

NOMENCLATURE OF SUBDIVISIONS WITHIN *PHACELIA* (BORAGINACEAE: HYDROPHYLLOIDEAE)

GENEVIEVE K. WALDEN

Department of Integrative Biology, University of California, Berkeley, CA 94720
gkwalden@berkeley.edu

ROBERT PATTERSON

Department of Biology, San Francisco State University, 1600 Holloway Avenue,
San Francisco, CA 94132

ABSTRACT

Nomenclature of subdivisions within *Phacelia* Juss. (Boraginaceae: Hydrophylloideae) reflects an update to the classification of the genus, based largely upon the structure offered in summary by Ferguson. We consider this proposed classification a continuation of efforts to better understand interrelationships within the genus and tribe Romanzoffieae Dumort., and anticipate future research offering insights into systematics of *Phacelia*. New names, changes in status, and combinations include the following: ***Phacelia* sect. *Baretiana*** Walden & R. Patt., **sect. nov.**; ***P.* subsect. *Bipinnatifidae*** (Small) Walden & R. Patt., **stat. nov.**; ***P.* subsect. *Cosmantha*** (Nolte ex A. de Candolle) Walden & R. Patt., **stat. nov.**; ***P.* subsect. *Cosmanthoides*** (A. Gray) Walden & R. Patt., **stat. nov.**; ***P.* subsect. *Dubiae*** (Small) Walden & R. Patt., **stat. nov.**; ***P.* subsect. *Eutoca*** (R. Br.) Walden & R. Patt., **stat. nov.**; ***P.* sect. *Glandulosae*** (Rydb.) Walden & R. Patt., **stat. nov.**; ***P.* subsect. *Humiles*** Walden & R. Patt., **subsect. nov.**; ***P.* subsect. *Lineares*** (Rydb.) Walden & R. Patt., **stat. nov.**; ***P.* sect. *Pachyphyllae*** Walden & R. Patt., **sect. nov.**; ***P.* subg. *Pulchellae*** (Rydb.) Walden & R. Patt., **stat. nov.**; ***P.* sect. *Ramosissimae*** (Rydb.) Walden & R. Patt., **stat. nov.**; ***P.* subsect. *Ranunculacea*** Walden & R. Patt., **subsect. nov.**; and ***P.* subsect. *Sericeae*** (Rydb.) Walden & R. Patt., **stat. nov.**.

Key Words: Boraginaceae, Hydrophyllaceae, Hydrophylloideae, *Phacelia*, Romanzoffieae.

Philippe Commerson (variously Commerson, Commercon, or Commerçon) and Jeanne Baret (variously Jean Baret, Jeanne Baré, Bonnefoi, or Bonnefoy) collected the first specimens of *Phacelia* Juss. in the Straits of Magellan in the winter of 1767–1768 (Lamarck 1792). Commerson was the naturalist on the Bougainville expedition and called his own fascination with plants a “botanomania” (Bougainville 1771; Oliver and Elliot 1909). Baret, mistress of and field assistant to her “lover-master” Commerson, was disguised as a man for the majority of the lengthy sea journey and identified as a woman only when the expedition reached Tahiti (Dunmore 2002; Schieberger 2003). Baret was the first woman to voyage around the world and was lauded as a skilled botanist (Bougainville 1771; Dunmore 2002; Schieberger 2003; Ridley 2010; Tepe et al. 2012). Botanical collections from Brazil were lost on a return voyage across the Atlantic, and Commerson retained the remainder of his collections, including those from the Straits of Magellan, until his death (Godley 1965). Commerson willed his herbarium to the Muséum national d’Histoire naturelle in Paris, and from these collections de Jussieu described *Phacelia* as a genus; *P. secunda* was later described and designated the type species (Jussieu 1789; Gmelin 1791; Laissus 1978). Taxonomic confusion began at the very formation of *Phacelia*, as researchers

proposed different classifications and alliances for the variation observed from the Commerson collection. “L’*Hydrophylle de Magellan*” (*Hydrophyllum magellanicum* Lam.) was also published from “l’herbier de Commerson,” (Lamarck 1792; Coville 1893; Degnani 1982). Although the informal “*Magellanicae*” has been generally adopted for the group of perennial species (e.g., *Phacelia magellanica* polyploid complex, *Phacelia* “species group *Magellanicae*”), the type species of the genus is also included within the subdivision and so the epithet for the subsection is *Phacelia* (Heckard 1960; Constance and Chuang 1982).

Gray (1875) combined the genera of A. de Candolle (1845) within *Phacelia* as subgenera, establishing a structure within the genus that has remained largely unchanged. In the first edition of the Manual of Botany, Gray (1848) noted subgenera and sections with the same mark, §. Clarification came in the second edition, with subgenera and sections both noted with §, but subgenera in all capitals (Gray 1856). In the Synoptical Flora, Gray (1878) defined the use of symbols and rank: “The characters of sections of genera, when of comparatively high rank, are designated by the sectional mark (§) and printed in the larger type; and those of first importance, such as may be termed subgenera, are distinguished by having a substantive name. Subsections, and also primary divisions when of low

rank, are in small type." These clarifications with discussion illustrated the need for hierarchical subdivisions in *Phacelia* and demonstrated acknowledgment of the intended use in the field (Candolle 1867; Brizicky 1968, 1969). Gray's taxonomy developed with each iteration of published subdivisions within *Phacelia*, although adoption and application were not standardized. Nomenclature provided structure and guidance as contemporaries of Gray followed or challenged his revisions and additions to the flora of North America. The taxonomy of *Phacelia* was complicated when Bentham and Hooker (1876) inadvertently recombined taxa by citing the subgenera of Gray (1875) but mistakenly translated (§) at sectional status, considered a bibliographic error of citation, but a valid publication with priority (Brizicky 1968, 1969; Moore 2001; McNeill et al. 2006). Gray (1878) combined subgenera at sectional rank, citing himself, in his next publication, making these sectional names later isonyms, which may be disregarded (Bentham and Hooker 1876; McNeill et al. 2006). Later authors, such as Brand (1913), followed and perpetuated sectional combinations of Gray, which resulted in common use of names with no nomenclatural standing. We correct the sectional nomenclature of *Phacelia* in the taxonomic treatment.

Brand's (1913) classification of sections, informal "conspectus varietatum," and informal "systema speciei" has been the basis and inspiration for revisional taxonomic work in the genus, due in part to the large scale of his revision within Hydrophyllaceae. Characters of importance used to separate subdivisions in *Phacelia* were ovule and seed number, seed shape and surface morphology, and corolla scales (known as corolla squamae, corolla plicae, interstaminal scales, appendages, or lamellae) (Candolle 1845; Gray 1875, 1878; Munz 1935; Constance 1949; Gillett 1968; Hoffmann 1999).

Rydberg (1917) limited his flora to species occurring within geographical bounds of the Rocky Mountains and organized *Phacelia* into seven unranked, but validly published, named subdivisions. Following a long-term study of chromosome numbers, Constance (1963) proposed a classification of three subgenera and ten informal "species groups." Investigations of pollen surface morphology, trichomes, and seed surface morphology resulted in expanded taxonomic characters for the genus (Atwood 1975; Halse 1979; Constance and Chuang 1982; Di Fulvio and Dottori 1995). Ferguson (1998) offered an update to Constance's classification, and although not a formal taxonomic revision, the synopsis of subdivisions in *Phacelia*, recognized to contain three subgenera, five sections, and six informal species groups, and broad sampling of genera within Hydrophyllaceae,

offered a structure for future taxonomic directions in the genus. The monospecific *Phacelia* subg. *Howellanthus* Constance (1953) has since been removed to *Howellanthus* (Constance) Walden & R. Patt., and although we assigned the genus to tribe Phacelieae Benth. ex A. Gray (1875), Reveal's *Indices Supragenericorum Nomina Plantarum Vascularium* (2012) identified Romanzoffieae Dumort. (Dumortier 1829) as having priority at rank tribe, and we correct our error here (Walden and Patterson 2010). *Phacelia* subg. *Cosmanthus* (Nolte ex A. de Candolle) A. Gray contains 20 species, *P.* subg. *Phacelia* encompasses the remaining 187 species across five sections, and 50 species were not assigned to a species group within *P.* sect. *Phacelia* (Ferguson 1998). By reviewing protologues, revisions, and molecular studies, we clarify the status of those unassigned taxa within this proposed classification. With additional species descriptions and systematic studies in *Phacelia* since Ferguson (1998), there is a need to formally recognize subdivisions in the genus, combine some previously separate subdivisions (*P.* subg. *Phacelia* and *P.* subg. *Eutoca*), provide names for other subdivisions (see Appendix 1 for outline), and note traditional taxonomic characters that are useful for classification and identification in a key to subdivisions.

PHACELIA SUBG. PHACELIA

Howell published revisions on two groups of annual species with entire-margined leaves from *P.* sect. *Euphacelia* (Howell 1943b) and *P.* sect. *Eutoca* (Howell 1945), later combined as the informal "species group *Humiles*" by Constance (1963). Lee (1986) examined the systematics of "species group *Humiles*" using corolla venation patterns and identified five morphological groups. Molecular studies of *Phacelia* support a sister relationship between the annual "species group *Humiles*" and perennial "species group *Magellanicae*," which we recognize formally here as *P.* subsect. *Humiles* and *P.* subsect. *Phacelia* within *P.* sect. *Phacelia* (Ferguson 1998; Gilbert et al. 2005; Walden 2010). It is clear that the nomenclature and taxonomic relationships of South America annual and perennial taxa should be reconsidered (Deginani 1982).

Molecular studies have supported a clade consisting of three perennial species: *P. hydrophyloides* Torr. ex A. Gray, *P. procera* A. Gray, and *P. bolanderi* A. Gray (Ferguson 1998; Gilbert et al. 2005; Walden 2010). These species have been traditionally included within *Phacelia* subg. *Eutoca* A. Gray, and were described together in one publication (Gray 1875). We treat this perennial group as *P.* sect. *Baretiana* within *P.* subg. *Phacelia*, named to honor the contributions of Baret to the botanical history of the genus, her

long life, and long journey to public recognition (Walden 2010).

“Species group *Crenulatae*” is an assemblage of 50 species, traditionally grouped by the morphological characteristics of trichomes stipitate-glandular with unicellular or multicellular heads, plants generally mephitic or malodorous, seeds cymbiform and excavated along one or both sides of a central adaxial ridge, seed surface reticulate-pitted and sometimes alveolate, and $n = 11$ (Voss 1937a, b; Atwood 1975; Garrison 2007; Walden 2010). Brand (1913) first grouped species within the informal “*P. crenulata conspectus varietatum*,” “*P. glandulosa systema speciei*,” and “*P. neo-mexicana systema speciei*,” in his monograph of Hydrophyllaceae. Rydberg’s (1917) *Phacelia* [unranked] *Glandulosae* somewhat encompassed the informal groupings of Brand (1913). Voss (1937a, b) revised the “*Phacelia Crenulatae* group,” an informal name that has stayed with the subdivision (Constance 1963; Atwood 1975). Taxa are distributed from Wyoming to México, with an amphitropical disjunction of three taxa in South America (*P. artemisioides* Griseb., *P. pinnatifida* Griseb. ex Wedd., and *P. setigera* Phil.) (Deglinani 1982). Molecular studies have supported sampled “species group *Crenulatae*” as monophyletic, although clearly not limited to a four-seeded capsule, and sister to a monophyletic “species group *Tanacetifoliae*” [treated here as *P. sect. Ramosissimae*] (Gilbert et al. 2005; Garrison 2007; Hansen et al. 2009; Walden 2010). We treat Rydberg’s validly published name as the basionym for *P. sect. Glandulosae* within *P. subg. Phacelia*.

When Gray (1875) established *P. subg. Cosmanthus* and *P. subg. Cosmanthoides*, he did so by splitting *Cosmanthus* Nolte ex A. de Candolle sect. *Eucosmanthus*, and assigning the majority of species to *P. subg. Cosmanthoides*. The typification of each subdivision has not been made explicit, and we provide lectotypification here. Orthographic changes in gender are required in subdivisions combined from *Cosmanthus* to *Phacelia*. In the preface to his Manual, Small (1933) wrote: “Complex genera have been divided into more natural groups, both for convenience of study and also in order to make the genera, as far as possible, correspond to the great majority of groups of species now recognized as genera by most present-day botanists.” The unranked subdivisions of Small (1933) are treated as the basionyms for *P. subsect. Bipinnatifidae* and *P. subsect. Dubiae*. Constance (1949, 1950) authored revisions of *P. subg. Cosmanthus*, documenting the distribution of the group from northeastern United States into México and Guatemala. Gillett (1968, pg. 368) noted “a basis for deleting the subgenus *Cosmanthus* as a systematic group”; in its place he proposed five

informal groups from biosystematic studies (Gillett 1964, 1965a, b, 1968). Molecular studies have maintained the monophyly of this subdivision, although with limited sampling, supported as sister to Gillett’s “species group *Franklinii*” (treated here as *P. sect. Eutoca*) and nested within *P. subg. Phacelia* (Ferguson 1998; Gilbert et al. 2005; Hansen et al. 2009; Walden 2010). We treat *P. sect. Cosmanthus* within *P. subg. Phacelia*. Gillett’s “*P. ranunculacea* Group” has been further explored by Sewell and Vincent (2009), and by Glass and Levy (2011), and we treat this clade as *P. subsect. Ranunculacea* within *P. sect. Cosmanthus*.

Gray (1875) included *Eutoca* R.Br. within *Phacelia*, justifying the merger by noting that *Phacelia* and *Eutoca* were “polymorphous” (Gray 1875). Rydberg’s (1917) *Phacelia* [unranked] *Lineares* and *Phacelia* [unranked] *Sericiae* were investigated in a series of biosystematic studies by Gillett (1960a, b, 1961, 1962, 1963) as the informal “species group *Franklinii*.” We treat Rydberg’s taxa as *P. subsect. Lineares* and *P. subsect. Sericeae* within *P. sect. Eutoca*.

PHACELIA SUBG. *MICROGENETES*

Molecular studies have supported a monophyletic clade formed of three species: *P. pachyphylla* A. Gray, *P. calthifolia* Brand, and *P. neglecta* M. E. Jones, sister to *P. sect. Euglypta* and *P. sect. Miltitzia* (Demey 1996; Ganong 2002; Gilbert et al. 2005). Gray (1883) noted in his description of *P. pachyphylla*, “A most peculiar species, to be placed at the end of the *Microgenetes* section.” Howell (1942) provided a diagnosis for the informal group within a key when forming the “compact triad among our desert phacelias,” and Gilbert et al. (2005) noted, “All analyses supported Howell’s (1946) *Phacelia pachyphylla* complex as a distinct lineage.” We treat this group as *P. sect. Pachyphyllae* within *P. subg. Microgenetes*.

PHACELIA SUBG. *PULCHELLAE*

Rydberg’s (1917) *Phacelia* [unranked] *Pulchellae*, diagnosed within keys, contained ten species of annual or perennial plants of low habit, corollas open-campanulate to tubular, corollas with stamens included, reticulate-pitted seeds, leaves long-petiolate, and leaf margins entire to lobed. Although only implied, the sharing of similar characteristics of *Phacelia* [unranked] *Pulchellae* to *Phacelia* [unranked] *Bicolores* suggested a close relationship between the two subdivisions (Torrey 1871; Gray 1875; Rydberg 1917). In discussion, Howell (1943a) referred to the “section *Pulchellae*” of Rydberg, but it does not appear that was a formal publication at that rank. Howell’s (1943a) revision included 19

species of annual or perennial plants with tubular corollas, stamens included, styles shallowly bifid, leaf margins entire to shallowly lobed, capsules elliptic or oblong, and ovules more than four per ovary. *Phacelia* [unranked] *Pulchellae*, *P.* sect. *Euglypta*, *P.* sect. *Miltizia*, and *Romanzoffia* Cham. have tricolpate pollen without pseudocolpi; the remainder of sampled *Phacelia* share tricolpate-tripseudocolpate pollen (Ferguson 1998). *Phacelia* [unranked] *Pulchellae*, consisting of the species around which Howell (1943a) centered his revision, was supported to have basal placement within the genus in molecular studies, sister to *P.* subg. *Phacelia* (Ferguson 1998; Gilbert et al. 2005; Walden 2010). We treat Rydberg's validly published name as the basionym for *P.* subg. *Pulchellae*.

TAXONOMIC TREATMENT

Phacelia Juss., Gen. Pl. 129. 1789. —Type (lectotype designated by J. F. Gmelin 1791): *Phacelia secunda* J. F. Gmel., Syst. Nat. ed. 13. 2:330. 1791.

Aldea Ruiz & Pavón, Fl. Peruv. Prodr. 16–17. 1794[1798]. —Type (lectotype designated by Ruiz & Pavón, 1799): *Aldea pinnata* Ruiz & Pavón, Fl. Peruv. 2:8, pl. 114 [CXIV], fig. a. 1799 (refers to p. 19 of the protologue in error).

Phacelia Juss. subg. *Phacelia*.

Phacelia Juss. sect. *Phacelia*.

Phacelia Juss. subsect. *Phacelia*.

Phacelia [unranked] *Heterophyllae* Rydb., Fl. Rocky Mts. 702. 1917. —Type: *Phacelia heterophylla* Pursh, Fl. Amer. Sept. 140. 1814.

Included taxa: *Phacelia argentea* A. Nelson & J. F. Macbr., *P. californica* Cham., *P. capitata* Kruckeb., *P. corymbosa* Jeps., *P. egena* (Brand) J. T. Howell, *P. hastata* Douglas ex Lehm., *P. hastata* var. *hastata*, *P. hastata* var. *charlestontensis* Cronquist, *P. hastata* var. *compacta* (Brand) Cronquist, *P. heterophylla* Pursh, *P. heterophylla* var. *heterophylla*, *P. heterophylla* var. *virgata* (Greene) Dorn, *P. imbricata* Greene, *P. imbricata* var. *imbricata*, *P. imbricata* var. *bernardina* (Greene) Walden & R. Patt., *P. imbricata* var. *patula* (Brand) Walden & R. Patt., *P. leptosepala* Rydb., *P. mutabilis* Greene, *P. nemoralis* Greene, *P. nemoralis* var. *nemoralis*, *P. nemoralis* var. *oregonensis* (Heckard) Walden & R. Patt., *P. secunda* J. F. Gmel., *P. secunda* var. *secunda*, *P. secunda* var. *pinnata* (Vahl) Deglinani.

***Phacelia* Juss. subsect. *Humiles* Walden & R. Patt., subsect. nov.** —Type: *Phacelia humilis* Torr. & A. Gray, in War Department (U.S.), Pacif. Railr. Rep. 2:122. 1855.

Plants annual; herbage mephitic or unscented. Stems decumbent to ascending to erect, sometimes

wiry, simple, or branched; hirtellous to hispidulous to hirsute, eglandular or glandular, glands colorless- to amber- or dark-tipped. Leaves rosulate, or opposite proximally and alternate distally, or alternate and caudine; petiolate or subsessile; blade linear to lanceolate to oblong or narrowly ovate, simple and margins entire, or margins shallowly pinnatifid or toothed or shallowly lobed with 1–4 pairs, lobe margins entire, bases cuneate or attenuate, hirtellous to hispidulous to hirsute, eglandular or glandular. Inflorescence unit a cyme, secund or racemose, usually solitary, or sometimes geminate, ascending to erect, one- or two-ranked, extending or not beyond vegetation. Flowers pedicellate, pedicels short or long, spreading to ascending, or arcuate in fruit; calyx slightly accrescent or strongly accrescent in fruit, lobes equal or unequal, linear to oblanceolate to spatulate to obovate, sometimes foliaceous, hirsute and glandular, margins ciliate; corollas deciduous or marcescent, campanulate to open-campanulate to subrotate, white or blue or lavender or purple, lamina sometimes with translucent areas, glabrous adaxially, puberulent to sparsely hirsute abaxially, lobe margins entire or erose; nectary gland usually absent, rarely present (*P. douglasii*); corolla scales usually present, sometimes absent, linear to lanceolate to ovate, adjacent scale edges divergent or not across base of filament, glabrous or ciliate; stamens included or exsert, filaments equal or unequal in length, glabrous or papillate, anthers bronze; style included or exsert, branched 1/2 length to branched nearly to base, hirsute proximally; ovules 2–12 per placenta. Fruits ellipsoid to ovoid and compressed along sutures, or globose and plump, hirsute and sparsely glandular. Seeds 2–20, brown, oblong or ovoid, rounded or truncate at ends, sometimes angled, surface finely or coarsely reticulate-pitted, reticulations rarely in transverse striations. *n* = 7, 8, 9, 10, 11.

Included taxa: *Phacelia austromontana* J. T. Howell, *P. brachyantha* Benth., *P. breweri* A. Gray, *P. congdonii* Greene, *P. curvipes* Torr. ex S. Watson, *P. davidsonii* A. Gray, *P. divaricata* (Benth.) A. Gray, *P. douglasii* (Benth.) Torr., *P. eisenii* Brandegee, *P. exilis* (A. Gray) G. J. Lee, *P. greenei* J. T. Howell, *P. grisea* A. Gray, *P. humilis* Torr. & A. Gray, *P. humilis* var. *humilis*, *P. humilis* var. *dudleyi* J. T. Howell, *P. inconspicua* Greene, *P. insularis* Munz, *P. insularis* var. *insularis*, *P. insularis* var. *continentis* J. T. Howell, *P. leonis* J. T. Howell, *P. marcescens* Eastw. ex J. F. Macbr., *P. minutissima* L. F. Hend., *P. mohavensis* A. Gray, *P. novenmillensis* Munz, *P. orogenes* Brand, *P. peckii* J. T. Howell, *P. phaceliooides* A. Gray, *P. pringlei* A. Gray, *P. purpusii* Brandegee, *P. quickii* J. T. Howell, *P. racemosa* (Kellogg) Brandegee, *P. stebbinsii* Constance & Heckard, *P. stellaris* Brand, *P. vallicola* Congdon ex Brand, *P. verna* J. T. Howell.

Phacelia Juss. sect. **Baretiana** Walden & R. Patt., **sect. nov.** —Type: *Phacelia hydrophyloides* Torr. ex A. Gray, Proc. Amer. Acad. Arts 7(2):400. 1868.

Plants perennial; herbage malodorous. Stems decumbent to ascending to erect; usually hirtellous to hirsute, glandular, glands colorless- to amber- to dark-tipped, sometimes glabrate proximally. Leaves petiolate; blade oblong to ovate to subrhombic, simple or pinnatifid to lyrate or pinnate with 1–3 pairs of leaflets at base, leaflets oblong to ovate, bases attenuate or truncate to subcordate, margins usually incised or serrate or dentate, rarely subentire, faces usually hirtellous to hirsute, sometimes glabrate, margins sometimes hispid-ciliate, glandular. Inflorescence unit a cyme, paniculate or capitate, solitary or in 2–3 clusters. Flowers pedicellate, pedicels short or long, straight in fruit; calyx slightly accrescent in fruit, lobes equal, linear to oblanceolate to oblong to narrowly spatulate, hirsute and glandular, margins hispid-ciliate, tips spreading; corollas deciduous, rotate to open-campanulate, white to cream to green-white or pale blue to lavender, throat sometimes fading brown in age, glabrous adaxially, puberulent abaxially, lobe margins entire or erose, spreading or revolute; nectary gland absent; corolla scales present, oblong, adjacent scale edges divergent across bases of filaments, scale edges sometimes adnate and forming a narrow sac, glabrous; stamens slightly exsert to exsert, filaments equal or slightly unequal, glabrous or hirsute, anthers blue or purple-brown or white; style included or exsert, branched 1/2 to 3/4 length, hirsute proximally; ovules 3–30 per placenta. Fruits plumply ovoid to subglobose, apiculate, hirsute. Seeds 3–60, brown or black, oblong to ellipsoid to irregularly cylindrical, angled, acute at both ends, adaxial surface sometimes with shallow keel, surface shallowly foveolate or finely scrobiculate, reticulate-pitted. $n = 11$.

Included taxa: *Phacelia bolanderi* A. Gray, *P. hydrophyloides* Torr. ex A. Gray, *P. procera* A. Gray.

Phacelia Juss. sect. *Cosmantha* (Nolte ex A. de Candolle) Benth. & Hook.f., Gen. Pl. 2:828. 1876. *Cosmanthus* Nolte ex A. de Candolle, Prodr. 9:296. 1845. *Phacelia* subg. *Cosmanthus* (Nolte ex A. de Candolle) A. Gray, Proc. Amer. Acad. Arts 10:320. 1875 (as § 2. COSMANTHUS). —Type (lectotype designated here): *Phacelia fimbriata* Michx., Fl. Bor.-Amer. 1:134. 1803.

Phacelia subsect. **Cosmantha** (Nolte ex A. de Candolle) Walden & R. Patt., **stat. nov.** *Phacelia* [unranked] *Fimbriatae* Small, Man. S.E. Fl. 1097. 1933. —Type (lectotype designated here):

Phacelia fimbriata Michx., Fl. Bor.-Amer. 1:134. 1803.

Included taxa: *Phacelia fimbriata* Michx., *P. purshii* Buckley

Phacelia Juss. subsect. **Bipinnatifidae** (Small) Walden & R. Patt., **stat. nov.** *Phacelia* [unranked] *Bipinnatifidae* Small, Man. S.E. Fl. 1097. 1933. —Type: *Phacelia bipinnatifida* Michx., Fl. Bor.-Amer. 1:134. 1803.

Included taxon: *Phacelia bipinnatifida* Michx.

Phacelia Juss. subsect. **Cosmanthoides** (A. Gray) Walden & R. Patt., **stat. nov.** *Phacelia* subg. *Cosmanthoides* A. Gray, Proc. Amer. Acad. Arts 10:320. 1875 (as § 3. COSMANTHOIDES). *Phacelia* sect. *Cosmanthoides* (A. Gray) Benth. & Hook.f., Gen. Pl. 2:828. 1876. —Type (lectotype designated here): *Phacelia platycarpa* (Cav.) Spreng., Syst. Veg. (ed. 16) [Sprengel] 1:584. 1824 [1825].

Included taxa: *Phacelia altotonga* B. L. Turner, *P. austrotexana* (J. A. Moyer) B. L. Turner, *P. carmenensis* B. L. Turner, *P. gilioides* Brand, *P. glabra* Nutt., *P. hirsuta* Nutt., *P. laxa* Small, *P. neffii* B. L. Turner, *P. patuliflora* A. Gray, *P. platycarpa* (Cav.) Spreng., *P. platycarpa* var. *platycarpa*, *P. platycarpa* var. *bursifolia* (Willd. ex Roem. & Schult.) Constance, *P. platycarpa* var. *madrensis* (Greenm.) Constance, *P. pulcherrima* Constance, *P. strictiflora* (Engelm. & A. Gray) A. Gray, *P. strictiflora* var. *strictiflora*, *P. strictiflora* var. *connexa* Constance, *P. strictiflora* var. *lundelliana* Constance, *P. strictiflora* var. *robbinsii* Constance, *P. teucriifolia* I. M. Johnst., *P. zaragozana* B. L. Turner.

Phacelia Juss. subsect. **Dubiae** (Small) Walden & R. Patt., **stat. nov.** *Phacelia* [unranked] *Dubiae* Small, Man. S.E. Fl. 1097. 1933. —Type: *Phacelia dubia* (L.) Trel. & Small, Rep. (Annual) Arkansas Geol. Surv. (for 1888). 4:205. 1891.

Included taxa: *Phacelia dubia* (L.) Trel. & Small, *P. dubia* var. *dubia*, *P. dubia* var. *georgiana* McVaugh, *P. dubia* var. *interior* Fernald, *P. maculata* Wood.

Phacelia Juss. subsect. **Ranunculacea** Walden & R. Patt., **subsect. nov.** —Type: *Phacelia ranunculacea* (Nutt.) Constance, Rhodora 42:39. 1940.

Plants annual, (5)10–25 cm; herbage unscented. Stems prostrate to erect; hirsute and glandular, glands colorless-tipped. Leaves blade oblong to ovate, pinnatifid or pinnate with 2–6 pairs of leaflets, lobes oblong to round, bases cuneate, margins entire or toothed, hirsute and glandular.

Inflorescence unit a cyme, secund, 1–6 flowers. Flowers pedicellate, pedicels short or long, reflexed to pendent in fruit; calyx slightly accrescent in fruit, lobes unequal, linear to lanceolate, hirsute and sparsely glandular; corollas tubular-campanulate, pale violet or lavender, lobe margins entire; stamens included, filaments equal, glabrous; style included, branched 1/3 to 2/3 length, glabrous; ovules 2 per placenta. Fruits depressed globose, hirsute. Seeds 2–4, globose to ovoid, surface finely reticulate-pitted. $n = 6, 14$.

Included taxa: *Phacelia covillei* S. Watson ex A. Gray, *P. ranunculacea* (Nutt.) Constance.

Phacelia Juss. sect. *Eutoca* (R. Br.) Benth. & Hook. f., Gen. Pl. 2: 828. 1876. *Eutoca* R. Br., Narr. Journey Polar Sea. 764–765, tab. 27. 1823. *Eutoca* R. Br. sect. *Ortheutoca* A. de Candolle, Prodr. 9:296. 1845. *Phacelia* subg. *Eutoca* (R. Br.) A. Gray, Proc. Amer. Acad. Arts 10:322. 1875 (as § 6. EUTOCA). —Type: *Phacelia franklinii* (R. Br.) A. Gray, Manual ed. 2:329. 1856.

Phacelia subsect. **Eutoca** (R. Br.) Walden & R. Patt., stat. nov. —Type: *Phacelia franklinii* (R. Br.) A. Gray, Manual ed. 2:329. 1856.

Included taxon: *Phacelia franklinii* (R. Br.) A. Gray.

Phacelia Juss. subsect. **Lineares** (Rydb.) Walden & R. Patt., stat. nov. *Phacelia* [unranked] *Lineares* Rydb., Fl. Rocky Mts. 702. 1917. —Type: *Phacelia linearis* (Pursh) Holz., Contr. U.S. Natl. Herb. 3:242. 1895.

Included taxon: *Phacelia linearis* (Pursh) Holz.

Phacelia Juss. subsect. **Sericeae** (Rydb.) Walden & R. Patt., stat. nov. *Phacelia* [unranked] *Sericeae* Rydb., Fl. Rocky Mts. 702. 1917. —Type: *Phacelia sericea* (Graham) A. Gray, Amer. J. Sci. Arts, ser. 2. 34(101):254. 1862.

Included taxa: *Phacelia idahoensis* L. F. Hend., *P. lenta* Piper, *P. lyallii* Rydb., *P. mollis* J. F. Macbr., *P. sericea* (Graham) A. Gray, *P. sericea* var. *sericea*, *P. sericea* var. *ciliosa* Rydb.

Phacelia Juss. sect. **Glandulosae** (Rydb.) Walden & R. Patt., stat. nov. *Phacelia* [unranked] *Glandulosae* Rydb., Fl. Rocky Mts. 702. 1917. —Type: *Phacelia glandulosa* Nutt., J. Acad. Nat. Sci. Philadelphia, ser. 2, 1:160. 1847.

Included taxa: *Phacelia alba* Rydb., *P. amabilis* Constance, *P. anelsonii* J. F. Macbr., *P. argylensis* N. D. Atwood & S. L. Welsh, *P. argillacea* N. D. Atwood, *P. arizonica* A. Gray, *P. artemisioides* Griseb., *P. bakeri* (Brand) J. F. Macbr., *P. bombycinia* Wooton & Standl., *P. cloudermannii*

N. D. Atwood, *P. coerulea* Greene, *P. congesta* Hook., *P. constancei* N. D. Atwood, *P. corrugata* A. Nelson, *P. cottamii* N. D. Atwood, *P. coulteri* Greenm., *P. crenulata* Torr. ex S. Watson, *P. crenulata* var. *crenulata*, *P. crenulata* var. *ambigua* (M. E. Jones) J. F. Macbr., *P. crenulata* var. *angustifolia* N. D. Atwood, *P. crenulata* var. *minutiflora* (J. W. Voss ex Munz) Jeps., *P. denticulata* Osterh., *P. formosula* Osterh., *P. furnissii* N. D. Atwood, *P. glandulosa* Nutt., *P. glandulosa* var. *glandulosa*, *P. glandulosa* var. *deserta* Brand, *P. gypsogenia* I. M. Johnst., *P. higginsii* N. D. Atwood, *P. hintoniorum* B. L. Turner, *P. howelliana* N. D. Atwood, *P. hughesii* N. D. Atwood, *P. infundibuliformis* Torr., *P. infundibuliformis* var. *infundibuliformis*, *P. infundibuliformis* var. *phanerandra* I. M. Johnst., *P. integrifolia* Torr., *P. integrifolia* var. *integrifolia*, *P. integrifolia* var. *texana* (J. W. Voss) N. D. Atwood, *P. mammillarensis* N. D. Atwood, *P. marshall-johnstonii* N. D. Atwood & Pinkava, *P. marshall-johnstonii* var. *marshall-johnstonii*, *P. marshall-johnstonii* var. *deliciosa* B. L. Turner, *P. neomexicana* Thurb. ex Torr., *P. orbicularis* Rydb., *P. pallida* I. M. Johnst., *P. palmeri* Torr. ex S. Watson, *P. pedicellata* A. Gray, *P. petrosa* N. D. Atwood, F. J. Sm., & T. A. Knight, *P. pinkavae* N. D. Atwood, *P. pinnatifida* Griseb. ex Wedd., *P. popei* Torr. & A. Gray, *P. potosina* B. L. Turner, *P. rafaelensis* N. D. Atwood, *P. robusta* (J. F. Macbr.) I. M. Johnst., *P. rupestris* Greene, *P. sanzinii* Hicken, *P. scariosa* Brandegee, *P. serrata* J. W. Voss, *P. setigera* Phil., *P. setigera* var. *setigera*, *P. setigera* var. *humahuquense* Deginani, *P. sinuata* Phil., *P. sivinskii* N. D. Atwood, P. J. Knight, & Lowrey, *P. sonoriensis* S. P. McLaughlin, *P. splendens* Eastw., *P. utahensis* J. W. Voss, *P. vossii* N. D. Atwood, *P. welshii* N. D. Atwood.

Phacelia Juss. sect. **Gymnobytha** (A. de Candolle) Benth. & Hook. f., Gen. Pl. 2:828. 1876. *Cosmanthus* Nolte ex A. de Candolle sect. *Gymnobythus* A. de Candolle, Prodr. 9:296. 1845. *Phacelia* subg. *Gymnobythus* (A. de Candolle) A. Gray, Proc. Amer. Acad. Arts 10:321. 1875 (as § 4. GYMNOBYTHUS). —Type: *Phacelia viscosa* (Benth.) Torr., Rep. U.S. Mex. Bound., Bot. (Emory) 143. 1859.

Included taxa: *Phacelia grandiflora* (Benth.) A. Gray, *P. viscosa* (Benth.) Torr., *P. viscosa* var. *viscosa*, *P. viscosa* var. *albiflora* (Nutt.) A. Gray.

Phacelia Juss. sect. **Ramosissimae** (Rydb.) Walden & R. Patt., stat. nov. *Phacelia* [unranked] *Ramosissimae* Rydb., Fl. Rocky Mts., 702. 1917. —Type: *Phacelia ramosissima* Douglas ex Lehm., Nov. Stirp. Pug. (Lehmann) 2:21. 1830.

Included taxa: *Phacelia cedrosensis* Rose, *P. cicutaria* Greene, *P. cicutaria* var. *cicutaria*,

P. cicutaria var. *hispida* (A. Gray) J. T. Howell, *P. ciliata* Benth., *P. cinerea* Eastw. ex J. F. Macbr., *P. cryptantha* Greene, *P. distans* Benth., *P. floribunda* Greene, *P. gentryi* Constance, *P. hirtuosa* A. Gray, *P. hubbyi* (J. F. Macbr.) L. M. Garrison, *P. ixodes* Kellogg, *P. lyonii* A. Gray, *P. malvifolia* Cham. *P. malvifolia* var. *malvifolia*, *P. malvifolia* var. *loasifolia* (Benth.) Brand, *P. phyllomanica* A. Gray, *P. platyloba* A. Gray, *P. pauciflora* S. Watson, *P. ramosissima* Douglas ex Lehm., *P. ramosissima* var. *ramosissima*, *P. ramosissima* var. *austrolitoralis* Munz, *P. ramosissima* var. *eremophila* (Greene) J. F. Macbr., *P. ramosissima* var. *latifolia* (Torr.) Cronquist, *P. ramosissima* var. *montereyensis* Munz, *P. rattanii* A. Gray, *P. tanacetifolia* Benth., *P. thermalis* Greene, *P. umbrosa* Greene, *P. vallis-mortae* J. W. Voss.

Phacelia Juss. sect. *Whitlavia* (Harv.) Benth. & Hook.f., Gen. Pl. 2:828. 1876. *Whitlavia* Harv., London J. Bot. 5:311–312, pl. 11. 1846. *Phacelia* subg. *Whitlavia* (Harv.) A. Gray, Proc. Amer. Acad. Arts 10:321. 1875 (as § 5. WHITLAVIA). —Type: *Phacelia minor* (Harv.) Thell. ex F. Zimm., Ber. Bayer. Bot. Ges. 14:79. 1914.

Phacelia subsect. *Whitlaviae* (Harv.) G. W. Gillett, Univ. Calif. Publ. Bot. 28:60. 1955. —Type: *Phacelia minor* (Harv.) Thell. ex F. Zimm., Ber. Bayer. Bot. Ges. 14:79. 1914.

Included taxa: *Phacelia minor* (Harv.) Thell. ex F. Zimm., *P. parryi* Torr.

Phacelia Juss. subsect. *Campanulariae* G. W. Gillett, Univ. Calif. Publ. Bot. 28:62. 1955. —Type: *Phacelia campanularia* A. Gray, Syn. Fl. N. Amer. 2(1):164. 1878.

Included taxa: *Phacelia campanularia* A. Gray, *P. campanularia* var. *campanularia*, *P. campanularia* var. *vasiformis* (G. W. Gillett) Walden & R. Patt., *P. longipes* Torr. ex A. Gray, *P. nashiana* Jeps.

Phacelia Juss. subg. *Microgenetes* (A. de Candolle) A. Gray, Proc. Amer. Acad. Arts 10:326. 1875 (as § 7. MICROGENETES). *Microgenetes* A. de Candolle, Prodr. 9: 292–293. 1845. —Type (lectotype designated by J. T. Howell 1946): *Phacelia cumingii* (Benth.) A. Gray, Syn. Fl. N. Amer. 2(1):169. 1878.

Phacelia Juss. sect. *Euglypta* S. Watson, Botany (Fortieth Parallel) 254. 1871. *Phacelia* sect. *Microgenetes* (A. de Candolle) Benth. & Hook.f., Gen. Pl. 2:828. 1876. —Type (lectotype designated by J. T. Howell 1946): *Phacelia cumingii* (Benth.) A. Gray, Syn. Fl. N. Amer. 2(1):169. 1878.

Phacelia [unranked] *Bicolores* Rydb., Fl. Rocky Mts. 702. 1917.—Type: *Phacelia bicolor* Torr. ex S. Watson, Botany (Fortieth Parallel) 255. 1871.

Included taxa: *Phacelia affinis* A. Gray, *P. bicolor* Torr. ex S. Watson, *P. brachyloba* (Benth.) A. Gray, *P. cephalotes* A. Gray, *P. cumingii* (Benth.) A. Gray, *P. fremontii* Torr., *P. glandulifera* Piper, *P. gymnoclada* Torr. ex S. Watson, *P. ivesiana* Torr., *P. leibergii* Brand, *P. nana* Wedd.

Phacelia Juss. sect. *Miltitzia* (A. de Candolle) J. T. Howell, Leafl. W. Bot. 4:15. 1944. *Miltitzia* A. de Candolle, Prodr. 9:296. 1845. *Emmenanthe* Benth. subg. *Miltitzia* (A. de Candolle) A. Gray, War Department (U.S.), Pacif. Railr. Rep. 1854–5, 6:84–85. 1857 (Gray wrote, “It will be seen that I incline to the latter view; but should retain *Miltitzia* as a subgenus.”). —Type: *Phacelia lutea* (Hook. & Arnott) J. T. Howell, Leafl. W. Bot. 4:15. 1944.

Included taxa: *Phacelia adenophora* J. T. Howell, *P. glaberrima* (Torr. ex S. Watson) J. T. Howell, *P. inundata* J. T. Howell, *P. inyoensis* (J. F. Macbr.) J. T. Howell, *P. lutea* (Hook. & Arnott) J. T. Howell, *P. lutea* var. *lutea*, *P. lutea* var. *calva* Cronquist, *P. lutea* var. *mackenzieorum* J. W. Grimes & P. L. Packard, *P. lutea* var. *purpurascens* J. T. Howell, *P. monoensis* Halse, *P. salina* (A. Nelson) J. T. Howell, *P. scopulina* (A. Nelson) J. T. Howell, *P. submutica* J. T. Howell, *P. tetramera* J. T. Howell.

Phacelia Juss. sect. *Pachyphyllae* Walden & R. Patt., sect. nov. —Type: *Phacelia pachyphyllea* A. Gray, Proc. Amer. Acad. Arts 19:88. 1883.

Plants annual, 3–35 cm, herbage mephitic. Stems erect, hirsute and glandular, glands colorless- to amber- to black-tipped. Leaves rosulate and long-petiolate proximally, reduced and subsessile distally, petioles stout, proximal petioles usually channeled; blade broadly ovate or reniform or round, simple, bases truncate or cordate, margins undulate to shallowly lobed or crenate or serrulate, thick and succulent to coriaceous, hirtellous and glandular adaxially, glabrate and glandular abaxially, veins impressed adaxially. Inflorescence unit a cyme, secund, erect, solitary or in 2–3 clusters, compact and not elongate proximally, extending or not beyond vegetation. Flowers pedicellate, pedicels short, spreading to arcuate proximally in fruit; calyx slightly accrescent in fruit, lobes equal, oblong to oblanceolate, pubescent to hirsute and glandular; corollas deciduous, funnelform-campanulate or open-campanulate or subrotate, tube white to purple, lobes white to purple, glabrous adaxially, puberulent abaxially, lobe margins entire; nectary gland absent; corolla scales reduced and narrow, adjacent scale

edges sometimes divergent and adnate across base of filament, hirsute or ciliate; stamens included, filaments subequal or unequal, glabrous or puberulent, anthers yellow or violet; style included, branched 1/2 to 3/4 length, hirtellous and glandular; ovules 50–120. Fruits plumply ovoid to globose, prominently sulcate, puberulent and glandular. Seeds dark brown, 30–120, ellipsoid to ovoid, angular, surface transversely corrugated, corrugations 4–8. $n = 11, 12$.

Included taxa: *Phacelia calthifolia* Brand, *P. neglecta* M. E. Jones, *P. pachyphylla* A. Gray.

Phacelia Juss. subg. **Pulchellae** (Rydb.) Walden & R. Patt., stat. nov. *Phacelia* [unranked] *Pulchellae* Rydb., Fl. Rocky Mts. 702. 1917. —Type: *Phacelia pulchella* A. Gray, Proc. Amer. Acad. Arts 10:326. 1875.

Included taxa: *Phacelia barnebyana* J. T. Howell, *P. beatleyae* Reveal & Constance, *P. cookei* Constance & Heckard, *P. cronquistiana* S. L. Welsh, *P. demissa* A. Gray, *P. demissa* var. *demissa*, *P. demissa* var. *heterotricha* J. T. Howell, *P. demissa* var. *minor* N. D. Atwood, *P. filiae* N. D. Atwood, F. J. Sm., & T. A. Knight, *P. filiformis* Brand, *P. geraniifolia* Brand, *P. glechomifolia* A. Gray, *P. incana* Brand, *P. indecora* J. T. Howell, *P. keckii* Munz & I. M. Johnst., *P. laxiflora* J. T. Howell, *P. lemmonii* A. Gray, *P. mustelina* Coville, *P. parishii* A. Gray, *P. peirsoniana* J. T. Howell, *P. perityloides* Coville, *P. pulchella* A. Gray, *P. pulchella* var. *pulchella*, *P. pulchella* var. *gooddingii* (Brand) J. T. Howell, *P. rotundifolia* Torr. ex S. Watson, *P. sabulonum* (J. T. Howell) N. D. Atwood, *P. saxicola* A. Gray, *P. suaveolens* Greene.

KEY TO SUBDIVISIONS IN *PHACELIA*

- Plants 3–35 cm; corolla tubular to campanulate; corolla scales reduced and narrow, or absent; stamens included, subequal to unequal in length; style shallowly 2-lobed to branched 1/2 length; capsule costate and longitudinally sulcate
2. Annuals or perennials; seed compressed or angled, surface reticulate-pitted or foveolate..... *Phacelia* subg. *Pulchellae*
- Annuals; seeds terete and plump, surface transversely corrugated or transversely striate..... *Phacelia* subg. *Microgenetes*
- Leaf blades round, simple, bases cordate; corolla not yellow at base, tube white or purple; style branched 1/2 length; capsule globose, plump, exceeding calyx lobes; seeds 30–120 per capsule..... *Phacelia* sect. *Pachyphyllae*
- Leaf blades oblong to ovate, usually pinnatifid to pinnate to bipinnatifid, rarely simple, bases cuneate to truncate; corolla yellow at base, tube white or yellow or blue; style shallowly 2-lobed to branched 1/4 length; capsule oblong to ellipsoid to cylindric, not plump, not exceeding calyx lobes (except *P. tetramera*); seeds 4–30 per capsule
 - Stems prostrate to ascending; herbage neither mephitic nor malodorous; corolla tardily deciduous or marcescent in fruit, lobes white or yellow to yellow-purple. *Phacelia* sect. *Miltitzia*
 - Stems ascending to erect; herbage usually mephitic or malodorous; corolla readily deciduous in fruit, lobes white or pink or purple or blue *Phacelia* sect. *Euglypta*
- Plants 5–200 cm; corolla tubular or campanulate or rotate; corolla scales present in pairs along lateral veins of lamina (10 total in 5 pairs), reduced, or absent; stamens usually exsert, usually equal in length; style branched 1/4 length to parted nearly to base; capsule ecostate and shallowly longitudinally sulcate..... *Phacelia* subg. *Phacelia*
- Annuals; corolla scales absent; seed surface shallowly reticulate-pitted and foveolate
 - Staminal appendages at base of filaments absent; seeds 40–200 per capsule, ovules 50–120 per placenta *Phacelia* sect. *Gymnobrytha*
 - Staminal appendages at base of filaments present; seeds 10–90 per capsule, ovules 5–45 per placenta *Phacelia* sect. *Whitlavia*
 - Corolla usually purple, rarely white, corolla markings opposite corolla lobes or none; staminal appendages hairy; seeds 1–1.5 mm *Phacelia* subsect. *Whitlaviae*
 - Corolla white or pink to pale violet or bright blue, corolla markings opposite corolla sinuses or none; staminal appendages glabrous; seeds 1.5–2 mm *Phacelia* subsect. *Campanulariae*
- Annuals, biennials, or perennials; corolla scales usually present, wholly or partially adnate to corolla tube along one or both scale edges, sometimes reduced or absent; seed surface reticulate-pitted, alveolate, or foveolate
 - Nectary gland present on lamina midvein, sometimes reduced to minute ridge; corolla scale distal edges bordering or overlapping midvein, not divergent proximally across base of filament
 - Corolla scales wholly adnate along one edge to lateral vein, distal free edge overlapping midvein or nectary gland; seeds 6–60 per capsule; western North America (usually west of Great Plains, except some *P. franklinii* populations) *Phacelia* sect. *Eutoca*
 - Perennials; nectary gland surface hairy; stamens exsert, filaments glabrous or glabrate..... *Phacelia* subsect. *Sericaeae*
 - Annuals or biennials; nectary gland surface glabrous; stamens included or equal to corolla, filaments hairy
 - Annuals; stamens included, filaments stipitate-glandular; seeds 6–15 per capsule, surface coarsely reticulate-pitted *Phacelia* subsect. *Lineares*

- 11' Biennials; stamens equal to corolla, filaments eglandular; seeds 40–60 per capsule, surface finely reticulate-pitted *Phacelia* subsect. *Eutoca*
- 9' Corolla scales usually wholly adnate along one or both edges to lateral vein, free edge bordering and not overlapping midvein or nectary gland, sometimes each reduced to a ridge; seeds 2–20 per capsule; eastern North America (east of Great Plains), México, and Guatemala *Phacelia* sect. *Cosmantha*
12. Annual or biennial herbs; seeds 2–4 per capsule, ovules 2 per placenta; seed globose or ovoid, not angled
13. Corolla tubular-campanulate; stamens included, filaments glabrous; seed adaxial keel absent *Phacelia* subsect. *Ranunculacea*
- 13' Corolla open-campanulate to rotate-campanulate; stamens equal to corolla or exsert, filaments hairy; seed adaxial keel present.
14. Biennial herbs; corolla lobe margins entire or erose; stamens exsert; seed surface coarsely reticulate-pitted, excavated along one side of adaxial keel *Phacelia* subsect. *Bipinnatifidae*
- 14' Annual herbs; corolla lobe margins fimbriate; stamens equal to corolla; seed surface finely reticulate-pitted, not excavated alongside adaxial keel *Phacelia* subsect. *Cosmantha*
- 12' Annual or perennial herbs; seeds usually 5–20 per capsule, ovules usually 4–14 per placenta, rarely ovules 2 per placenta and seeds (2–3)4 per capsule (*P. zaragozana*); seed ovoid or ellipsoid, angled
15. Annual herbs; plants usually east of Mississippi River (not of México or Guatemala). *Phacelia* subsect. *Dubiae*
- 15' Annual or perennial herbs; plants usually west of Mississippi River (except some populations of *P. strictiflora* var. *lundelliana*, also of México, Guatemala) *Phacelia* subsect. *Cosmanthoides*
- 8' Nectary gland usually absent on lamina midvein, rarely present (*P. douglasii*); corolla scales usually divergent proximally across base of filament, distal scale edges between filaments free or connate, sometimes reduced or absent
16. Seed cymbiform (shallowly cymbiform in *P. sonotensis* and *P. infundibuliformis*), usually excavated along one or both sides of adaxial ridge, forming two longitudinal grooves, sometimes shallowly excavated (*P. bakeri*), surface reticulate-pitted or alveolate, adaxial ridge sometimes corrugated, seeds sometimes marginate, margins sometimes corrugated *Phacelia* sect. *Glandulosae*
- 16' Seed terete or carinate or angled, not cymbiform, sometimes shallowly excavated alongside adaxial ridge or keel, surface reticulate-pitted or foveolate or alveolate or scrobiculate or rugose, adaxial ridge or keel not corrugated, seeds rarely marginate, margins not corrugated
17. Leaves cauline, alternate, usually pinnatifid or pinnate or bipinnatifid, rarely simple (*P. bolanderi*, *P. malvifolia*, and *P. rattanii*), margins lobed or pinnatifid
18. Annuals or perennials; annuals with seeds 1–40 per capsule, perennials with seeds 1–4 per capsule; calyx usually strongly accrescent in fruit, lobes usually unequal *Phacelia* sect. *Ramosissimae*
- 18' Perennials; seeds 3–60 per capsule; calyx slightly accrescent in fruit, lobes equal *Phacelia* sect. *Baretiana*
- 17' Leaves in basal rosette or rosulate, or first pair opposite to subopposite, or leaves cauline and alternate, simple or shallowly lobed and margins entire, or pinnatifid to pinnate and leaflet margins entire. *Phacelia* sect. *Phacelia*
19. Perennials or biennials; stamens exsert; seeds (1–2)3–4 per capsule, ovules 2 per placenta. *Phacelia* subsect. *Phacelia*
- 19' Annuals; stamens included or exsert; seeds (1–2)3–20 per capsule, ovules 2–20 per placenta. *Phacelia* subsect. *Humiles*

ACKNOWLEDGMENTS

We thank Frank Cipriano, Dennis Desjardin, Ellen Dean, Bruce Baldwin, Diane Ferguson, Richard Olmstead, Leigh Johnson, Laura Garrison, Debra Hansen, John Dempcy, Deb Trock, Nancy Morin, Ron Hartman, Jim Linnberg, and Trigger (service dog of GKW). We are grateful to archivists, librarians, and curators at many institutions for access to books, databases, specimens, and loans supporting this research. This represents, in part, a master's thesis by GKW (2010) submitted to SFSU, and is in support of the FNANM treatment of *Phacelia* by both authors. Funding was provided in part by NSF GK12, NSF TREE, NSF GRF, and UC Berkeley Chancellor's

Fellowships, and by research grants from the California Native Plant Society (CNPS Bristlecone Chapter, CNPS Marin County Chapter, and CNPS Orange County Chapter), Colorado Native Plant Society, Conservation Genetics Laboratory at SFSU, Lawrence R. Heckard Endowment Fund of the Jepson Herbarium, Nevada Native Plant Society, Southern California Botanists, SFSU Department of Biology, and UC Valentine Eastern Sierra Reserve to GKW. We thank Hartmut Hilger for directing our attention to the earlier tribe name on Jim Reveal's INSG site. We especially thank John Strother for comments on later drafts of this manuscript, and conversations on nomenclature and taxonomy.

LITERATURE CITED

- ATWOOD, N. D. 1975. A revision of the *Phacelia Crenulatae* group (Hydrophyllaceae) for North America. *Great Basin Naturalist* 35:127–190.
- BENTHAM, G. AND J. D. HOOKER. 1876. *Genera Plantarum: ad exemplaria imprimis in Herberiis Kewensibus servata definita, auctorisbus G. Bentham et J. D. Hooker. Sistens dicotyledonum gamopetalorum ordines xxxix, Stylidieas-Plantagineas.* 3 vols., Vol. 2, pt. 2. Reeve, and Company, London, UK.
- BOUGAINVILLE, L. A. DE. 1771. *Voyage de Bougainville, capitaine de vaisseau, autour de monde par La Boudeuse et L'Etoile (années 1766, 1767, 1768, et 1769).* Paris, FR.
- BRAND, A. 1913. Hydrophyllaceae. A. Engler (ed.). *Das Pflanzenreich*, IV, Vol. 251 (Heft 59). Verlag von Wilhelm Engelmann, Leipzig, DE.
- BRIZICKY, G. K. 1968. 1805, a proposed starting point for the nomenclature of subgeneric taxa of vascular plants. *Taxon* 17:659–660.
- . 1969. Subgeneric and sectional names: their starting points and early sources. *Taxon* 18: 643–660.
- CANDOLLE, A. DE. 1845. Hydrophyllaceae. In *Prodromus systematis naturalis regni vegetabilis*, A. P. de. Candolle (ed). Fortin, Masson, and Company, Paris, FR.
- . 1867. Laws of botanical nomenclature, adopted by the International Botanical Congress, held at Paris in August 1867, together with an historical introduction and a commentary. English translation by H. A. Weddell, Vol. 2. Paris, FR.
- CONSTANCE, L. 1949. A revision of *Phacelia* subgenus *Cosmanthus* (Hydrophyllaceae). Contributions from the Gray Herbarium 168:1–48.
- . 1950. Some interspecific relationships in *Phacelia* subgenus *Cosmanthus*. Proceedings of the American Academy of Arts and Sciences 78:135–147.
- . 1953. *Howellanthus*, a new subgenus of *Phacelia*. *Madroño* 11(5):198–203.
- . 1963. Chromosome number and classification in Hydrophyllaceae. *Brittonia* 15:273–285.
- . AND T.-I. CHUANG. 1982. SEM survey of pollen morphology and classification in Hydrophyllaceae (Waterleaf Family). *American Journal of Botany* 69:40–53.
- COVILLE, F. V. 1893. Botany of the Death Valley Expedition. Contributions from the United States National Herbarium 4:1–318.
- DEGINANI, N. B. 1982. Revisión de las especies argentinas del género *Phacelia* (Hydrophyllaceae). *Darwiniana* 24:405–496.
- DEMPCY, J. M. 1996. Phylogenetic relationships in *Phacelia* section *Euglypta* (Hydrophyllaceae). M.S. Thesis, San Francisco State University, San Francisco, CA.
- DI FULVIO, T. E. AND N. DOTTORI. 1995. Contribución al conocimiento de tricomas y emergencias en Hydrophyllaceae. Clasificación y consideraciones taxonómicas. *Kurtziana* 24:19–24.
- DUMORTIER, B. C. 1829. Analyse des familles des plantes, avec l'indication des principaux genres qui s'y rattachent. Tournay, FR.
- DUNMORE, J. 2002. Monsieur Baret: first woman around the world 1766–68. Heritage Press, Auckland, NZ.
- FERGUSON, D. M. 1998. Phylogenetic analysis and relationships in Hydrophyllaceae based on *ndhF* sequence data. *Systematic Botany* 23:253–268.
- GANONG, C. K. 2002. Phylogenetic analysis of *Phacelia* section *Miltizia*. M.S. Thesis, San Francisco State University, San Francisco, CA.
- GARRISON, L. M. 2007. Phylogenetic relationships in *Phacelia* (Boraginaceae) inferred from *nITS* sequence data. M.S. Thesis, San Francisco State University, San Francisco, CA.
- GILBERT, C., J. M. DEMPcy, C. K. GANONG, R. PATTERSON, AND G. S. SPICER. 2005. Phylogenetic relationships within *Phacelia* subgenus *Phacelia* (Hydrophyllaceae) inferred from nuclear rDNA ITS sequence data. *Systematic Botany* 30:627–634.
- GILLETT, G. W. 1960a. Flowering responses in *Phacelia sericea* and *P. idahoensis*. *Madroño* 62:245–249.
- . 1960b. A systematic treatment of the *Phacelia franklinii* group. *Rhodora* 62:205–222.
- . 1961. An experimental study of variation in the *Phacelia sericea* complex. *American Journal of Botany* 48:1–7.
- . 1962. Evolutionary relationships of *Phacelia linearis*. *Brittonia* 14:231–236.
- . 1963. Flowering responses and phylogeny in the *Phacelia franklinii* group (Hydrophyllaceae). *American Journal of Botany* 50:798–801.
- . 1964. Genetic barriers in the *Cosmanthus phacelias* (Hydrophyllaceae). *Rhodora* 66:359–368.
- . 1965a. Genotypic variation in the *Phacelia hirsuta* complex. *Rhodora* 67:42–48.
- . 1965b. Genotypic variation in the *Phacelia strictiflora* complex. *Rhodora* 67:139–145.
- . 1968. Systematic relationships in the *Cosmanthus phacelias* (Hydrophyllaceae). *Brittonia* 20:368–374.
- GLASS, P. M. AND F. LEVY. 2011. Correspondence of morphology, phylogeny, and reproductive barriers in *Phacelia* subgenus *Cosmanthus* (Hydrophyllaceae). *Journal of the Torrey Botanical Society* 138:341–352.
- GMELIN, J. F. 1791. *Phacelia*. C. von Linné and J. F. Gmelin, (eds.). *Systema Naturae ... editio decima tertia, aucta, reformata*, Vol. 2. Lipsiae [Leipzig], Impensis Georg. Emanuel. Beer.
- GODLEY, E. 1965. Botany of the Southern Zone: exploration to 1843. *Tuatara* 13:140–181.
- GRAY, A. 1848. A manual of the botany of the Northern United States, first edition, from New England to Wisconsin and south to Ohio and Pennsylvania inclusive, according to the natural system, 2nd ed. James Munroe and Company, Boston & Cambridge, MA.
- . 1856. A manual of the botany of the Northern United States, second edition, including Virginia, Kentucky, and all east of the Mississippi, arranged according to the natural system, 2nd ed. George P. Putnam and Company, New York, NY.
- . 1875. A conspectus of the North American Hydrophyllaceae. *Proceedings of the American Academy of Arts and Sciences* 10:312–332.
- . 1878. *Synoptical flora of North America*, Vol. II, pt. I. Smithsonian Institute, Washington, DC.

- . 1883. Contributions to North American botany. Proceedings of the American Academy of Arts and Sciences 19:1–97.
- HALSE, R. R. 1979. Taxonomy of *Phacelia* section *Miltizia* (Hydrophyllaceae). Ph.D. Dissertation, Oregon State University, Corvallis, OR.
- HANSEN, D. R., G. S. SPICER, AND R. PATTERSON. 2009. Phylogenetic relationships between and within *Phacelia* Sections *Whitlavia* and *Gymnobrythus* (Boraginaceae). Systematic Botany 34:737–746.
- HECKARD, L. R. 1960. Taxonomic studies in the *Phacelia magellanica* polyploid complex, with special reference to the California members. University of California Publications in Botany 32:1–126.
- HOFFMANN, M. 1999. Flower and fruit development in the genus *Phacelia* (Phacelieae, Hydrophyllaceae): characters of systematic value. Systematics and Geography of Plants 68:203–212.
- HOWELL, J. T. 1942. Southwest botanical odyssey. Leaflets of Western Botany 3:132–137.
- . 1943a. Studies in *Phacelia*: a revision of species related to *P. pulchella* and *P. rotundifolia*. American Midland Naturalist 29:1–26.
- . 1943b. A systematic study of *Phacelia humilis* and its relatives in Sertulum Greeneanum. American Midland Naturalist 30:6–18.
- . 1945. Studies in *Phacelia*: revision of species related to *P. douglasii*, *P. linearis*, and *P. pringlei*. American Midland Naturalist 33:460–494.
- . 1946. A revision of *Phacelia* section *Euglypta*. American Midland Naturalist 36:381–411.
- JUSSIEU, A. L. DE. 1789. Genera plantarum secundum ordines naturales disposita. Herissant and Barrois, Paris, FR.
- LAISSUS, Y. 1978. Catalogue des manuscrits de Philibert Commerson (1727–1773) conservés à la Bibliothèque centrale du Muséum national d'Histoire naturelle (Paris). Revue d'histoire des sciences 31:131–162.
- LAMARCK, J. B. P. A. DE. 1792. Sur les relations dans leur port ou leur aspect, que les plantes de certaines contrées ont entre elles, et sur une nouvelle espèce d'*Hydrophyllie*. *Hydrophyllum Magellanicum*. Journal d'histoire naturelle 1:371–376, plate 19.
- LEE, G. J. 1986. Systematic studies in the *Phacelia humilis* group (Hydrophyllaceae): Corolla venation patterns. American Journal of Botany 73:230–235.
- MCNEILL, J., F. R. BARRIE, H. M. BURDET, V. DEMOULIN, D. L. HAWKSWORTH, K. MARHOLD, D. H. NICOLSON, J. PRADO, P. C. SILVA, J. E. SKOG, J. H. WIERSEMA, and N. J. TURLAND (EDS.). 2006. International code of botanical nomenclature (Vienna code). Regnum Vegetabile. Vol. 146: A. R. G. Gautner Verlag KG.
- MOORE, G. 2001. A review of the nomenclatural difficulties associated with misplaced rank-denoting terms. Taxon 50:495–505.
- MUNZ, P. A. 1935. A manual of southern California botany. Claremont Colleges, Scripps Publishing Fund, Claremont, CA.
- OLIVER, S. P. AND G. F. S. ELLIOT. 1909. The life of Philibert Commerson, D.M., naturalist du roi: an old-world story of French travel and science in the days of Linneaus. J. Murray, London, UK.
- REVEAL, J. 2012. Indices Nominum Supragenericorum Plantarum Vascularium. Website: <http://www.plantsystematics.org/reveal/pbio/fam/allspgnames.html> [accessed 15 April 2012].
- RIDLEY, G. 2010. The discovery of Jeanne Baret: a story of science, the high seas, and the first woman to circumnavigate the globe. Crown Publishers, New York, NY.
- RYDBERG, P. A. 1917. Flora of the Rocky Mountains and adjacent plains. Published by the author, New York, NY.
- SCHIEBINGER, L. 2003. Jeanne Baret: the first woman to circumnavigate the globe. Endeavour 27:22–25.
- SEWELL, M. AND M. A. VINCENT. 2009. Biosystematics of the *Phacelia ranunculacea* complex (Hydrophyllaceae). Castanea 71:192–209.
- SMALL, J. K. 1933. Manual of the southeastern flora; being descriptions of the seed plants growing naturally in Florida, Alabama, Mississippi, eastern Louisiana, Tennessee, North Carolina, South Carolina, and Georgia. Published by the author, New York, NY.
- TEPE, E., G. RIDLEY, AND L. BOHS. 2012. A new species of *Solanum* named for Jeanne Baret, an overlooked contributor to the history of botany. PhytoKeys 8:37–47.
- TORREY. 1871. Botany. In United States geological exploration [sic] of the Fortieth Parallel, S. Watson (ed.). Washington, DC.
- VOSS, J. W. 1937a. A revision of the *Phacelia Crenulata* group for North America. Bulletin of the Torrey Botanical Club 64:81–96.
- . 1937b. A revision of the *Phacelia Crenulata* group for North America (Concluded). Bulletin of the Torrey Botanical Club 64:133–144.
- WALDEN, G. K. 2010. Phylogeny of infrageneric relationships within *Phacelia* (Boraginaceae) inferred from chloroplast sequence data. M.S. Thesis, San Francisco State University, San Francisco, CA.
- . AND R. PATTERSON. 2010. *Howellanthus dalesianus*, recognition of a new genus and species in tribe Phacelieae (Boraginaceae). Madroño 57:268–273.

APPENDIX 1

CLASSIFICATION OF *PHACELIA*

- Phacelia* Juss.
Phacelia subg. *Phacelia*
Phacelia sect. *Phacelia*
Phacelia subsect. *Phacelia*
Phacelia subsect. *Humiles* Walden & R. Patt.
Phacelia sect. *Baretiana* Walden & R. Patt.
Phacelia sect. *Cosmantha* (Nolte ex A. de Candolle) Benth. & Hook.f.
Phacelia subsect. *Cosmantha* (Nolte ex A. de Candolle) Walden & R. Patt.
Phacelia subsect. *Bipinnatifidae* (Small) Walden & R. Patt.
Phacelia subsect. *Cosmanthoides* (A. Gray) Walden & R. Patt.
Phacelia subsect. *Dubiae* (Small) Walden & R. Patt.
Phacelia subsect. *Ranunculacea* Walden & R. Patt.

Phacelia sect. *Eutoca* (R. Br.) Benth. & Hook.f.
Phacelia subsect. *Eutoca* (R. Br.) Walden & R. Patt.
Phacelia subsect. *Lineares* (Rydb.) Walden & R. Patt.
Phacelia subsect. *Sericeae* (Rydb.) Walden & R. Patt.
Phacelia sect. *Glandulosae* (Rydberg) Walden & R. Patt.
Phacelia sect. *Gymnobrytha* (A. de Candolle) Benth. & Hook.f.
Phacelia sect. *Ramosissimae* (Rydberg) Walden & R. Patt.

Phacelia sect. *Whitlavia* (Harv.) Benth. & Hook.f.
Phacelia subsect. *Whitlaviae* (Harv.) G. W. Gillett
Phacelia subsect. *Campanulariae* G. W. Gillett
Phacelia subg. *Microgenetes* (A. de Candolle) A. Gray
Phacelia sect. *Euglypta* S. Watson
Phacelia sect. *Miltizia* (A. de Candolle) J. T. Howell
Phacelia. sect. *Pachyphyllae* Walden & R. Patt.
Phacelia subg. *Pulchellae* (Rydb.) Walden & R. Patt.



BHL

Biodiversity Heritage Library

Walden, Genevieve K and Patterson, Robert. 2012. "Nomenclature of Subdivisions Within Phacelia (Boraginaceae: Hydrophylloideae)." *Madroño; a West American journal of botany* 59, 211–222.
<https://doi.org/10.3120/0024-9637-59.4.211>.

View This Item Online: <https://www.biodiversitylibrary.org/item/185599>

DOI: <https://doi.org/10.3120/0024-9637-59.4.211>

Permalink: <https://www.biodiversitylibrary.org/partpdf/169170>

Holding Institution

Smithsonian Libraries and Archives

Sponsored by

Biodiversity Heritage Library

Copyright & Reuse

Copyright Status: In Copyright. Digitized with the permission of the rights holder

Rights Holder: California Botanical Society

License: <http://creativecommons.org/licenses/by-nc/3.0/>

Rights: <https://www.biodiversitylibrary.org/permissions/>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.