, 1886.” Since CAS 131 does exist, however, with no suggestion of material having been removed, it should be the lectotype.

Ravenella griffinii (Morin) Morin, **comb. nov.** *Campanula griffinii* Morin, Madroño 27: 160. 1980. *Campanula angustiflora* Eastwood var. *exilis* J.T. Howell, Leafl. W. Bot. 2: 101. 1938. **TYPE: California.** San Benito Co.: the Pinnacles, 19 May 1937, *Howell 12938* (holotype: CAS 254819!; isotypes: GH 33007!, RSA 2264!, US 1765657!).

Ravenella sharsmithiae (Morin) Morin, **comb. nov.** *Campanula sharsmithiae* Morin, Madroño 27:159. 1980. **TYPE: California.** Stanislaus Co.: Red Mountains, 27 km (17 mi) above mouth of Arroyo del Puerto, Mt. Hamilton Range, 420 m, rocky, almost barren talus slope, associated with *Clarkia breweri*, 19 May 1935, *C.W. and H.K. Sharsmith 3144* (holotype: UC 571938!; isotypes: CAS 4008!; GH 33016!).



Figure 9. *Ravenella exigua*. Photo ©Neal Kramer.

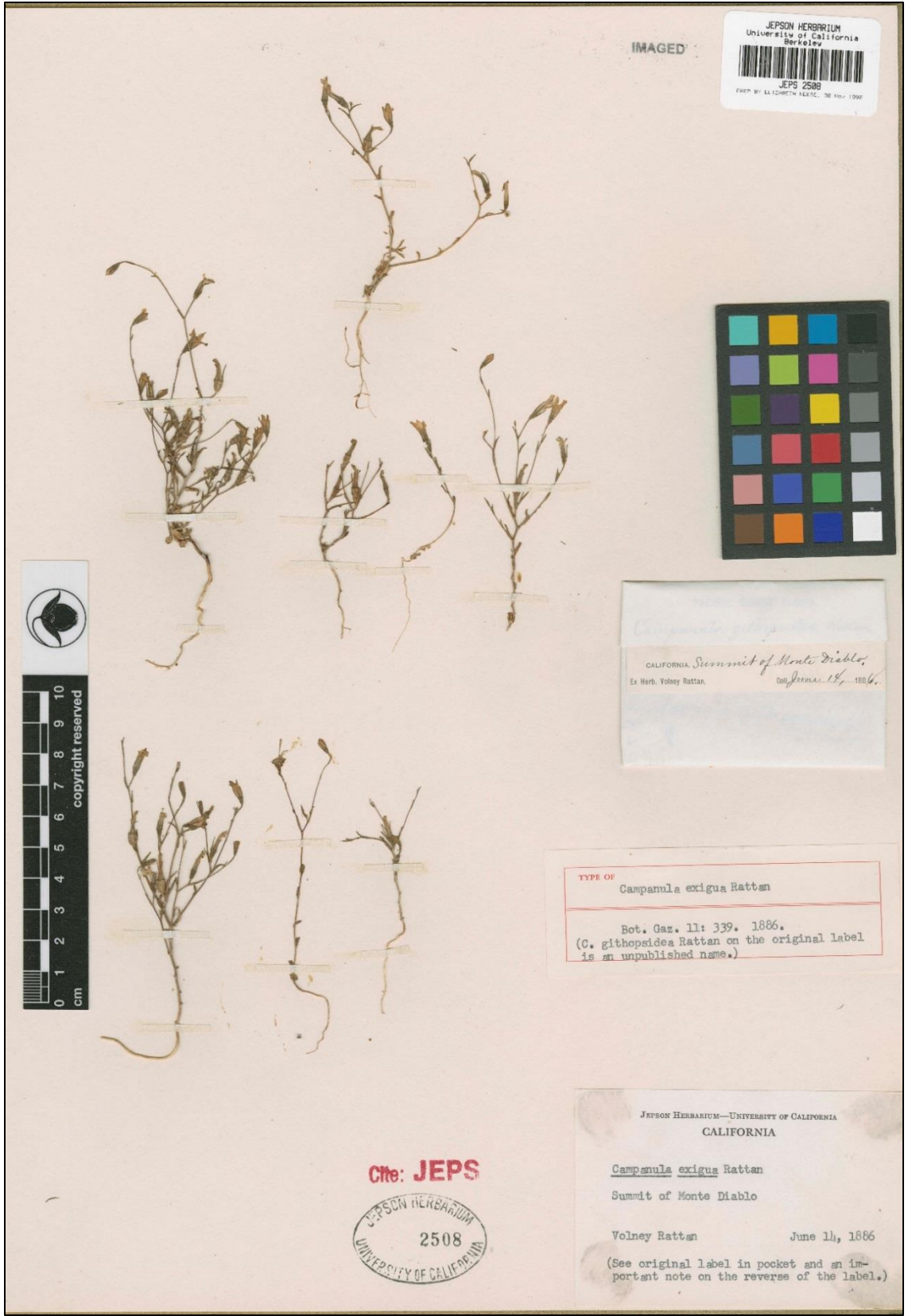


Figure 10. Holotype of *Ravenella exigua* (Rattan s.n., JEPS 2508).



Figure 11. *Ravenella griffinii*. Photo T. Gosliner.



Figure 12. *Ravenella sharsmithiae*. Photo A. Schusteff.



Figure 13. *Ravenella angustiflora*. Photo D. Greenberger.

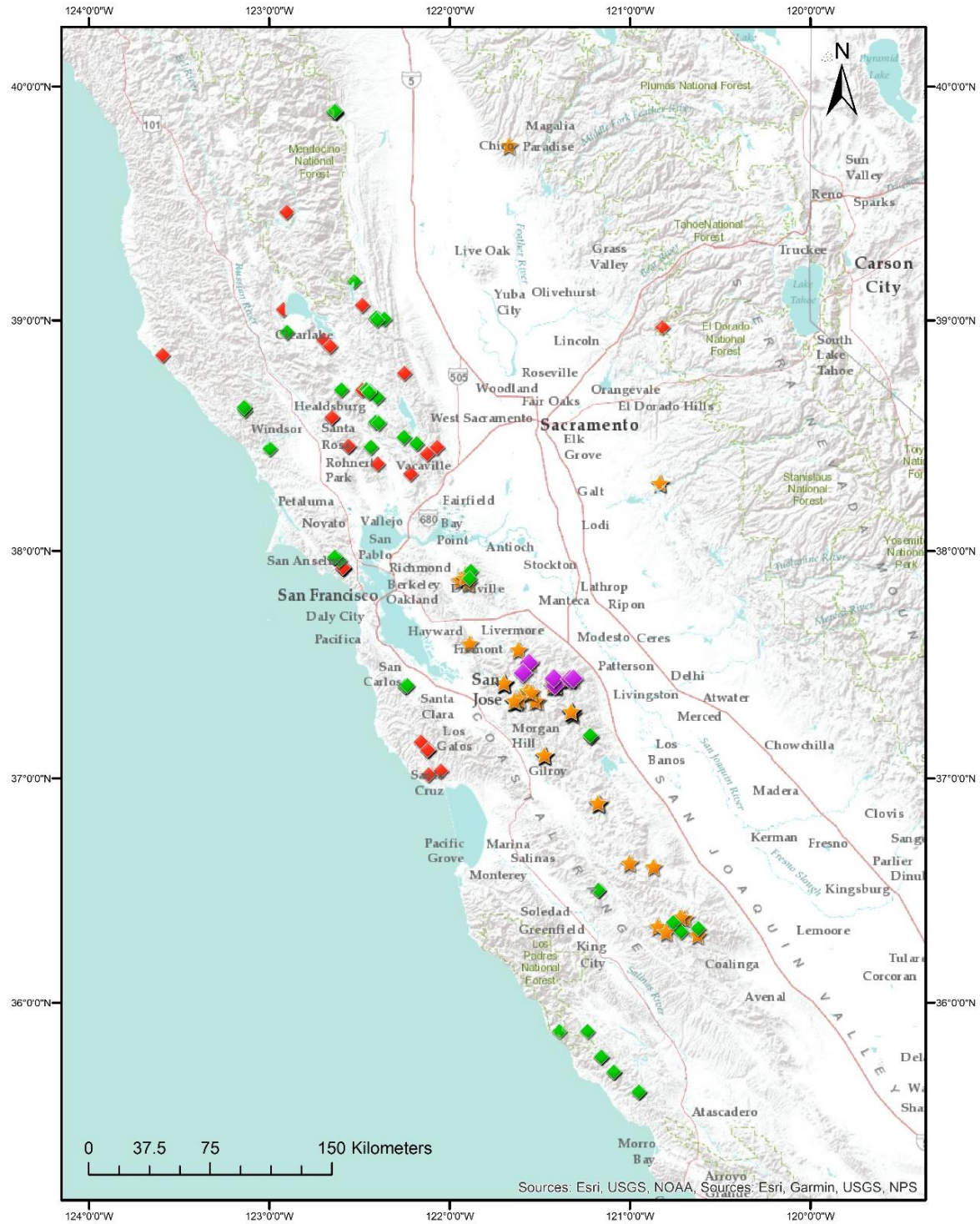


Figure 14. Distribution of *Ravenella*. *Ravenella griffinii*, green diamonds, *R. angustiflora*, red diamonds; *R. exigua*, orange stars; *R. sharsmithiae* purple diamonds. Consortium of California Herbaria (2020).

Campanula prenanthoides* and *Campanula wilkinsiana

McVaugh (1944) transferred *Campanula prenanthoides* to *Asyneuma* Griseb. & Schenk. He did not say explicitly which characters he thought *C. prenanthoides* shared with *Asyneuma*, but he

pointed out that *Asyneuma* was distinguished from *Campanula* by its deeply divided corolla with tardily separating lobes, and from *Phyteuma* L. by a narrowly paniculate rather than capitate or spicate inflorescence. Damboldt (1968) defined *Asyneuma* as species having corolla lobes connate less than $\frac{1}{4}$ their length and/or the capsule opening with medial or apical pores. *Campanula prenanthoides* does superficially resemble *Asyneuma*, and in the past I have followed McVaugh in keeping it as *Asyneuma* (Morin 2012), based on its having sulcate stems, flowers sometimes in condensed short shoots, the corolla deeply divided, and the style long-exserted, character states found in various species of *Asyneuma*. In looking more closely at *Asyneuma*, however, I find clear differences. In *Asyneuma* the corolla is divided clear to the base, with the lobes rotate, whereas in *C. prenanthoides* the corolla is divided (66--75 (--90)%, the lobes are erect distal to the tube and then flare out or reflex. In *Asyneuma* the dilated filament bases are large, often pigmented, and form a structure around the base of the style, the undilated portion immediately distal to this is also stiff and erect; in *C. prenanthoides* the filament bases are dilated but do not form a definite structure, and the rest of the filament is lax. Both *Asyneuma* and *C. prenanthoides* have long-exserted styles; in *Asyneuma*, the papillae are in a clearly defined distal zone, whereas in *C. prenanthoides* the papillae become increasingly less dense proximally. *Campanula prenanthoides* (Figs. 18, 19) has oblong to nearly round capsules (in longitudinal section) that are 3-lobed in cross-section and cordate at base, whereas most *Asyneuma* species have capsules that are obconical and terete in cross-section. *Asyneuma argutum* Bornm., *A. japonicum* (Miq.) Briq., and *A. amplexicaule* (Willd.) Hand.-Mazz. have hemispherical capsules somewhat cordate at base, but none of these species seems to belong in *Asyneuma*, judging from their position in recent phylogenies, and they are not closely related to *C. prenanthoides* (Crowl et al. 2016; Jones et al. 2017). *Campanula prenanthoides* does not belong in either *Campanula* or *Asyneuma*.

Yoo et al. (2018), placed *Campanula wilkinsiana* (Figs. 16, 17) in the equivalent of Wendling et al.'s *Rapunculus* 2A. Wendling et al. (2011) and Yoo et al. (2018) show *C. wilkinsiana* as sister to *C. prenanthoides*. *Campanula wilkinsiana* grows near standing or flowing water, has a woody caudex and thin rhizomes. Stems and leaves are generally glabrous, and leaves are densely arranged at the base of the stem, then evenly distributed distally. Its corolla lobes are not as deeply cut, and not as narrow as in *C. prenanthoides*, the style is exserted but not as far, the hypanthium is ribbed but more obconic than *C. prenanthoides*. *Campanula wilkinsiana* is known from only two clusters of populations on Mt. Shasta, in northern California. Margins of distal leaves on *Campanula wilkinsiana* have one or two pairs of sharp teeth that extend from the margin rather than being incised in it, and one pair near the apex, a character state also found in *Ravenella exigua*. It may be that *C. wilkinsiana* is the result of ancient hybridization or other gene flow among *Eastwoodiella californica*, *C. prenanthoides*, and/or *Ravenella exigua*. *Campanula prenanthoides* and *C. wilkinsiana* are here placed in a new genus, as follows.

SMITHIASTRUM Morin, **gen. nov.**

Type species, *Smithiastrum prenanthoides* (Durand) Morin

Diagnosis: *Smithiastrum* is similar to *Eastwoodiella* and *Palustricodon* in being a slender perennial, lacking a basal rosette, and having cauline leaves sessile or subsessile. It differs from them and other Campanuloideae in the combination of having the flowers terminal or axillary, pedicellate or nearly sessile, sometimes both in one inflorescence, solitary or in interrupted spikelike clusters, sometimes somewhat capitate, or inflorescence paniculate with longer pedicels, the hypanthium widely cylindrical or obconic, base squared and somewhat cordate, sepals very narrowly lanceolate, corolla with petals distinct in distal 66--90% of length, tube cylindrical or somewhat funnellform, sometimes slightly constricted below lobes, lobes linear or narrowly lanceolate, spreading to recurved; capsule hemispherical, oblong, or obconic, dehiscing by pores central or apical in center of the area between each lobe or broad rib.

Etymology: *Smithiastrum* is named in honor of James Payne Smith, Jr., emeritus faculty member in the Biology Department of Humboldt State University; a pioneer in plant conservation, authority on uses of plants especially by native peoples and on the toxicity of plants. The name also alludes to the star-shaped quality of the flowers.

Species 2, coniferous forests, California in the western Sierra Nevada, Cascade Range, Klamath Range, North Coast Range, and western Oregon in the Coast and Cascade Ranges (Fig. 15).

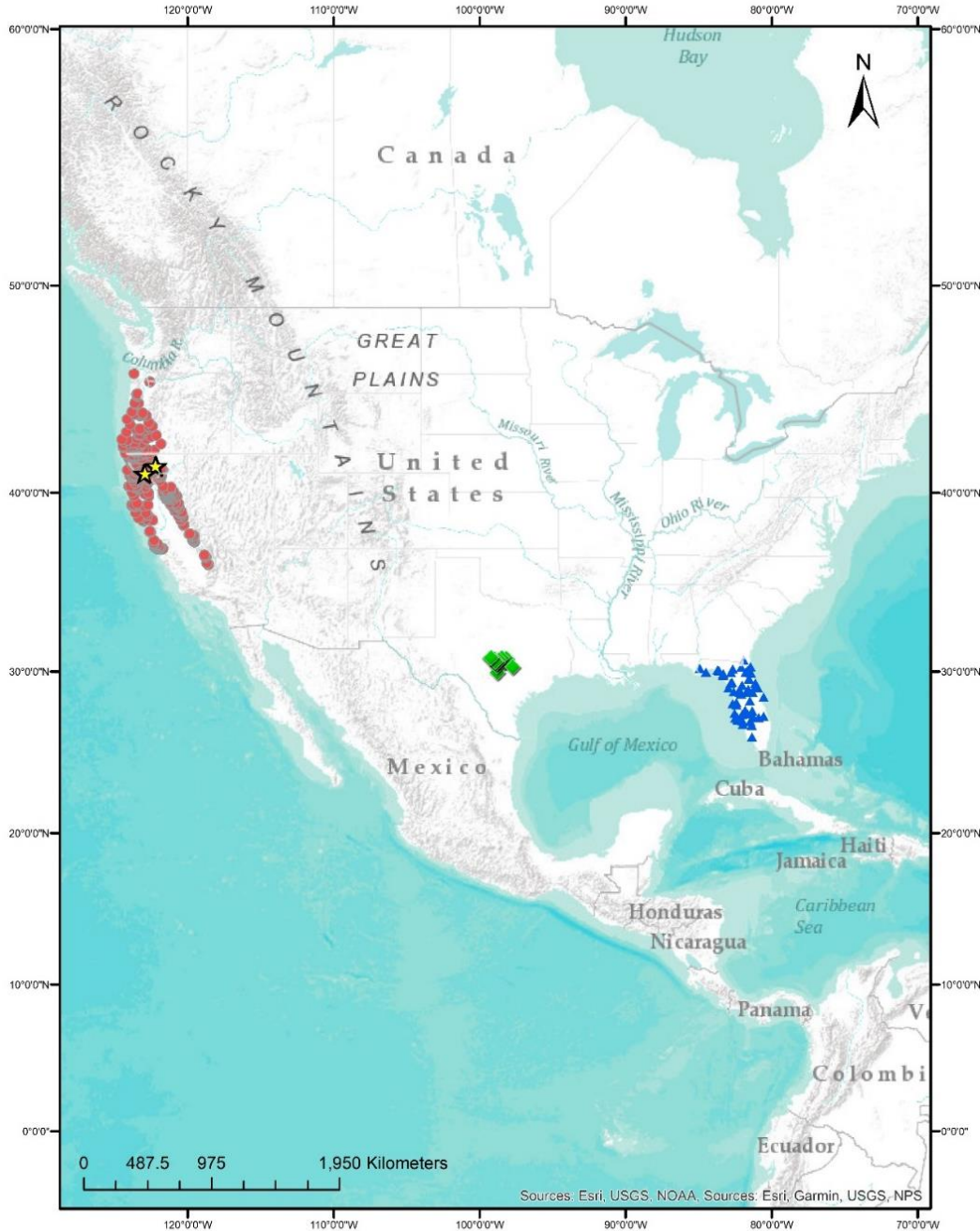


Figure 15. Distribution of *Smithiastrum*, *Poolea*, *Rotantheella*. Red circles, *Smithiastrum prenanthoides*; yellow stars, *Smithiastrum wilkinsiana* (Consortium of California Herbaria 2020; Consortium of Pacific Northwest Herbaria, 2020). Green diamonds, *Poolea reverchonii* (specimen records from BRIT). Blue triangles, *Rotantheella floridana* (Wunderlin et al. 2020).



Figure 16. *Smithiastrum wilkinsiana*. Photo E. White.

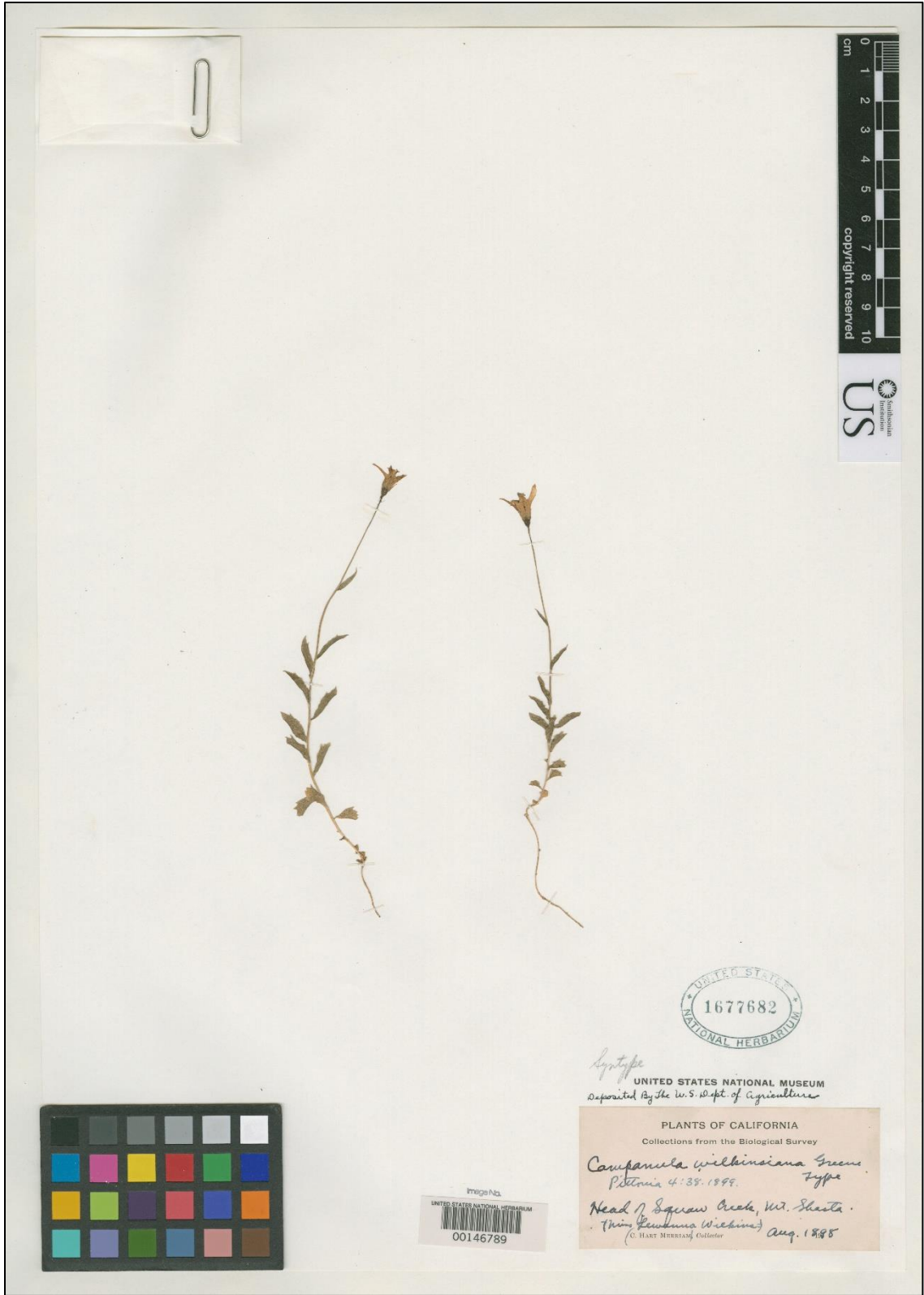


Figure 17. Representative specimen of *Smithiastrum wilkinsiana* (C. Hart Merriam Aug. 1885. US1677682).

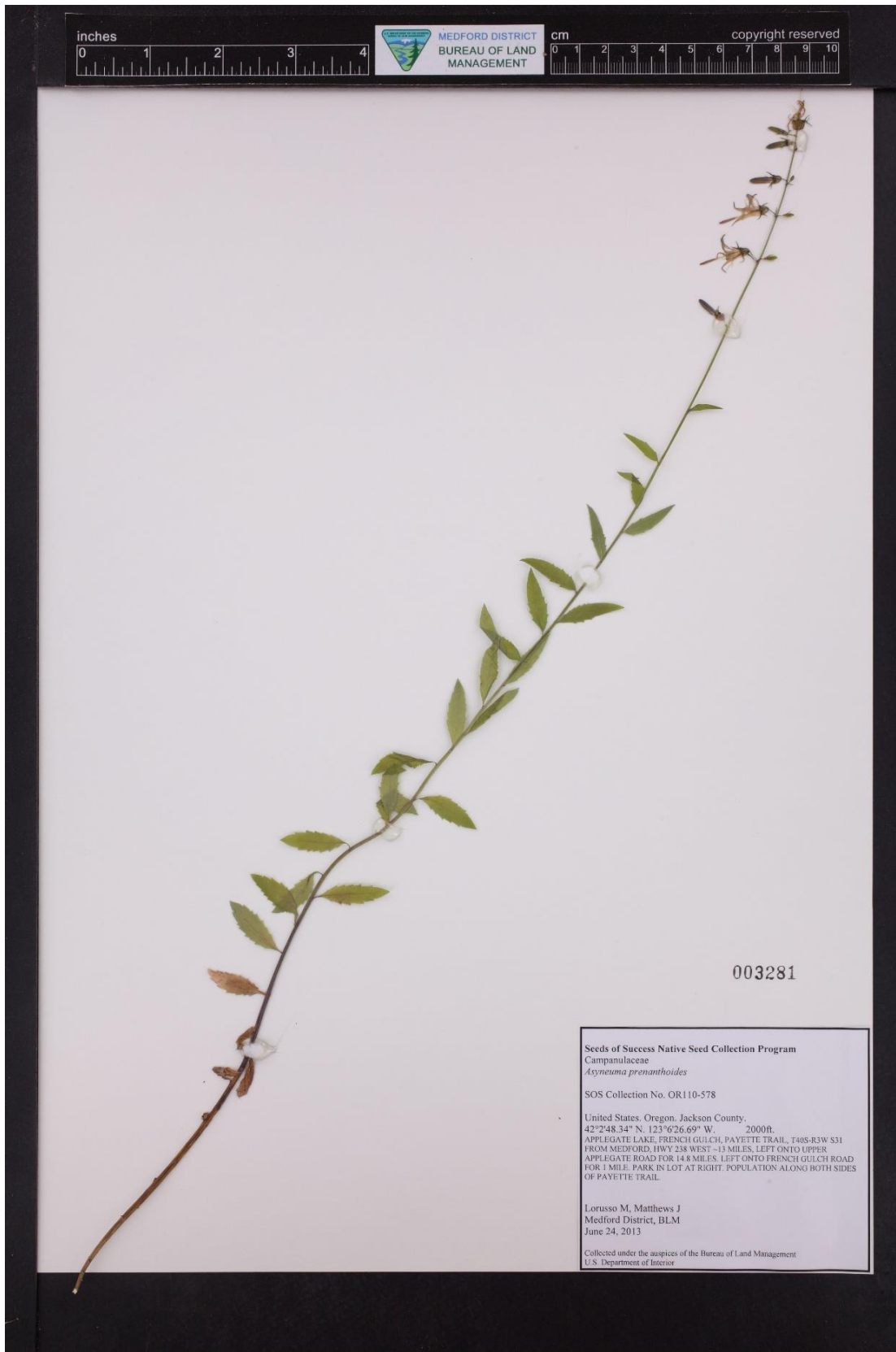


Figure 18. Representative specimen of *Smithiastrum prenanthoides* (BLM MD003281).



Figure 19. *Smithiastrum prenanthoides*. Photo S. Matson.

Smithiastrum prenanthoides (Durand) Morin, **comb. nov.** *Campanula prenanthoides* Durand, Pl. Pratten. Calif. 93. June 1855; J. Acad. Nat. Sciences, Philadelphia, ser. 2, 3:93. December 1855. **LECTOTYPE** (designated here): **California**, Nevada City, *s.d.*, Pratten *s.n.* (Barcode PH 414!, specimen stamp M1038627) containing Durand's handwritten Latin description and handwritten ticket; *Asyneuma prenanthoides* (Durand) McVaugh.

Smithiastrum wilkinsiana (Greene) Morin, **comb. nov.** *Campanula wilkinsiana* Greene, Pittonia 4:33. 1899. **LECTOTYPE** (designated here): **California**. Head of Squaw Creek, Mt Shasta, Aug 1898, L. Wilkins *s.n.* (US 1677682! image 146789).

Greene mentioned two specimens, both from Squaw Creek, one from August and one from September. The August specimen has good flowers and well-pressed leaves; the September specimen has developing capsules, poorly preserved. The August 1898 specimen is therefore chosen as the lectotype.

Campanula baileyi Eastw., Bull. Torrey Bot. Club 29: 525. 1902. **TYPE: California**. Trinity Co.: Mountains at the head of Canyon Creek, Aug 1899, V. Bailey *s.n.* (holotype: CAS 133).

Campanula reverchonii* and *Campanula floridana

Wendling et al.'s (2011) clade Rapunculus 2B is close but not immediately adjacent to the taxa discussed above. It contains the North American *Triodanis*, *Campanula reverchonii*, *Campanula floridana*, and *Campanulastrum americanum* (Table 2), which together are sister to European *Legousia* and more distantly related to *Asyneuma*. *Popoviocodonia uyemurae* (Kudô) Fed. is sister to the larger clade (Crowl et al. 2016 and Mansion et al. 2012, although Jones et al. 2017 has it as sister to *Campanula uniflora*).

Triodanis is an annual that generally grows in dry areas, often in grassland. It has clusters of chasmogamous and cleistogamous flowers that are sessile in axils of broad, nearly round bracts or narrower, lanceolate bracts, in an unbranched, spikelike inflorescence; the hypanthium and capsule are broadly cylindrical or clavate but not narrow and not or barely narrower below the sepals, corollas are light or mid-blue or lavender, the lobes elliptic to narrowly elliptic, the center paler but not a bright white, sharply defined eye, lobes distinct nearly to base; capsule broadly cylindrical or clavate, pores near the base, central, or near the apex, round, broadly oblong, slit-like, or capsule splitting from top. The Texan *Triodanis coloradoensis* (Buckley) McVaugh diverges from these patterns and is more similar to *Legousia falcata* (Ten.) Fritsch: the central white area of the corolla is slightly more defined than in other *Triodanis*, the hypanthium is longer, much thinner than other *Triodanis* and similar in length and width to *L. falcata*, the flowers terminal on branches from the axils of narrow bracts or sessile in axils, distal ones chasmogamous, proximal ones cleistogamous. *Triodanis leptocarpa* Nieuwl. also has a narrow hypanthium and narrow leaves and bracts, spicate inflorescence, and both chasmogamous and cleistogamous flowers. Of the seven species, Mansion et al. (2012) included *T. coloradoensis*, *T. leptocarpa*, *T. biflora*, and *T. perfoliata*, but without much resolution.

The European genus *Legousia* is a small annual with flowers sessile in axils of moderately narrow bracts in a branched or unbranched inflorescence, all chasmogamous, with corollas that are deep blue-purple, the lobes nearly round or very broadly elliptic, with a sharply delineated white center, the lobes distinct nearly to the base, the hypanthium and capsule cylindrical and very narrow, constricted just below the sepals, pore small, near apex. *Legousia falcata*, which McVaugh (1945) treated in *Triodanis*, supported by Haberle et al.'s analysis (2009), differs in having flowers with broad blue corolla lobes, the central white area less distinctly demarcated, the hypanthium cylindrical but broader than core *Legousia*, the flowers terminal on elongated axillary branches, distal flowers chasmogamous, proximal flowers cleistogamous. Wahlsteen and Tyler (2019) revisited the circumscription of taxa in *Legousia*.

Campanulastrum Small is a tall, coarse annual or biennial, with flowers in spikes composed fascicles of 1–5-flowered cymes in axils of lanceolate bracts, all chasmogamous, with corollas that are pale to bright, light blue or lavender blue, generally with a white central area, the lobes nearly rotate, distinct nearly to the base, lanceolate to deltate-ovate, hypanthium and capsules narrowly obconic, pores near the apex. The style of *Campanulastrum* is very long, declined and upcurved, a character state seen in *Campanula aurita* and *C. versicolor* (Janković et al. 2019).

Campanula reverchonii, a divaricately branching annual (Fig. 20) of xeric habitats, has terminal flowers, all chasmogamous, with narrowly campanulate, light lavender-blue corollas with longitudinal cream-colored areas and a dark purple ring at the base adaxially, the lobes distinct for 50–60% of the length (Fig. 21), differs from any *Campanula*, *Triodanis*, or *Legousia* in the shape of its narrowly ellipsoid hypanthium and capsule. It resembles *Triodanis* only in the shape of its seeds, which are lenticular, and in the dehiscence of the capsule. In both *T. coloradoensis* and *C. reverchonii* the pore opens from the top down, whereas in all other Campanuloideae in which dehiscence is by pores, the pores open from the bottom up (Shetler 1963; Shetler & Morin 1986).

Campanula floridana is a weak-stemmed, prostrate or clambering perennial of marshes, swamps, and similar wet areas, with flowers terminal, all chasmogamous, hypanthium and capsule obconic, corolla lobes distinct nearly to base, dark purple, linear-lanceolate. The capsule opens by a wide pore initiated near the base that occupies most of the space between the ribs. The seeds have seed coats with large lumina and irregularly shaped foramina in the walls, the surface rugose (Shetler & Morin 1986).

Campanula floridana and *C. reverchonii* cannot be kept as *Campanula*, neither fits into the other genera in this clade, and they do not resemble each other morphologically or in habit. Each is placed in a monotypic genus here.

POOLEA Morin, **gen. nov.**

Type species, *Poolea reverchonii* (A. Gray) Morin, **comb. nov.**

Diagnosis: *Poolea* is similar to *Githopsis*, *Ravenella*, and *Heterocodon* in being an erect annual with sympodial branching. It is similar to *Githopsis* and *Ravenella* in having narrow bracts and leaves. It differs from these genera in having an inflorescence with long internodes and in the shape of the hypanthium and capsule. It differs from *Triodanis* in having sympodial branching and in lacking cleistogamous flowers. It differs from *Rotanthea* in being annual and erect rather than perennial and clambering or prostrate. *Poolea* differs from these genera and from all other Campanuloideae in the combination of having the hypanthium and capsule ellipsoid with the pores near the apex and the valve opening at the top, curving down.

Etymology: *Poolea* is named in honor of Jackie M. Poole, botanist with the Texas Parks and Wildlife Department for more than thirty years, an effective and passionate advocate for plant conservation, especially of the Texas flora.

Poolea has one species. It is endemic to the Llano Uplift area of the Edwards Plateau, in central Texas (Fig. 15).

Poolea reverchonii (A. Gray) Morin, **comb. nov.** *Campanula reverchonii* A. Gray, Syn. Fl. N. Amer. 2(1): 396. 1886 (as "*Reverchoni*"). **TYPE: Texas.** Llano, 1885, *J. Reverchon s.n.* (holotype: GH [barcode 00348407]).

This specimen has a handwritten label, with "*Campanula reverchoni* n. sp." Gray wrote: "On granitic rocks, House Mountain, Llano and Burnet Co. Reverchon 1885" in the original description. Duplicates of the May 1885 collection under the number 1548 were widely distributed with a printed label headed "Texas Plants" and "*Campanula reverchoni*, Gray n. sp. Clefts of granitic rocks, House Mountain, Llano Co., May [no year given]." (duplicates are at CAS, CM, F, MO-3 sheets, NY-2 sheets, UC, US-2 sheets). It seems probable that Reverchon sent Gray one specimen, the one with the handwritten label, and after receiving the determination from Gray, produced the printed labels, which accompanied the duplicates he distributed. Therefore, the GH specimen is the one Gray would have seen. A sheet at MO (3460223) has an entirely handwritten label that reads "*Campanula reverchoni* Gr, granitic soil, House Mt., Llano (crossed out) Mason Co., May 1884-fr Burnet Co July 1884." A sheet at Kew has a label printed ex herb A. Gray and handwritten "*Campanula reverchoni* n. sp. A. G., Reverchon 1885, Texas" (image K000814507). Reverchon apparently collected this taxon in July 1884, Burnet Co., Texas, also numbered 1548, specimen at Missouri Botanical Garden (image MO 3460224). He may have mentioned this collection to Gray, which would account for the inclusion of Burnet Co. in the original description.



Figure 20. *Poolea reverchonii*. Holotype, Reverchon s.n., 1885 (GH).



Figure 21. *Poolea reverchonii*. Photo C. Chang.

ROTANTHELLA Morin, **nom. nov.**, a replacement name for *Rotantha* Small, Man. S.E. Fl. [Small] 1289. 1933, non *Rotantha* Baker, J. Linn. Soc. Bot. 25: 317. 1890.

Type species, *Rotanthea floridana* (S. Wats. ex A. Gray) Morin

Rotanthea is similar to some *Triodanis* in having an obconic hypanthium and capsule and corolla rotate with lobes distinct almost to base. It differs from *Triodanis* in being perennial, prostrate to clambering, lacking cleistogamous flowers, and its aquatic or mesic habitat. It differs from all other Campanuloideae in the combination of perennial habit, prostrate or clambering stems, basal rosette of leaves absent, cauline leaves evenly distributed, hypanthium obconic, corolla rotate or nearly so, petals free to base, capsule obconic to oblong-obconic, opening by oblong pores that occupy most of the space between ribs.

Etymology: Small did not give a reason for his choice of *Rotantha* as the name for this genus. The corollas of *Rotanthea floridana* are markedly rotate and the name may have alluded to that.

Rotanthea has one species, occurring in shallow water and wet ditches throughout most of Florida (Fig. 15), with outlying populations reported from Georgia, North Carolina, and Alabama (no precise localities, not shown on map).



Figure 22. *Rotanthea floridana*. Photo M. Groeneveld.



Figure 23. *Rotanthea floridana*. Photo A. de la Paz.



Figure 24. Representative specimen of *Rotanthea floridana* (Lakela 25900, USF).

Rotanthea floridana (S. Wats. ex A. Gray) Morin, **nom. nov.** *Campanula floridana* S. Wats. ex A. Gray, Syn. Fl. N. Amer. 2(1): 13. 1878. *Rotanthea floridana* (S. Wats. ex A. Gray) Small, Man. S.E. Fl. [Small] 1289. 1933. **Lectotype** (designated here): “East Florida, coll. Edward Palmer, M.D., 1874, Indian River, *C. floridana* n. sp. S.W.” (GH, image GH 68140!).

This sheet appears to have four collections on it, two of which are by A.P. Garber, and the other two, by Palmer and Feay, are cited in the original description by Gray. The Palmer collection is a plant with small, elliptic leaves. It is nearest the label and is the least ambiguous as to collector. It has both a flower and a capsule. The Feay collection is in an envelope. Florida, Pease River, Dr. Feay, GH image GH68140!; K, image K000814514, NY, image NY00232343 (from Chapman Herbarium in the Columbia College Herbarium). Specimens labeled *Campanula calycosa* Torr., n.sp., “East Florida (from Dr. Torrey 1859)”, at GH (image HUH1795516) and one labeled “*Campanula calycosa* Torr. & Gr. n. sp., = *floridana* A. Gray 1841” at Kew (image: K000814515) are also *Rotanthea floridana*.

Campanula uniflora

Campanula uniflora, Wendling et al.’s (2011) Rapunculus 2C clade, which is circumarctic and occurs in the high alpine regions of western North America, was, with *Petromarula* Vent. ex R. Hedw., sister to *Asyneuma*, *Physoplexis*, and *Phyteuma* in Schneeweiss et al. (2013), and in a clade with *Petromarula* and *Asyneuma japonicum* in Yoo et al. (2018). *Campanula uniflora* is unique in having a dark blue hypanthium, the capsule clavate, becoming nearly black, pore near apex. *Campanula uniflora* is not similar in any way to these other genera. Fedorov (1957) assigned *Campanula uniflora* to *Campanula* subsect. *Melanocalyx*, which is elevated to genus here.

MELANOCALYX (Fed.) Morin, **stat. nov.** *Campanula* L. subsect. *Melanocalyx* Fed., Flora S.S.R. XXIV: 467. 1957. **Type species:** *Melanocalyx uniflora* (L.) Morin

Melanocalyx uniflora (L.) Morin, **comb. nov.** *Campanula uniflora* L., Sp. Pl. 1: 231. 1753. **LECTOTYPE:** Herb. Linnaeus No. 221.2 (LINN [digital image!]), Ferrer-Gallego (2019).

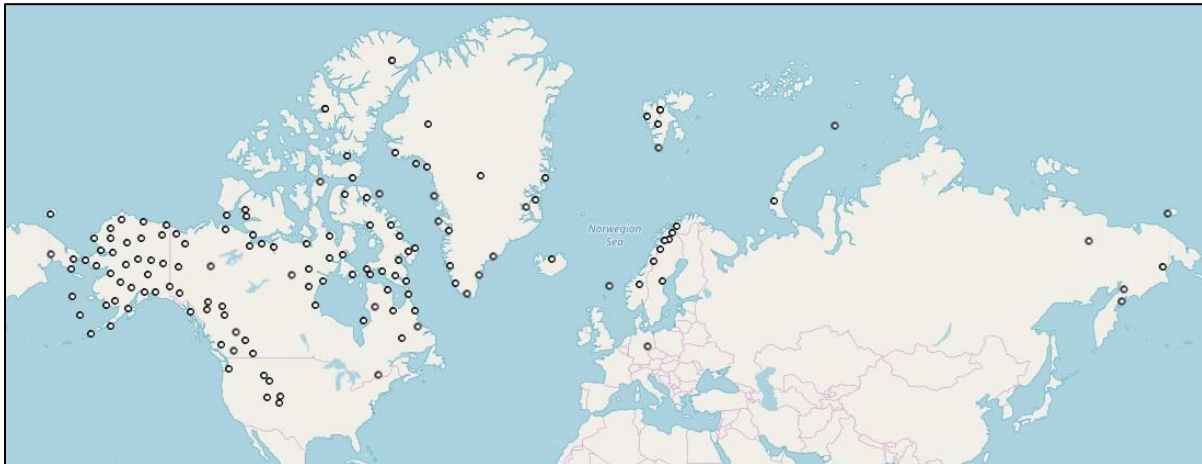


Figure 25. Distribution of *Melanocalyx uniflora* (GBIF 2020; Consortium of Pacific Northwest Herbaria 2020; Consortium of Northeastern Herbaria, 2020; SEINet 2020).



Figure 26. Representative specimen of *Melanocalyx uniflora* (Patterson & Beaty, August 1882. UVMVT158007).

DISCUSSION

Wendling et al. (2011) suggested that campanuloid ancestors colonized North America at least six times:

1. *Campanula chamissonis*, the Aleutian species of the *Campanula* clade, with an east Asian origin (Yoo et al. 2018).
2. Rapunculus 2A, which, based on Yoo et al. 2018, would have a Eurasian origin through an ancestor shared with *Peracarpa*.
3. Rapunculus 2B, from an introduction of a relative of the Macaronesian/Mediterranean *Legousia* (Jones, 2017).
4. Rapunculus 2C, *Campanula uniflora*, from east Asia (Roquet et al. 2008; Wendling et al. 2011; Yoo et al. 2018).
5. Rapunculus 1A, the “Cordilleran” species, high elevation and alpine taxa.
6. Rapunculus 1B, *Campanula rotundifolia*, also with a European origin.

Earlier authors also had hypothesized multiple introductions less explicitly (e.g., Morin, 1983; Shetler & Morin 1986; Eddie et al. 2003; Haberle et al. 2009; Mansion et al. 2012).

Wendling et al.’s Rapunculus 2A Clade

Phylogenetic analysis of Peracarpeae (Zhou et al. 2012) showed that the eastern Asian monotypic *Peracarpa* constituted a clade with North American *Heterocodon*, *Githopsis*, and three species now in new genera: *Protocodon*, *Ravenella*, and *Smithiastrum*, supporting a Campanuloideae disjunction between Eurasia and North America 16.84 (13.12–20.97) m.y.a. (Zhou et al. 2012). Yoo et al. (2018) suggested this split occurred earlier, more than 30 m.y.a. Yoo et al. (2018) estimated that *Palustricodon*, now widespread in central and eastern North America, separated from *Protocodon*, now limited to a small area in Florida, about 18 m.y.a. *Protocodon* appears to be a relict in the Brooksville Range, which may have remained above sea level during the Pleistocene (James 1961). It exhibits characters that appear again in various other North American taxa, such as occurrence in wet habitats, annual habit, clambering aspect, sympodial branches, leaves evenly distributed on the stem, cleistogamy, and specialized seeds (Table 1).

The *Palustricodon/Protocodon* clade is sister to the remaining species in Rapunculus 2A, all western taxa (Yoo et al. 2018). The similarity in habit, habitat, and special features like retrorse hairs shared by *Eastwoodiella* and *Palustricodon* suggests that these two taxa have retained some characters from a common ancestor. *Ravenella*, *Smithiastrum*, *Heterocodon*, and *Githopsis* diverged from *Protocodon/Palustricodon* about 22 m.y.a. (Yoo et al. 2018); perennial, woodland *Smithiastrum prenanthoides* split from *Ravenella/Heterocodon/Githopsis*, all annuals, about 10 m.y.a. (Yoo et al. 2018). *Eastwoodiella*, limited to coastal California, was not included in the more recent studies but is placed in this clade by Mansion et al. (2012) and Crowl et al. (2016); its 3-lobed hypanthium and capsule suggest a relationship with the more widespread *Smithiastrum prenanthoides*. *Ravenella* and *Githopsis* both show the rapid speciation typical of annuals adapted to xeric conditions and specialized soil types in the California Floristic Province (Raven & Axelrod 1978). The presence in *Ravenella* of a chromosome number of $2n = 34$ (Morin 1980) and pantoporate pollen in all but *R. angustiflora*, which has $2n = 30$ and 4–6 zonoporate pollen (Nowicke et al. 1992), suggests there is more complexity in this genus that needs study. *Ravenella* and *Githopsis* have both self-pollinating and outcrossing species (Morin 1980, 1983). *Githopsis tenella*, known from only three populations in Kern and Tulare counties, California, shares the presence of both chasmogamous and cleistogamous flowers and broad bracts (Morin 1983) with the widespread *Heterocodon*, which has predominantly cleistogamous flowers.

Wendling et al.'s *Rapunculus* 2B clade

Legousia, a European genus of annuals, is sister to the North American taxa in *Rapunculus* 2B, the separation occurring about 20 m.y.a. (Yoo et al. 2018). *Campanulastrum* is basal to the North American portion of the clade, with *Poolea* sister to *Triodanis* and *Rotanthea*. Except for *Poolea*, these taxa share an obconic or cylindrical hypanthium and capsule and a deeply divided corolla (Table 2). Barnard-Kubow et al. (2015) suggested that the distribution of *Campanulastrum* represented multiple lineages that survived the Last Glacial Maximum in at least three refugia in the Appalachians and on the Atlantic and Gulf Coasts, which subsequently migrated north. *Poolea*, a relict annual limited to the Llano Uplift of central Texas, split from annual *Triodanis* and perennial *Rotanthea* more than 10 m.y.a. (Yoo et al. 2018). The center of diversity of *Triodanis* is in Texas (McVaugh 1945; Haberle et al. 2009): *Triodanis coloradoensis* and *T. texana* McVaugh are limited to central Texas and the remaining five species are more or less widespread, with their distribution including Texas. They all occupy relatively xeric habitats. *Rotanthea*, in contrast, is perennial and occurs in wet habitats. Its position in the clade might argue for inclusion in *Triodanis*, but its distinctive growth form, flower morphology, and habitat suggest it is on a different evolutionary path from *Triodanis*.

Wendling et al.'s *Rapunculus* 2C clade

The relationships of the arctic-alpine *Melanocalyx uniflora* to other Campanuloideae is unclear. It is placed in a clade with *Petromarula*, *Phyteuma*, and *Physoplexis* in Wendling et al. (2011). *Melanocalyx* is not similar morphologically to any of these.

Additional considerations

Campanuloideae taxa in North America have been separated from Eurasian relatives for millions of years (Yoo et al. 2018). Within North America, some of them are separated from each other by vast distances and dramatically different topography. Over geologic time their populations will have expanded and contracted, so even geographically distant species, or their ancestors, may have grown together at one time or another. The western species in *Rapunculus* 2 often grow sympatrically with each other or in close approximation in various combinations, although usually occupying different microhabitats. In the east, distributions of *Campanulastrum* and *Triodanis* overlap, as do the *Triodanis* and *Poolea* distributions. Some taxa in Wendling et al.'s (2011) *Rapunculus* 1 clade (the “cordilleran” species and *C. divaricata*, as well as *C. rotundifolia*) are sympatric with *Rapunculus* 2 species. Flower morphology is distinctive in some of these species, but the general pollination mechanism is similar in all of them and there is no reason to suppose that cross-pollination cannot occur. The possibility of historic gene flow should be kept in mind when untangling relationships in the remaining North American campanuloids.

CONCLUSION

These new North American genera reflect habitat similarities, geographic distribution, morphological similarities, and genetic affinities as expressed in phylogenetic analyses. They differ morphologically from each other and from other Campanuloideae at least as much as, or more than, most other genera in the subfamily. Retaining them in *Campanula* obscures their relationships and makes it difficult to portray phytogeographic patterns. Recognizing them as new, well-defined genera will facilitate consideration of evolutionary patterns in the family and on the continent.

ACKNOWLEDGEMENTS

I am grateful to Tina J. Ayers and William M.M. Eddie for reviewing the manuscript and for their helpful comments. I thank Kanchi Gandhi for his help with nomenclature and typification. Jennifer H. Richards and Tatyana V. Shulkina provided helpful advice on morphology.

I thank the following herbaria for loaning specimens to MO for my study: ALA, ARIZ, ASU, AUA, BM, CAN, CAS, CHSC, CHSD, CM, COLO, DAV, DES, DS, DUKE, DUL, F, FLAS, FSU, FTG, GA, GFND, GH, HSC, ID, IDS, JEPS, JSU, LAF, LL, LSU, LTU, MICH, MIN, MNA, MONT, MONTU, NCSC, NCU, NDA, NEB, NLU, NO, NY, OBI, OKL, OMA, ORE, OSC, OSU, PAC, PH, POM, PUA, RM, RSA, SDC, SLU, SMU, TAES, TAMU, TENN, TEX, UARK, UC, UCHT, UMO, UNA, UNLV, UNM, US, USF, UT, UTC, VDB, VPI, WCW, WILLU, WS, WTS, WTU, WVA. I thank Missouri Botanical Garden (MO), Deaver Herbarium (ASC), UC/JEPS herbaria, California Academy of Sciences (CAS), National Museum of Natural History—Smithsonian Institution (US), Natural History Museum (BM), Royal Botanic Gardens, Kew (K); Muséum National d'Histoire Naturelle—Paris (P); Herbarium, Conservatoire de Jardin botanique de la Ville de Genève (G), and Royal Botanic Gardens, Edinburgh (E), for allowing me to work in their herbaria for extended periods.

LITERATURE CITED

- Akcin, T. 2009. Seed coat morphology of some Turkish *Campanula* (Campanulaceae) species and its systematic implication. *Biologia* 64: 1089–1094.
- Barnesky, A.L. and T.G. Lammers. 1997. Revision of the endemic Asian genus *Peracarpa* (Campanulaceae: Campanuloideae) via numerical phenetics. *Bot. Bull. Acad. Sin.* 38: 49–56.
- Borsch, T., N. Korotkova, T. Raus, W. Lobin, and C. Löhne. 2009. The petD group II intron as a species level marker: Utility for tree inference and species identification in the diverse genus *Campanula* (Campanulaceae). *Willdenowia* 39: 7–33.
- Cellinese, N., S.A. Smith, E.J. Edwards, S.-T. Kim, R.C. Haberle, M. Avramakis, M.J. Donoghue. 2009. Historical biogeography of the endemic Campanulaceae of Crete. *J. Biogeogr.* 36: 1253–1269.
- Chapman, J.L. 1966. Palynology in Campanulaceae. *Trans. Kansas Acad. Sci.* 69: 197–200.
- Consortium of California Herbaria. 2020. Consortium database (data provided by the participants of the Consortium). <ucjeps.berkeley.edu/consortium/>
- Consortium of Pacific Northwest Herbaria. 2020. Consortium database (data provided by the participants of the Consortium). <<http://pnwherbaria.org>>
- Consortium of Northeastern Herbaria. 2020. Consortium database (data provided by the participants of the Consortium). <portal.neherbaria.org>
- Contandriopoulos, J. 1984. Polyphylétisme des campanules annuelles. *Bull. Soc. Bot. Fr.* 131, *Lettres bot.*, 1984 (4/5): 315–324.
- Cosner, M.E., R.K. Jansen, and T.G. Lammers. 1994. Phylogenetic relationships in the Campanulales based on *rbcL* sequences. *Pl. Syst. Evol.* 190: 79–85.
- Cosner, M.E., L.A. Raubeson, and R.K. Jansen. 2004. Chloroplast DNA rearrangements in Campanulaceae: Phylogenetic utility of highly rearranged genomes. *BMC Evol. Biol.* 4: 27.
- Crowl, A.A., E. Mavrodiev, G. Mansion, R. Haberle, A. Pistarino, G. Kamari, D. Phitos, T. Borsch, N. Cellinese. 2014. Phylogeny of Campanuloideae (Campanulaceae) with emphasis on the utility of nuclear pentatricopeptide repeat (PPR) gene. *PLoS ONE* 9: 1–14.
- Crowl, A.A., N.W. Miles, C.J. Visger, K.Hansen, T. Ayers, R. Haberle, and N. Cellinese. 2016. A global perspective on Campanulaceae: Biogeographic, genomic, and floral evolution. *Amer. J. Bot.* 103: 233–245.
- Dambolt J. 1968. Vorarbeiten zu einer revision der gattung *Asyneuma* (Campanulaceae). I. *Willdenowia* 5: 35–54.

- De Candolle, A. 1830. Monographie des Campanulées. Viii + 384 pp. + plates 1–20. Veuve Desray, Paris.
- De Chaine, E.G., B.M. Wendling, and B.R. Forester. 2014. Integrating environmental, molecular, and morphological data to unravel an ice-age radiation of arctic-alpine *Campanula* in western North America. *Ecol. Evol.* 20: 3940–3959.
- Eddie, W.M.M. 1997. A global reassessment of the generic relationships in the bellflower family (Campanulaceae). Ph.D. thesis, University of Edinburgh.
- Eddie, W.M.M., T. Shulkina, J. Gaskin, R.C. Haberle, and R.K. Jansen. 2003. Phylogeny of Campanulaceae s.str. inferred from ITS sequences of nuclear ribosomal DNA. *Ann. Missouri Bot. Gard.* 90: 554–575.
- Eddie, W.M.M., and M.J. Ingrouille. 2008. Polymorphism in the Aegean “five-loculed” species of the genus *Campanula*, Section *Quinqueloculares* (Campanulaceae). *Nordic J. Bot.* 19: 153–169.
- Fedorov, A.A. 1957. Family CLVIII. Campanulaceae. Pp. 128–475 in B.K. Shishkin (ed.). *Flora of the U.S.S.R.*, Vol. XXIV, Dipsacaceae, Cucurbitaceae, Campanulaceae. [English translation published by the Israel Program for Scientific Transitions.]
- Fedorov, A.A. and M. Kovanda. 1976. *Campanula*. Pp. 4–93 in T.G. Tutin, N.A. Burges, A.O. Chater, J.R. Edmondson, V.H. Heywood, D.M. Moore, D.H. Valentine, S.M. Walters, and D.A. Webb (eds.). *Flora Europaea*, Vol. 4.
- Ferrer-Gallego, P. P. 2019. Typification of Linnaean specific names in the genus *Campanula* (Campanulaceae). *Taxon* 68: 1350–1358.
- Gadella, T.W.J. 1964. Cytotaxonomic studies in the genus *Campanula*. *Wentia* 11: 1–104.
- GBIF.org (20 June 2020). GBIF Occurrence Download <<https://doi.org/10.15468/dl.2b8tv4>>
- Haberle, R.C., A. Dang, T. Lee, C. Penaflor, H. Cortes-Burns, A. Oestreich, L. Raubeson, N. Cellinese, E.J. Edwards, S.T. Kim, W.M.M. Eddie, and R.K. Jansen. 2009. Taxonomic and biogeographic implications of a phylogenetic analysis of the Campanulaceae based on three chloroplast genes. *Taxon* 58: 715–734.
- Hong, De-Yuan. 2015. A Monograph of *Codonopsis* and Allied Genera (Campanulaceae). Science Press, Beijing.
- Hong, De-Huan and Q. Wang. 2015. A new taxonomic system of the Campanulaceae s.s. *J. Syst. Evol.* 53: 203–209.
- Janković, I. Z. Satovic, Z. Liber, N. Kuzmanović, R. Di Pietro, I. Radosavljević, Z. Nikolov, and D. Lakušić. 2019. Genetic and morphological data reveal new insights into the taxonomy of *Campanula versicolor* s.l. (Campanulaceae). *Taxon* 68: 340–369.
- Jones, K.E., N. Korotkova, J. Petersen, T. Henning, T. Borsch, and N. Kilian. 2017. Dynamic diversification history with rate upshifts in Holarctic bell-flowers (*Campanula* and allies). *Cladistics* 33: 1–30.
- Kunzer, J.M., R.P. Wunderlin, L.C. Anderson, and J.R. Burkhalter. 2009. New and noteworthy plants from Florida. *J. Bot. Res. Inst. Texas* 3: 331–337.
- Lakušić, D., W.M.M. Eddie, L. Shuka, M. Lazarević, and Z. Barina. 2019. The evolving “fate” of *Asyneuma comosiforme*: Validation of *Hayekia*, a new monotypic genus of Campanulaceae from Albania. *Willdenowia* 49: 81–93.
- Lammers, T.G. 2007. World checklist and bibliography of Campanulaceae. Royal Botanic Gardens, Kew, Richmond.
- Liveri E., A. Crawl, and N. Cellinese. 2019. Past, present, and future of *Campanula* systematics. *Bot. Chron.* 21: 209–222.
- Mansion, G., G. Parolly, A.A. Crawl, E. Mavrodiev, N. Cellinese, M. Oganessian, K. Fraunhofer, G. Kamari, D. Phitos, R. Haberle, G. Akaydin, N. Ikinici, T. Raus, and T. Borsch. 2012. How to handle speciose clades? Massive taxon-sampling as a strategy towards illuminating the natural history of the bell flowers (*Campanula*, Campanuloideae). *PLoS ONE* 7: 1–23. <<https://doi.org/10.1371/journal.pone.0050076>>
- McVaugh, R. 1944. Notes on North American Campanulaceae. *Bartonia* 23: 36–40.

- McVaugh, R. 1945. The genus *Triodanis* Rafinesque, and its relationships to *Specularia* and *Campanula*. *Wrightia* 1: 13–52.
- McVaugh, R. 1948. Generic status of *Triodanis* and *Specularia*. *Rhodora* 50: 38–49.
- Menezes, T., M.M. Romeiras, M.M. de Sequeira, and M. Moura. 2018. Phylogenetic relationships and phylogeography of relevant lineages within the complex Campanulaceae family in Macaronesia. *Ecol. Evol.* 2018: 88–108.
- Morin, N.R. 1980. Systematics of the annual California Campanulas (Campanulaceae). *Madroño* 127: 149–163.
- Morin, N.R. 1983. Systematics of *Githopsis* (Campanulaceae). *Syst. Bot.* 8: 436–468.
- Morin, N.R. 2012. Campanulaceae (except *Downingia* and *Lobelia*). Pp. 588–598, in B.G. Baldwin, D.H. Goldman, D.J. Keil, R. Patterson, T.J. Rosatti, and D. H. Wilken (eds.). *The Jepson Manual: Vascular Plants of California* (ed. 2). Univ. of California Press, Berkeley.
- Nowicke J.W., S.G. Shetler, and Morin N. 1992. Exine structure of pantoporate *Campanula* (Campanulaceae) species. *Ann. Missouri Bot. Gard.* 79: 65–80.
- Park, J.-M., S. Kovačić, Z. Liber, W.M.M. Eddie, and G.M. Schneeweiss. 2006. Phylogeny and biogeography of isophyllous species of *Campanula* (Campanulaceae) in the Mediterranean area. *Syst. Bot.* 31: 862–880.
- Raven, P.H. and D.I. Axelrod. 1978. Origin and relationships of the California flora. *Univ. California Pub. Bot.* 72: 1–134.
- Roquet, C., I. Sanmartin, N. Garcia-Jacas, L. Sáez, A. Susana, N. Wikström, and J. J. Aldasoro. 2009. Reconstructing the history of Campanulaceae with a Bayesian approach to molecular dating and dispersal-vicariance analyses. *Mol. Phylogenet. Evol.* 52: 575–587.
- Rosatti, T.J. 1986. The genera of Sphenocleaceae and Campanulaceae in the southeastern United States. *J. Arnold Arb.* 67:1–64.
- Schneeweiss, G.M., C. Pachschwöll, A. Tribsch, P. Schönswetter, M.H.J. Barfuss, K. Esfeld, H. Weiss-Schneeweiss, and M. Thiv. 2013. Molecular phylogenetic analyses identify alpine differentiation and dysploid chromosome number changes as major forces for the evolution of the European endemic *Phyteuma* (Campanulaceae). *Mol. Phylog. Evol.* (2013). <<http://dx.doi.org/10.1016/j.ympev.2013.07.015>>
- Schweingruber, F.H., P. Řiha, and J. Doležal. 2014. Variation in stem anatomical characteristics of Campanuloideae species in relation to evolutionary history and ecological preferences. *PLoS ONE* 9:e88199. <<https://doi:10.1371/journal.pone.0088199>>
- SEINet. 2020. Southwest Environmental Information Network. Managed at Arizona State Univ., Tempe. <<http://swbiodiversity.org/seinet/index.php>>
- Shetler, S.G. 1963. A checklist and key to the species of *Campanula* native or commonly naturalized in North America. *Rhodora* 65: 319–337.
- Shetler, S.G. and N.R. Morin. 1986. Seed morphology in North American Campanulaceae. *Ann. Missouri Bot. Gard.* 7: 653–688.
- Shulkina, T.V. 1980. The significance of life-form characters for systematics, with special reference to the family Campanulaceae. *Plant Syst. Evol.* 136: 233–246.
- Shulkina, T.V., J.F. Gaskin, and W.M.M. Eddie. 2003. Morphological studies toward an improved classification of Campanulaceae *s.str.* *Ann. Missouri Bot. Gard.* 90: 576–591.
- Small, J.K. 1933. *Manual of the Southeastern Flora*. Univ. of North Carolina Press, Chapel Hill.
- USDA NRCS. 2020. The PLANTS Database. National Plant Data Team, Greensboro, North Carolina. <<http://plants.usda.gov>> Accessed June 2020.
- Wahlsteen, E. and T. Tyler. 2019. Morphometric analysis and species delimitation in *Legousia* (Campanulaceae). *Willdenowia* 49:21–33.
- Wendling, B.M., K.E. Galbreath, and E.G. DeChaine. 2011. Resolving the evolutionary history of *Campanula* (Campanulaceae) in Western North America. *PLoS ONE* 6(9): e23559. <doi:10.1371/journal.pone.0023559>

- Wunderlin, R.P., B.F. Hansen, A.R. Franck, and F B. Essig. 2020. Atlas of Florida Plants (<http://florida.plantatlas.usf.edu/>). [S.M. Landry and K.N. Campbell (application development), USF Water Institute.] Institute for Systematic Botany, Univ. of South Florida, Tampa.
- Yoo, K.O., A.A. Crowl, K.-A. Kim, K-S. Cheon, and N. Cellinese. 2018. Origins of East Asian Campanuloideae (Campanulaceae) diversity. *Mol. Phylogen. Evol.* 127: 468–474.
- Zhou, Z., J. Wen, L. Guodong, and H.S. Source. 2012. Phylogenetic assessment and biogeographic analyses of tribe Peracarpeae (Campanulaceae). *Pl. Syst. Evol.* 298: 323–336.

Table 1. Wendling et al.'s (2011) *Rapunculus* Clade 2A, part 1. **Annuals**.

	<i>Protocodon</i>	<i>Ravenella</i>	<i>Heterocodon</i>	<i>Githopsis</i>
Duration	annual	annual	annual	annual
Height/length	3--26 cm	2--25 cm	1.5--30 cm	1--40 cm
Habit	clambering	erect	erect	erect
Roots	fibrous	slender taproot	slender taproot	slender taproot
Leaf distribution	evenly distributed	below inflorescence	evenly distributed (bracts leaflike)	below inflorescence
Cauline leaf shape	elliptic to narrowly lanceolate	linear-subulate to oblong-ovate	round to ovate	oblong to ovate
Leaf blade length	5--10 mm	2--11 mm	2--10 mm	3.5--20 mm
Inflorescence*	sympodial/leader replaced (flower offset)	sympodial/leader replaced or dichotomous	sympodial/leader replaced (flower offset)	sympodial/leader replaced (flower offset) or dichotomous
Flowers/axis	many	many	many	many
Cleistogamous flowers	present	absent	present	absent (present)
Hypanthium shape	spheric (cl), cylindrical cordate (ch)	oblong, turbinate, or rhomboid	obconic to cylindrical	cylindric or obconic
Corolla length	4--5 mm	2.2--18 mm	3--5 mm	2.5--24 mm
Petals %distinct	85--95%	30--60%	30--40%	20--80%
Corolla shape	campanulate	funnelform-campanulate or cylindrical	cylindric-campanulate	cylindric, funnelform, or campanulate
Corolla lobe shape	narrowly elliptic	deltate	triangular or ovate-triangular	elliptic to deltate
Style exertion**	included	included	included	included or exerted
Style curved	straight	straight	straight	straight
Stigma	25--33%	10--30%	25%	10--15%

Table 1. Wendling et al.'s (2011) *Rapunculus* Clade 2A, part 1. **Annuals, continued.**

	<i>Protocodon</i>	<i>Ravenella</i>	<i>Heterocodon</i>	<i>Githopsis</i>
Capsule shape	globose or urceolate	oblong, oblong-obconic, obovoid to spheric	urceolate or cylindrical	cylindric, funnellform, or campanulate
Hypanthium ribs	absent	narrow, dark, interspersed with pale inter-rib areas	raised, flat/sulcate inter-rib areas	prominent, adjacent (inter-rib areas absent or narrow)
Sepal aspect	forming a beak	erect or forming a beak	rotate	erect to spreading
Capsule pore position	basal	central	basal	base of style
Capsule pore extent	small	small	small	n/a
Seeds	triangular in x-section, angles sharp, conspicuous protruberances on angles	fusiform, round in x-section, striate or smooth	elliptical, terete in x-section, smooth	fusiform, terete in x-section, striate
Habitat	riparian	xeric	mesic	xeric
Geographic distribution	Florida: Brooksville Ridge	central California	Rocky Mountains west	western states

*Sympodial (flower offset): New branch from axil of leaf/bract straight and continuous with main axis, flower offset opposite leaf/bract. Dichotomous: new branch from axil of leaf/bract appears to fork, giving dichotomous appearance.

**Style exsertion depends on both shape of corolla (rotate or open cup vs. narrow tube) and relative length of style.

Table 1. Wendling et al.'s (2011) *Rapunculus* Clade 2A, part 2. **Perennials.**

	<i>Palustricodon</i>	<i>Eastwoodiella</i>	<i>Smithiastrum</i> <i>prenanthoides</i>	<i>Smithiastrum</i> <i>wilkinsiana</i>
Duration	perennial	perennial	perennial	perennial
Height/length	10--300 cm	10--30 cm	20--80 cm	5--30 cm
Habit	clambering	clambering	erect or spreading	erect
Roots	slender rhizomes	slender rhizomes	from woody caudex	from woody caudex
Leaf distribution	evenly distributed	evenly distributed	evenly distributed	concentrated proximally
Cauline leaf shape	elliptic to linear	elliptic	ovate to lanceolate	ovate-lanceolate to lance-oblong
Leaf blade length	6--45 mm	10--20 mm	10--60 mm	12--20 mm
Inflorescence*	sympodial/ appearing dichotomous	monopodial becoming dichotomous/ leader replaced	monopodial	monopodial
Flowers/axis	many	single	many	single
Cleistogamous flowers	absent	absent	absent	absent
Hypanthium shape	obconic becoming semi-globose	hemispheric	cylindric, base cordate	obconic to cylindric
Corolla length	5--15 mm	8--15 mm	7--14 mm	12--15 mm
Petals %distinct	75--80%	50--70%	66--90%	50%
Corolla shape	bowl-shaped	campanulate to funnellform	tube cylindrical	funnelform
Corolla lobe shape	deltate	oblong-deltate	linear to linear-lanceolate	narrowly lanceolate
Style exertion**	exposed	included	long-exserted	slightly exerted
Style curved	straight	straight	straight or curved	straight
Stigma	33%	15%	10%	15--30%
Capsule shape	globose or urceolate	cup-shaped, 3-lobed in cross section	cylindric to hemispheric, 3-lobed in cross section	narrowly obconic to oblong, terete

Table 1. Wendling et al.'s (2011) Rapunculus Clade 2A, part 2. **Perennials, continued.**

	<i>Palustricodon</i>	<i>Eastwoodiella</i>	<i>Smithiastrum</i>	<i>Smithiastrum</i>
			<i>prenanthoides</i>	<i>wilkinsiana</i>
Hypanthium ribs	obscure	grouped alternating with inter-rib areas	grouped, prominent	dark
Sepal aspect	erect	spreading	rotate or reflexed	ascending
Capsule pore position	basal	basal	central	apical
Capsule pore extent	small or capsule wall disintegrates	small	medium	small
Seeds	± triangular in x-section, angles rounded, surface with ±hexagonal plates	elliptical to obovate, ovate in x-section, interrupted striate	oblong, ovate-flattened in x-section, surface striate	not known
Habitat	riparian	riparian	mesic	mesic, high elevation
Geographic distribution	c, e N. Amer.	California coast	California, Oregon	California: Mt. Shasta

*Sympodial (flower offset): New branch from axil of leaf/bract straight and continuous with main axis, flower offset opposite leaf/bract. Dichotomous: new branch from axil of leaf/bract appears to fork, giving dichotomous appearance.

**Style exertion depends on both shape of corolla (rotate or open cup vs. narrow tube) and relative length of style.

Table 2. Wendling et al.'s (2011) Rapunculus Clade 2B and 2C.

	Rapunculus 2B				Rapunculus 2C
	<i>Campanulastrum</i>	<i>Triodanis</i>	<i>Poolea</i>	<i>Rotanthea</i>	<i>Melanocalyx</i>
Duration	annual/ biennial	annual	annual	perennial	perennial
Height/length	(20--) 210 cm	5--100 cm	5--35 cm	15--40 cm	4--10(--15) cm
Habit	erect	erect	erect	clambering/ prostrate	erect
Branching	monopodial	monopodial	sympodial dichotomous	sympodial dichotomous	unbranched from woody, branched caudex
Leaf distribution	evenly distributed	evenly distributed	below infl.	evenly distributed	mostly basal
Leaf shape	ovate to broadly lanceolate	lanceolate to suborbiculate	spatulate	broadly ovate to elliptic	broadly ovate to spatulate
Leaf blade length	60--120 mm	5--35 (-70) mm	5--15 mm	8--40 mm	7--30 mm
Inflorescence	flowers in axillary fascicles	flowers axillary, 1 or in fascicles	flowers terminal	flowers terminal	flowers terminal
Flowers/axis	many	many	many	many	one
Cleistogamous flowers	absent	present	absent	absent	absent
Hypanthium shape	obconic	obconic	ellipsoid	ovate-turbinate	oblong ellipsoid
Corolla length or diam.	20--30 mm diam.	10--24 mm diam.	12--16 mm long	14--18 mm diam.	6--12 mm long
Petals %distinct	80--90%	70--85%	55--65%	95%	33--55%
Corolla shape	rotate	rotate	funnelform to campanulate	± rotate	campanulate to funnelform
Corolla lobe shape	deltate-ovate	elliptic, ovate, or oblong	elliptic to ovate- lanceolate	narrowly oblong- lanceolate	narrowly triangular
Style exsertion	long-exserted	exserted	included	exserted	included
Style curved	sigmoidally curved	straight	straight	straight	straight
Stigma lobes	5--10%	15--17%	15%	10%	10%

Table 2. Wendling et al.'s (2011) Rapunculus Clade 2B and 2C, continued.

	Wendling et al.'s (2011) Rapunculus 2B				Rapunculus 2C
	<i>Campanulastrum</i>	<i>Triodanis</i>	<i>Poolea</i>	<i>Rotanthea</i>	<i>Melanocalyx</i>
Capsule shape	obconic	cylindrical to obovoid	ellipsoid to obovoid	hemispheric to obovoid	clavate (dark blue to black)
Hypanthium/capsule ribs	faint	capsule sulcate	faint	ribs thin, grouped	ribs thin, spaced
Sepal aspect	spreading	spreading	forming a beak	spreading	erect
Capsule pore position	apical	apical, central, below center (<i>T. coloradoensis</i> top down)	apical, opening top down	most of inter-rib area	apical
Capsule pore extent	medium	small to extensive	most of inter-rib	most of inter-rib	medium
Seeds	oblong, lenticular, pebbled	smooth or muricate; <i>T. texana</i> quadrangular, basket weave surface	broadly elliptical/roundish, lenticular, striate	broadly elliptical to quadrangular, terete-ovate, rugose	oblong, terete, striate
Habitat	mesic	xeric to mesic	xeric	aquatic	alpine
Geographic distribution	central/eastern North America	throughout North America	Llano uplift, Texas	Florida & adjacent states	circumboreal

*Sympodial (flower offset): New branch from axil of leaf/bract straight and continuous with main axis, flower offset opposite leaf/bract. Dichotomous: new branch from axil of leaf/bract appears to fork, giving dichotomous appearance.

**Style exsertion depends on both shape of corolla (rotate or open cup vs. narrow tube) and relative length of style.