

THE GENERA OF HYDROPHYLLACEAE AND POLEMONIACEAE IN THE SOUTHEASTERN UNITED STATES ¹

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HYDROPHYLLACEAE R. Brown ex Edwards (WATERLEAF FAMILY)

Annual, biennial or perennial herbs [or rarely shrubs] with alternate or opposite, entire, pinnately or palmately divided leaves. Inflorescences terminal, axillary, or opposite the leaves, the flowers in cymes, panicles, or solitary. Flowers bisexual, regular, 5-merous. Calyx 5-parted, the sinuses sometimes bearing appendages. Corolla rotate, campanulate or funnelform, 5-parted. Stamens 5, epipetalous. Gynoecium syncarpous; styles 2 (rarely more) or 1, terminal; ovary superior, 1-locular with 2 parietal placentae or 2-locular and the placentation axile. Ovules 4—many, anatropous or amphitropous. Fruit a capsule.

A family of about 18 genera and 250 species in three tribes, primarily of North America, but extending into South America, Asia, and Africa. The family is represented in the United States by 15 genera centered in the Southwest; six genera occur in our area.

The family is regarded as being closely allied to the Polemoniaceae and the Boraginaceae. It may be distinguished from them by the combination of bicarpellary 1- or 2-locular ovary (usually with numerous ovules) and the usually imbricate aestivation of the flowers which are generally borne on scorpioid cymes. Considerable variation is evident in the structure and nature of the ovary. The gynoecium is 2-carpellate; the placentae may be parietal and fleshy or they may be narrow, extending into the ovary to meet without fusing and partition the ovary into two locules. In *Hydrolea* further elaboration of the placentae, accompanied by a fusion of the dividing wall, has produced a 2-locular ovary with axile placentation.

The Hydrophyllaceae are cytologically perhaps the best known family of any size. Information on the chromosome numbers of the species in

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the family has been accumulating, and, along with morphological studies, has already contributed to the understanding of the group. Cytological information, for instance, supports the recognition of subg. *Cosmanthus* of *Phacelia*, and also points to the relationship of *Lemmonia* to *Nama*. A comprehensive knowledge of the cytology of the members of this family will give a clearer indication of the value of chromosomal data in systematic studies. Presently the chromosomes of about 67 per cent of the species (about 200) have been counted, and counts are available for at least one species in each of the described genera.

REFERENCES:

- BRAND, A. Hydrophyllaceae. Pflanzenr. IV. 251(Heft 59): 1-210. 1913.
 ———. Die Hydrophyllaceen der Sierra Nevada. Univ. Calif. Publ. Bot. 4: 209-227. 1912.
 CAVE, M. S., and L. CONSTANCE. Chromosome numbers in the Hydrophyllaceae. Univ. Calif. Publ. Bot. 18: 205-216. 1942; II. 18: 293-298. 1944; III. 18: 449-465. 1947; IV. 23: 363-382. 1950; V. 30: 233-258. 1959.
 CONSTANCE, L. The genera of the tribe Hydrophyllae of the Hydrophyllaceae. Madroño 5: 28-33. 1939. [Includes key to genera.]
 ———. Hydrophyllaceae. In L. Abrams, III. Fl. Pacific States 3: 476-532. 1951.
 ———. Hydrophyllaceae. Inst. Paran. Catal. Gen. 4: 1, 2. 1956.
 GRAY, A. A conspectus of the North American Hydrophyllaceae. Proc. Am. Acad. Arts Sci. 10: 312-332. 1875.
 PETER, A. Hydrophyllaceae. Nat. Pflanzenfam. IV. 3a: 54-71. 1897.
 SVENSSON, H. G. Zur Embryologie der Hydrophyllaceen, Boraginaceen und Heliotropiaceen mit besonderer Rücksicht auf die Endospermibildung. Uppsala Univ. Årsskr. 1925. 2(Math. Nat. 2): 1-176. 1925.

KEY TO THE GENERA OF HYDROPHYLLACEAE

- A. Leaves dissected, lobed or toothed; style 1, entire or 2-cleft.
 B. Placentae parietal, dilated, ovary 1-locular.
 C. Flowers in scorpioid cymes; stamens exserted; leaves mostly basal and alternate; seeds not cucullate; plants biennial or perennial. 1. *Hydrophyllum*.
 C. Flowers solitary opposite the leaves or terminal in a loose cyme; stamens included; leaves mostly cauline, all alternate or the lower opposite and the upper alternate; plants annual.
 D. Calyx sinuses auriculate; seeds cucullate; leaves all alternate. 2. *Nemophila*.
 D. Calyx sinuses without auricles; seeds not cucullate; leaves opposite below, alternate above. 3. *Ellisia*.
 B. Placentae parietal, narrow, projecting into ovary and partitioning it into 2 locules but not fusing; flowers in scorpioid cymes; calyx sinuses without auricles; seeds not cucullate; leaves alternate. 4. *Phacelia*.
 A. Leaves entire, simple; styles 2 (rarely 3-5).
 E. Flowers axillary, solitary or paired; placentae parietal, narrow, projecting into ovary and partitioning it into 2 locules but not fusing. . . . 5. *Nama*.
 E. Flowers in cymose inflorescences; ovary 2-locular; placentae axile. 6. *Hydrolea*.

Tribe HYDROPHYLLAE A. Gray

1. **Hydrophyllum** Linnaeus, Sp. Pl. 1: 146. 1753; Gen. Pl. ed. 5. 72. 1754.

Erect, perennial or biennial herbs with membranaceous, pinnate or pinnatifid basal leaves and alternate cauline leaves similar to the basal ones or orbicular to reniform, palmately lobed or divided. Inflorescences simple or branched cymes, terminal. Calyx campanulate, 5-lobed, at times the sinuses with a small appendage. Corolla campanulate, 5-parted, greenish-white or white to purple or violet, with a pair of elongated scales adnate to the corolla tube at the base of each filament. Stamens 5, exserted, the filaments more or less villous; pollen smooth, tricolpate. Style solitary, once branched at the apex, the stigmas capitate; ovary 1-locular with 2 parietal placentae. Fruit a globose, 1-3-seeded capsule. Seeds reticulate, without cucullus. (Including *Decemium* Raf.) TYPE SPECIES: *H. virginianum* L. (Name from Greek, *hydor*, water, and *phyllon*, leaf, in reference to the succulent stems and petioles of *H. virginianum*.) — WATERLEAF.

A genus of eight species in two sections with four species in eastern and four in western North America. All four of the eastern American species occur in our area, all in rich, moist woods. The species of *Hydrophyllum* are very similar in floral and fruit characters, but are distinguishable in the characters of the leaf and of pubescence.

Section HYDROPHYLLUM (perennial and rhizomatous, calyx rarely appendaged) includes seven species, four restricted to western North America, and three in our area. *Hydrophyllum virginianum* ($2n = 18$) ranges from Quebec west to eastern North and South Dakota and south to Maryland, Virginia, Tennessee, Arkansas, and Kansas. Deep-violet-flowered plants from the mountains of West Virginia, Virginia, and North Carolina have been described as *H. virginianum* var. *atranthum* (E. J. Alex.) Constance. Additional field study is needed to determine whether this is merely a color-form occurring among other forms (white to purple) or whether it is in fact the only representative of the species in its area and restricted in its distribution. *Hydrophyllum macrophyllum* Nutt. ranges from western Virginia and West Virginia, west to Illinois, and south to Georgia, Alabama, and Arkansas; and *H. canadense* L. ($2n = 18$) occurs from Massachusetts and Vermont to Ontario and Illinois south to northern Alabama and eastern Missouri.

Section DECEMIUM (Raf.) Gray (biennial with taproot, calyx always appendaged) includes only *Hydrophyllum appendiculatum* Michx. ($2n = 18$) which is distributed from Ontario to Minnesota, south to Pennsylvania, Tennessee, Missouri, and eastern Kansas. The presence of appendages in the sinuses of the calyx lobes and the biennial habit have served as characters in the recognition of the monotypic genus *Decemium* Raf. However, since appendages may occasionally be found in *H. canadense*

and other distinguishing features are only minor floral variations, *Decemium* is to be retained in *Hydrophyllum* which it closely resembles in all other respects.

REFERENCES:

- CONSTANCE, L. The genus *Hydrophyllum* L. Am. Midl. Nat. 27: 710-731. 1942. [Monograph.]
GARCIN, M. Étude anatomique de l'*Hydrophyllum canadense*. Bull. Soc. Bot. Lyon II. 5: 77-85. 1887.
SELBY, A. D. A peculiar *Hydrophyllum*. Jour. Columbus Hort. Soc. 8: 128-130. 1893-1894.*

2. *Nemophila* Nuttall in Barton, Fl. N. Am. 2: 71. 1822; Nuttall, Jour. Acad. Nat. Sci. Phila. 2: 179. 1822, nom. cons.

Weak, annual herbs with alternate [or opposite, or the lower opposite and the upper alternate] oblong to orbicular, pinnate, pinnatifid or lobed leaves. Flowers solitary on peduncles opposite the leaves or in terminal cymes. Calyx campanulate, deeply 5-parted, the sinuses auriculate [or exauriculate.] Corolla campanulate to rotate, 5-lobed, white or blue, with a pair of scales adnate to corolla lobes at the base of each filament. Stamens 5, included; pollen smooth, tricolpate. Style solitary, shallowly or deeply cleft; ovary 1-locular with 2 parietal placentae. Fruit an ovoid or globose, 1-4[-20]-seeded loculicidal capsule. Seeds cucullate, regularly [or irregularly] pitted [or without evident pits]. (*Viticella* Mitch., nom. rejic.; *Galax* L. 1753 [partim], 1754, nom. rejic.) TYPE SPECIES: *N. phacelioides* Nutt. in Barton. (Name from Greek, *nemos*, a grove, and *philein*, to love, in reference to the habitat of *N. phacelioides*.)

A genus of eleven species with nine in western North America and two in the southeastern United States. The species are distinguished on the basis of leaf shape and arrangement, nature of the seeds, color and shape of the corolla, nature of the auricles, and pubescence of the stems and leaves. A number of growth forms of various species have been described and named, mostly as a result of misinterpretation of the behavior of the species during the growing season. As the season progresses, most species pass from a small, erect, and unbranched stage to an elongated, decumbent, and branched one. The flowers also often become smaller and altered in their shape.

Our two species occur in moist and shaded woods. *Nemophila phacelioides* Nutt. ($2n = 14$) (corollas blue or purplish, 1-3 cm. broad, auricles prominent) ranges from southern Texas and Louisiana north to Arkansas and Oklahoma. It is cytologically unique in its seven pairs of chromosomes which are nearly twice as large as the nine pairs of the ten other species. *Nemophila microcalyx* (Nutt.) Fisch. & Mey. (corollas white, 0.5 cm. or less broad, auricles minute) ($2n = 18$) ranges from southeastern Texas north to Arkansas, and southeastern Missouri, east and north to Florida, Tennessee and Virginia.

REFERENCES:

- BERG, R. Y. Seed dispersal, morphology, and phylogeny of *Trillium*. Skr. Vid.-Akad. Oslo 1: 1-36. 1958. [Includes note on the dispersal of seeds of *Nemophila* by ants.]
- BIOLETTI, F. T. Notes on the genus *Nemophila*. Erythea 3: 139-142. 1895.
- CHANDLER, H. P. A revision of the genus *Nemophila*. Bot. Gaz. 34: 194-215. 1902.
- CONSTANCE, L. The genus *Nemophila* Nutt. Univ. Calif. Publ. Bot. 19: 341-398. 1941. [Monograph.]
- CRÉTÉ, P. Embryogénie des hydrophyllacées. Développement de l'embryon chez le *Nemophila insignis* Benth. Compt. Rend. Acad. Sci. Paris 224: 749-751. 1947.
- EASTWOOD, A. Observations on the habits of *Nemophila*. Erythea 3: 151-153. 1895. [Flowers of *N. insignis* (= *N. Menziesii*).]
- WULFF, H. D., and T. S. RAGHAVAN. Beobachtungen an Pollenschlauchkulturen von der Hydrophyllacee *Nemophila insignis*. Planta 27: 466-473. 1937.

3. *Ellisia* Linnaeus, Sp. Pl. ed. 2. 2: 1662. 1763, nom. cons.

Simple or diffusely branched, weak annual herbs with oblong to ovate or deltoid-ovate, pinnately divided leaves, the lower opposite and the upper alternate. Flowers solitary on peduncles opposite the leaves or in terminal cymes. Calyx campanulate, deeply 5-parted, auricles none. Corolla narrowly campanulate, 5-lobed, white or bluish, with a pair of minute scales adnate to each corolla lobe at the base of each stamen. Stamens 5, included; pollen smooth, tricolpate. Style solitary, 2-cleft; ovary 1-locular with 2 parietal placentae. Fruit a globose, usually 4-seeded capsule. Seeds without a cucullus, regularly reticulate. $2n = 20$. (*Macrocalyx* Ehret ex Trew, Nova Acta Acad. Leop.-Carol., nom rejic.; *Nyctelea* Scopoli.) TYPE AND SOLE SPECIES: *E. Nyctelea* (L.) L. (Named in honor of the English naturalist John Ellis, 1710-1776.)

A monotypic genus with disrupted distribution, occurring in rich woods and on stream banks from New Jersey and Pennsylvania to North Carolina (?) and on the prairies and plains of Manitoba to Alberta, southeast and south to Indiana, Illinois, Arkansas, Oklahoma, and New Mexico. It is also known as an adventive in disturbed areas in the northeastern United States.

Ellisia resembles *Pholistoma* and *Nemophila*, but is distinguished by its seeds which lack a cucullus, its unarmed capsules, and its hispid or glabrate stems. Although closely related to these groups, *Ellisia* is believed to be a distinct and natural genus.

REFERENCES:

- CONSTANCE, L. The genus *Ellisia*. Rhodora 42: 33-39. 1940.
- ROBERTSON, C. Flowers and insects. X. Bot. Gaz. 18: 47-54. 1893. [Pollination of *Ellisia* by bees.]

Tribe PHACELIEAE A. Gray

4. *Phacelia* Jussieu, Gen. Pl. 129. 1789.

Annual, biennial [or perennial] herbs with alternate, lobed or pinnately divided leaves. Inflorescences scorpioid cymes. Calyx deeply 5-parted. Corollas rotate to campanulate, 5-lobed, white to lavender or bluish violet, without scales, a gland bearing two parallel flaps adnate to the corolla tube between each pair of stamens. Stamens 5, exserted or included. Style 2-cleft; ovary with two 2–14-ovuled parietal placentae which meet and partition the ovary into 2 locules. Fruit an ovoid 4–many-seeded capsule. Seeds finely reticulate to alveolate or rugose. TYPE SPECIES: *P. secunda* J. F. Gmelin (*P. magellanica* (Lam.) Coville). (Name from Greek, *phacelos*, a fascicle, in reference to the cymose inflorescences.) — SCORPION WEED.

A genus of perhaps 100 species of temperate North and South America, placed by Brand in six sections. All of our species belong to subg. *Cosmanthus* (Nolte ex A. DC.) Constance (sect. *Cosmanthus* Nolte ex A. DC.). The genus itself is characterized by the scorpioid cymes and by the narrow placentae which project into the ovary and meet, thereby producing two locules.

Subgenus *COSMANTHUS*, with 14 species, occurs from the highlands of Guatemala and Mexico, north into Texas, east to Georgia and North Carolina, and north to Oklahoma, Missouri, Illinois, Ohio, Pennsylvania and New York, primarily in rich woods, clearings, and fields. Ten species and varieties occur in our area. All of our species are annuals, except *Phacelia bipinnatifida* Michx. (including *P. brevistyla* Buckl.) ($2n = 18$), a biennial distributed from West Virginia to Georgia and Alabama, west to Illinois, Missouri, and northeastern Arkansas. This species, formerly placed in sect. *PHACELIA* because of its prominent glands and their associated scales, belongs properly in subg. *COSMANTHUS* on the basis of its other morphological features and its distribution.

Phacelia Purshii Buckl. (including *P. Boykinii* (A. Gray) Small and *P. Bicknellii* Small) ($2n = 18$) is widely distributed in eastern North America. Both large-flowered plants of *P. Purshii* and similar small-flowered plants (*P. Bicknellii* ?) grow together in the vicinity of Nashville, Tennessee, suggesting the need for additional investigation. *Phacelia dubia* (L.) Trel. var. *dubia* ($2n = 10$) is also of wide distribution in eastern North America, while *P. dubia* var. *georgiana* McVaugh is an endemic of the granite flat rocks of Georgia and Alabama.

Phacelia strictiflora (Engelm. & Gray) Gray var. *Robinsii* Constance ($2n = 18$), of Alabama, Missouri, Oklahoma, and Texas, has characters intermediate between *P. strictiflora* var. *Lundelliana* Constance ($2n = 18$) (Texas and Oklahoma) and *P. hirsuta* Nutt. ($2n = 18$) (Missouri, Kansas, Arkansas, Louisiana, Oklahoma, Texas) and is suspected of having arisen through the hybridization of those two taxa. Similarly,

hybridization of *Phacelia hirsuta* and *P. Purshii* appears to have given rise to *P. gilioides* Brand ($2n = 18$) (Missouri, Kansas, Oklahoma).

Our other species are *Phacelia ranunculacea* (Nutt.) Constance (*P. Covillei* S. Wats.) ($2n = 28$), peculiar in its tubular-campanulate corolla, vestigial glands, semiglobose seeds, chromosome number, and disrupted distribution (Maryland, District of Columbia, Virginia and Indiana, Missouri, Tennessee, North Carolina, Arkansas); *P. maculata* Wood ($2n = 10$), from the southern Appalachians; *P. glabra* Nutt. ($2n = 16$), unique in its chromosome number; and *P. fimbriata* Michx. ($2n = 18$). In spite of the different chromosome numbers among the species in subg. *COSMANTHUS*, the absence of the number 11, which is common among the other members of the genus, supports the distinctness of the group. It is also the only group of *Phacelia* in which there is a 9-paired perennial species (*P. platycarpa* (Cav.) Spreng.).

REFERENCES:

- ALLARD, H. A. *Phacelia ranunculacea* (Nutt.) Constance, its length of day, temperature reactions and seasonal adaptations. *Castanea* 5: 94-97. 1940.
- CONSTANCE, L. A revision of *Phacelia* subgenus *Cosmanthus* (Hydrophyllaceae). *Contr. Gray Herb.* 168: 1-48. 1949.
- . Some interspecific relationships in *Phacelia* subgenus *Cosmanthus*. *Proc. Am. Acad. Arts Sci.* 78: 135-147. 1950.
- . *Howellanthus*, a new subgenus of *Phacelia*. *Madroño* 11: 198-203. 1952.
- CRÉTÉ, P. Embryogénie des hydrophyllacées. Développement de l'embryon chez le *Phacelia tanacetifolia* Benth. *Compt. Rend. Acad. Sci. Paris* 223: 459, 460. 1946.
- FERNALD, M. L. Overlooked species, transfers and novelties in the flora of eastern North America. *Rhodora* 46: 32-57. 1944. [51-56, The plants passing as *Phacelia hirsuta*.]
- GILLET, G. W. Variation and genetic relationships in the *Whitlavia* and *Gymnobythus* *Phacelias*. *Univ. Calif. Publ. Bot.* 28: 19-78. 1955. [$2n = 22$ in all 7 species.]
- GREENE, E. L. Some *Phacelia* segregates. *Pittonia* 5: 17-23. 1902.
- HECKARD, L. R. Cytotaxonomy of a polyploid complex. VIIIth Congr. Int. Bot. Rapp. & Comm. Sect. 9, 10: 72, 73. 1954. [*Phacelia magellanica* complex.]
- HOWELL, J. T. A revision of *Phacelia* sect. *Euglypta*. *Am. Midl. Nat.* 36: 381-411. 1946.
- . A revision of *Phacelia* section *Miltitzia*. *Proc. Calif. Acad. Sci.* IV. 25: 357-376. 1944.
- . Studies in *Phacelia* — I-IV. *Leafl. West. Bot.* 3: 95, 96, 1941; 117-120, 190-192. 1942; 4: 150-152. 1945.
- . Studies in *Phacelia* — revision of species related to *P. Douglasii*, *P. linearis* and *P. Pringlei*. *Am. Midl. Nat.* 33: 460-494. 1945.
- . Studies in *Phacelia* — a revision of species related to *P. pulchella* and *P. rotundifolia*. *Am. Midl. Nat.* 29: 1-26. 1943.
- . Sertulum Greeneanum. *Am. Midl. Nat.* 30: 6-39. 1943. [I. A systematic study of *Phacelia humilis* and its relatives. II. Types of *Phacelia* in the Greene herbarium.]
- JANOTA, D. Erste Erfahrungem mit dem Nektarbetrag der *Robinia pseudoacacia*

- und *Phacelia tanacetifolia*. (In Czech.) Brno. Vysoká Zeměděl. a Lesn. Fakul. Sborn. Rada A. 1956(4): 225–234. 1956.*
- KARTASHOVA, N. Minor elements and nectar-yielding *Phacelia*. (In Russian.) Sel'sk. Khoz. Sibiri 1958(8): 82–84. 1958.*
- KRUCKEBERG, A. R. Notes on the *Phacelia magellanica* complex in the Pacific Northwest. Madroño 13: 209–221. 1956. [I. A new *Phacelia* from southwestern Oregon. II. The hexaploid *Phacelia leptosepala* Rydberg.]
- LIVENTSEVA, E. On determining the seed germination of *Phacelia*. (In Russian.) Pchelovodstvo 29(3): 42–44. 1952.*
- QUICK, C. R. Germination of *Phacelia* seeds. Madroño 9: 17–20. 1947. [Seeds of many annual species will grow without special treatments; seeds of many perennial species must be stratified.]
- ROLLIN, P. Action qualitative de la lumière sur la germination des graines de *Phacelia tanacetifolia*. Compt. Rend. Acad. Sci. Paris 247: 1484–1487. 1958.
- Voss, F. W. A revision of the *Phacelia crenulata* group for North America. Bull. Torrey Bot. Club 64: 81–96. 1937.

5. **Nama** Linnaeus, Syst. Nat. ed. 10. 2: 950. 1759, partim, emend. Choisy in DC. Prodr. 10: 182. 1846, nom. cons.

Prostrate or ascending, annual [or perennial] herbs with alternate [rarely opposite] entire leaves. Flowers solitary or paired in the axils of leaves [or in reduced lateral or terminal cymes]. Calyx deeply 5-parted, accrescent. Corolla tubular, 5-lobed, purple or white. Stamens 5, included, unequally inserted on the corolla tube, the filament bases usually dilated, the adnate portion with [or without] free margins. Styles 2, free, or at times united about half their length [or completely united]; ovary multiovulate, appearing 2-locular as a result of the intrusion of the 2 parietal placentae. Fruit a loculicidal [or either loculicidal or septicidal] many-seeded capsule. Seeds variously pitted, alveolate [or reticulate to smooth]. (*Nama* L., 1753, *Conanthus* S. Wats., *Marilau-nidium* O. Ktze., nomina rejicienda; not *Nama* sensu Small = *Hydrolea* L.) TYPE SPECIES: *N. jamaicensis* L. (Name from Greek, *nama*, a river or stream, in reference to the habitat of *Nama zeylanica* L. [= *Hydrolea zeylanica* (L.) Vahl.] the only species mentioned by Linnaeus in 1753.)

A genus of about 35 species in five sections, primarily of Mexico and the southwestern United States, but also in South and Central America, the West Indies, and (one species) the Hawaiian Islands. In our area the genus is represented only by *Nama jamaicensis* L. ($2n = 28$), of sect. NAMA (leaves entire, styles free or only partially united, capsules membranous), which occurs in hammocks, roadsides, and disturbed areas, and ranges from El Salvador and the West Indies, north to Texas, Florida, and Louisiana.

REFERENCES:

- HITCHCOCK, C. L. A taxonomic study of the genus *Nama*. I. Am. Jour. Bot. 20: 415–430; II. 518–534. 1933. [Monograph.]
- . The perennial Mexican *namas*. Am. Jour. Bot. 26: 341–347. 1939.

Tribe HYDROLEAE Choisy

6. *Hydrolea* Linnaeus, Sp. Pl. ed. 2. 1: 328. 1762, nom. cons.

Annual or perennial herbs with alternate, simple leaves. Inflorescences axillary or terminal cymes. Calyx deeply 5-parted. Corolla rotate to campanulate, 5-parted, blue, rarely white, without scales. Stamens 5, exserted or included, the filament bases dilated, inserted on corolla tube. Styles 2, rarely 3–5; ovary 2-locular, multiovulate, placentation axile, the placentae 2-branched [or entire]. Fruit a 2–4-valved, or irregularly dehiscent capsule. Seeds longitudinally ribbed. (*Nama* L., 1753, not 1759, nom. rejic.) TYPE SPECIES: *H. spinosa* L. (Name from Greek, *hydor*, water, apparently in reference to the aquatic habitat.)

A genus of about 19 species (in two sections) in aquatic habitats in the tropics of the world. Section ATTALERIA Brand (placentae entire) with about five species, is entirely Old World (occurring primarily in Africa and Asia). Section HYDROLEA (sect. *Sagnonea* (Aubl.) Brand) (placentae divided into two parts) is limited to the Americas and contains about 14 species ranging from Paraguay and Uruguay, to Brazil, north to Mexico, the West Indies, and the eastern United States.

Hydrolea uniflora Raf. (*H. affinis* Gray) (Texas to Mississippi and northern Florida, north to Oklahoma, southern Missouri, southern Indiana, and southern Illinois) has glabrous stems and lance-ovate calyx lobes which equal the corolla in length. *Hydrolea quadrivalvis* Walt. ($2n = 20$) (northern Florida to Louisiana, north to southeastern Virginia) has stems which are villous-hispid, and linear or linear-lanceolate calyx lobes which equal the corolla. These two species seem to be very closely related and differ mainly in the pubescence of the stem. Field observations and collections of the two, particularly in the area where they overlap, should be valuable in clarifying their relationship. Our other two species are *H. ovata* Nutt. (Texas to Georgia, north to Missouri) with ovate leaves, pubescent stems and calyx segments shorter than the corolla, and *H. corymbosa* Macbride ex Elliott (southern Florida to Georgia and South Carolina) with elliptic to elliptic-lanceolate leaves, glabrate stems, and calyx segments shorter than the corolla.

Hydrolea spinosa L., of the American tropics, has also been reported to have 20 pairs of chromosomes.

POLEMONIACEAE Jussieu (PHLOX FAMILY)

Annual, biennial, or perennial herbs [shrubs, vines, or small trees], with opposite or alternate, simple or pinnately [or palmately] dissected leaves. Inflorescences cymose or flowers rarely solitary. Flowers bisexual. Calyx 5-parted. Corolla 5-parted, salverform to rotate, the aestivation contorted. Stamens 5, alternate with the corolla lobes, equally or unequally inserted on the corolla, the anthers introrse. Gynoecium syncar-

pous, stigmas 3[rarely 2]-lobed, style 1, ovary superior, 3[rarely 2]-locular, each locule with 1-many anatropous ovules, the placentation axile. Fruit a loculicidal capsule [rarely indehiscent]. Seeds with a straight embryo and abundant endosperm. TYPE GENUS: *Polemonium* L.

A family of about 300 species variously interpreted to represent about 12 to 23 genera placed in four tribes and two subfamilies by Brand, and in five tribes by Grant. The tribes COBAEAE Baill., CANTUEAE Peter and BONPLANDIEAE Baill. contain tropical genera of shrubs, vines or small trees (*Cobaea* Cav., *Cantua* Juss., *Huthia* Brand, *Bonplandia* Cav. and *Loeselia* L.) and range from Mexico south to Chile. The temperate, primarily herbaceous, genera fall in tribe POLEMONIEAE Baill., which includes the well-marked genera *Phlox* and *Polemonium*, and in the tribe GILIEAE Reichb., which includes *Gilia*, a genus which has been considered by some authors to include almost all of the remaining species in the subfamily, a complex of polymorphic species which is poorly understood. The Polemoniaceae are centered primarily in western North America, but extend south into Mexico, Peru, and southern Chile, east to eastern North America, and also into Asia and Europe. In our area the family is represented by *Phlox*, *Polemonium*, and *Ipomopsis*. The weedy *Colomia linearis* Nutt. ($2n = 16$) is known in Missouri and may perhaps also become established within our region.

The family has been a perplexing problem with respect to its phylogenetic relationships. It has been considered to be derived from a sympetalous relative of the Rosales, from the Geraniales, and from the Primulales. The Polemoniaceae seem to be allied to the Convolvulaceae, which they resemble in their inflorescences, corolla, stamens, and anatropous ovules. However, on the basis of a morphological study of the flowers, Dawson concluded that they are closely related to the Caryophyllaceae and Geraniaceae, and interpreted the family as representing an evolutionary line from a 3-carpellate caryophyllaceous stock which arose prior to the establishment of the free-central placentation of the Caryophyllaceae. *Cantua* and *Cobaea* were interpreted as primitive genera: they differ from other Polemoniaceae in their woody habit and in having two whorls of stamen traces. Cytologically, the subfamily COBAEOIDEAE differs in having a larger number of chromosomes which have a much smaller size than those of the genera of the POLEMONIOIDEAE.

The family is particularly popular in horticulture, and almost all of the genera are known in cultivation.

REFERENCES:

See also SOUÈGES under *Polemonium*.

BRAND, A. Polemoniaceae. Pflanzenr. IV. 250(Heft 27): 1-203. 1907.

DAWSON, M. L. The floral morphology of the Polemoniaceae. Am. Jour. Bot. 23: 501-511. 1936.

FLORY, W. S. Chromosome numbers in the Polemoniaceae. Cytologia Fujii Jubil. Vol. 1: 171-180. 1937.

- GRANT, V. Natural history of the *Phlox* family. I. Systematic Botany. 280 pp. The Hague. 1959. [Morphology, chromosome numbers, phylogeny, phyto-geography, taxonomy; not a taxonomic revision.]
- GRAY, A. Revision of the North American Polemoniaceae. Proc. Am. Acad. Arts Sci. 8: 247-282. 1870.
- HÜLLER, G. Beiträge zur vergleichenden Anatomie der Polemoniaceen. Beih. Bot. Centr. 21: 173-244. 1907.
- INGRAM, J. Notes on the cultivated Polemoniaceae. 1. A key to the genera. Baileya 7: 80-86. 1959.
- MASON, H. L. The genus *Eriastrum* and the influence of Bentham and Gray upon the problem of generic confusion in Polemoniaceae. Madroño 8: 65-91. 1945.
- . Polemoniaceae. In L. ABRAMS, III. Flora Pacif. States 3: 396-474. 1951.
- . Polemoniaceae. Inst. Paran. Catal. Gên. 5: 1, 2. 1956.
- and A. D. GRANT. Some problems in the genus *Gilia*. Madroño 9: 201-220. 1948.
- PETER, A. Polemoniaceae. Nat. Pflanzenfam. IV. 3a, b: 40-54. 1897.
- WHERRY, E. T. Picking out the Polemoniaceae. Bartonia 11: 1-4. 1929.
- . The Polemoniaceae of Pennsylvania. Proc. Penn. Acad. Sci. 9: 150-155. 1935.
- . The Polemoniaceae of Virginia. Claytonia 2: 3, 4, 11-14. 1935.
- . Polemoniaceae of the middle Appalachian region. Castanea 1: 13-15. 1936; 32-35. 1936.
- . Miscellaneous eastern Polemoniaceae. Bartonia 18: 52-59. 1936. [Includes key to native and adventive genera.]
- . A provisional key to the Polemoniaceae. Bartonia 20: 14-17. 1940.

KEY TO THE GENERA OF POLEMONIACEAE

- A. Leaves simple, opposite; perennials or annuals; stamens unequally inserted on the corolla tube. 1. *Phlox*.
- A. Leaves pinnately divided, alternate; stamens equally inserted on the corolla tube.
- B. Leaves once pinnately divided, the leaflets oval to lanceolate; flowers blue or white; perennial. 2. *Polemonium*.
- B. Leaves deeply pinnately dissected into narrow, linear lobes; flowers red, pink, or white; biennial. 3. *Ipomopsis*.

Tribe POLEMONIEAE Baill.

1. *Phlox* Linnaeus, Sp. Pl. 1: 151. 1753; Gen. Pl. ed. 5. 75. 1754.

Perennial or annual, herbaceous or more or less woody, erect, decumbent or trailing plants with opposite, alternate or subopposite sessile or petioled leaves. Inflorescences cymose, terminal or in the axils of the uppermost leaves. Calyx tubular, angled, 5-parted, not accrescent, rupturing as the capsule expands. Corolla salverform, 5-parted, purple, to lavender, to pink to white. Stamens 5, unequally inserted on the corolla tube, exserted or included. Style 1; stigmas 3; ovary 3-locular, each locule with 1-3 anatropous ovules. Fruit a loculicidal capsule. TYPE SPECIES: *P. glaberrima* L. (Name from Greek, *phlox*, flame, the ancient name for *Lychnis*, transferred to this genus.)

A genus of about 67 species primarily of North America, ranging from northern Mexico to the United States and southern Canada, and in Alaska to adjacent Yukon and Northwest Territories; a single species in northeastern Asia (Siberia). In our area the genus is represented by about seventeen species, most of which are known also in cultivation.

The genus has been variously subdivided into six sections by Peter; two subgenera, five sections and two subsections by Brand; and into three sections and eighteen subsections by Wherry. The major subgeneric divisions are based on such characters as the habit of the plant, the length of the style, the size of the seed and embryo, and the length of the stamens. Additional divisions are based on the shape of the corolla, minor leaf variations, as well as leaf arrangement, and pubescence. It seems questionable that the numerous subdivisions of the genus are natural and that all are worthy of taxonomic recognition. It is probable that a genetic study of the genus would help to clarify problems of interrelationships of the species which are not apparent on the basis of morphological studies alone.

The variation within the species of *Phlox* has often led to widely different taxonomic treatments. The variation in a population of *Phlox bifida* Beck from Tennessee has been interpreted as the result of introgressive hybridization with *P. amoena* Sims. Further studies of this kind are needed to help explain the nature of the variation in different species. *Phlox Drummondii* Hook., an annual native to Texas, is widely grown as an ornamental and has become naturalized as far east as Georgia and Florida. Hundreds of forms of *P. Drummondii*, differing in flower color, shape of the corolla, and pubescence have arisen in cultivation, and the remarkable variation in the species has been the subject of numerous studies. At least some of the corolla variations seem to be related to single genes.

Most of the species which have been examined cytologically are diploids ($2n = 14$). Both diploid and tetraploid ($2n = 14, 28$) plants have been reported in *Phlox Drummondii*, as well as in *P. subulata* L. A triploid known in cultivation may possibly represent a hybrid of *P. maculata* L. and *P. carolina* L., although tetraploids are not known in either of the supposed parental species. Short- and long-styled species of *Phlox* occur, but whether style-length serves as a barrier to fertilization, as has been suggested in *Polemonium*, is not known.

REFERENCES:

- AINSWORTH, W. Notes on color, lobing and freaks in *Phlox subulata*. *Bartonia* 28: 34, 35. 1957.
- ANDERSON, E., and A. GAGE. Introgressive hybridization in *Phlox bifida*. *Am. Jour. Bot.* 39: 399-404. 1952.
- BANCHER, E. Studien an der Blüte von *Phlox paniculata* hybr. *Österr. Bot. Zeitschr.* 100: 308-318. 1953.
- EIGSTI, O. J., and H. TAYLOR. The induction of polyploidy in *Phlox* by colchicine. *Proc. Okla. Acad. Sci.* 22: 120-122. 1942. [*P. Drummondii*.]

- FERNALD, M. L. Studies of eastern American plants. *Rhodora* 51: 61-83. 1949.
[Notes on *Phlox*, 78-82.]
- FLORY, W. S., JR. Chromosome numbers in *Phlox*. *Am. Nat.* 65: 473-476. 1931. [Counts for 25 varieties distributed among 13 species.]
- . A cytological study of the genus *Phlox*. *Cytologia* 6: 1-18. 1934.
- GABRIELSON, I. N. Some North American dwarf *Phlox*. *New Fl. Silva* 3: 157-164. 1931.
- GILBERT, A. W. Heredity of color in *Phlox Drummondii*. *Jour. Agr. Res.* 4: 293-302. 1915.
- KELLY, J. P. Cultivated varieties of *Phlox Drummondii*. *Jour. N. Y. Bot. Gard.* 16: 179-191. 1915. [Origin and history of the varieties.]
- . Further observations on *Phlox Drummondii*. *Ibid.* 18: 83-86. 1917.
- . A genetical study of flower form and flower color in *Phlox Drummondii*. *Genetics* 5: 189-248. 1920.
- . *Astylis Phlox*. The relation of this variation of *Phlox Drummondii* to the large-eyed flower. *Jour. Hered.* 13: 339-342. 1923.
- . Fasciation in *Phlox Drummondii*. The origin and nature of fasciation in *Phlox*. *Ibid.* 18: 323-327. 1927.
- . Single and semi-double flowers in *Phlox*. *Ibid.* 20: 549-554. 1929. [*P. Drummondii*.]
- . The "eye" of *Phlox*. *Ibid.* 25: 182-186. 1934. [*P. Drummondii*.]
- . Irregular flowers in *Phlox*. *Ibid.* 31: 169-171. 1940.
- . Hoodedness in *Phlox*. *Ibid.* 36: 25-28. 1945. [*P. Drummondii*.]
- KRAEMER, H. The histology of the rhizome and roots of *Phlox ovata* L. (*Phlox carolina* L.). *Am. Jour. Pharm.* 82: 470-475. 1910.*
- MAINS, E. B. *Phlox* resistant to powdery mildew. *Phytopathology* 32: 414-418. 1942. [*P. paniculata*, *P. maculata*, and *P. Drummondii*.]
- MEYER, J. R. Chromosome studies of *Phlox*. *Genetics* 29: 199-216. 1944.
- MILLER, H. A., and R. H. WETMORE. Studies in the developmental anatomy of *Phlox Drummondii* Hook. I. The embryo. *Am. Jour. Bot.* 32: 588-599; II. The seedling. 628-634. 1945; III. The apices of the mature plant. 33: 1-10. 1946.
- RAU, M. A. Studies in growth in vitro of excised ovaries. I. Influence of colchicine on the embryo and endosperm in *Phlox Drummondii* Hook. *Phytomorphology* 6: 90-96. 1956.*
- SEVERIN, H. H. P. Breaking in color of flowers of annual *Phlox* caused by the aster-yellow virus. *Phytopathology* 33: 741-743. 1943.
- STOUT, A. B. Variation in the moss pink, *Phlox subulata*. *Jour. N. Y. Bot. Gard.* 18: 75-83. 1917.
- WHERRY, E. T. The eastern subulate-leaved phloxes. *Bartonia* 11: 5-35. 1929.
- . The eastern short-styled phloxes. *Ibid.* 12: 36-53. 1930.
- . The eastern long-styled phloxes. I. *Ibid.* 13: 18-37. 1932. II. 14: 14-26. 1932.
- . The eastern veiny-leaved phloxes. *Ibid.* 15: 14-26. 1933.
- . A variety of *Phlox ovata* from the Alabama mountains. *Ibid.* 16: 37, 38. 1934. [*P. ovata* var. *pulchra*.]
- . Supplementary notes on the eastern phloxes. *Ibid.* 38-45. 1934.
- . Our native phloxes and their horticultural derivatives. *Natl. Hort. Mag.* 14: 209-231. 1935.
- . Variation in *Phlox floridana*. *Bartonia* 22: 1, 2, 1943.
- . The *Phlox carolina* complex. *Ibid.* 23: 1-9. 1945.

- . Rock garden phloxes. *Bull. Amer. Rock Gard. Soc.* 4: 17–31. 1946.
- . Subspecies of three eastern phloxes. *Castanea* 16: 97–100. 1951. [*P. subulata*, *P. bifida*, *P. maculata*.]
- . The genus *Phlox*. 174 pp. Morris Arb. Univ. Pa., Philadelphia. 1955. [Monograph.]
- . Validation of new combinations in *Phlox*. *Baileya* 4: 97, 98. 1956. [Validation of subspecific epithets published in "The genus *Phlox*."]
- WHITEHOUSE, E. Annual *Phlox* species. *Am. Midl. Nat.* 34: 388–401. 1945.

2. **Polemonium** Linnaeus, *Sp. Pl.* 1: 162. 1753; *Gen. Pl.* ed. 5. 76. 1754.

Perennial [or annual], erect or decumbent herbs with alternate, pinnately divided leaves. Inflorescences cymose, terminal or axillary. Calyx campanulate, herbaceous, accrescent. Corolla campanulate to funnel-form, 5-parted, blue or white, [yellow, pink, or purple]. Stamens 5, equally inserted on the corolla tube, included [or exerted]. Style 1; stigmas 3; ovary 3-locular, each locule with 1–10 ovules. Fruit a loculicidal capsule. TYPE SPECIES: *P. caeruleum* L. (Derivation of name uncertain; perhaps from Greek, *polemos*, war, or perhaps named for *Polemon*, an early Greek philosopher.) — JACOB'S LADDER, GREEK VALERIAN.

About 20 species, primarily of western North America, ranging from the mountains of Mexico north to Alaska and northern Canada, extending into eastern North America, and also into Asia and Europe; a single species in southern South America. Represented in our area by only one species, *Polemonium reptans* L., of rich woods and damp meadows from Wisconsin to New Hampshire, south to Oklahoma, Arkansas, Mississippi, Alabama, Georgia, and North Carolina.

The variation of most of the species of *Polemonium* has not been studied in great detail and, consequently, considerable confusion exists in the understanding of the species and their interrelationships. *Polemonium reptans* varies in its size, in the shape and number of the leaflets, in the shape of the sepals and in the degree and nature of pubescence. Varietas *villosum* E. L. Br. was described from Ohio and Kentucky and is characterized by its densely glandular-villous inflorescence. The correlation of the restricted distribution of var. *villosum* with the disjunct occurrence of other species which have been considered to have a relic distribution has led to the interpretation that its present range is a remnant of an earlier, more extensive one. The pubescence of some plants of the widespread *P. reptans* var. *reptans* in Ohio, and also in Pennsylvania, is considered to show evidence of introgression with var. *villosum*. Further studies of the variation of *P. reptans* in other areas should contribute more information on the validity of this hypothesis.

The species which have been examined cytologically have a chromosome number of $2n = 18$; polyploidy has been reported in *Polemonium californicum* Eastwood ($2n = 36$) and in *P. caeruleum* L. subsp. *Van-Bruntiae* (Britt.) Davidson (*P. Van-Bruntiae* Britt.) ($2n = 36$), of Maryland and West Virginia and north to Vermont.

REFERENCES:

- BRAUN, E. L. Variation in *Polemonium reptans*. *Rhodora* 58: 103-116. 1956.
- CLAUSEN, J. Genetic studies in *Polemonium*. III. Preliminary account on the cytology of species and specific hybrids. *Hereditas* 15: 62-66. 1931. [Notes on chromosome morphology, cytology and various crosses.]
- DAVIDSON, J. F. The genus *Polemonium* (Tournefort) L. Univ. Calif. Publ. Bot. 23: 209-282. 1950. [Monograph.]
- MARKOVA, L. G. On certain anomalies in the embryology of *Polemonium coeruleum* L. *Compt. Rend. Acad. URSS* 49: 144, 145. 1945.*
- OSTENFELD, C. H. Genetic studies in *Polemonium*. II. Experiments with crosses of *P. mexicanum* Cerv. and *P. pauciflorum* Wats. *Hereditas* 12: 33-40. 1929. [*P. pauciflorum* ♀ × *P. mexicanum* ♂ impossible, reciprocal cross fertile.]
- SOUÈGES, R. Les lois du développement chez le *Polemonium caeruleum* L. Affinités des polémoniacées. *Bull. Soc. Bot. France* 86: 289-297. 1939. [Allied with the Solanaceae and the Boraginaceae.]
- . Embryogénie des polémoniacées. Développement de l'embryon chez le *Polemonium caeruleum* L. *Compt. Rend. Acad. Sci. Paris* 208: 1338-1340. 1939.
- . Embryogénie des polemoniacees. Développement de l'embryon chez le *Polemonium pauciflorum* Wats. *Compt. Rend. Acad. Sci. Paris* 220: 897-900. 1945.
- WHERRY, E. T. *Polemonium* and *Polemoniella* in the eastern states. *Bartonia* 17: 5-12. 1936. [Includes *Polemonium* (*Polemoniella*) *micrantha* adventive in Massachusetts.]
- . The genus *Polemonium* in America. *Am. Midl. Nat.* 27: 741-760. 1942.

3. *Ipomopsis* Michaux, Fl. Bor.-Am. 1: 141. 1803.

Biennial [perennial, or annual] herbs with alternate pinnatifid leaves, the tips of the leaf segments bearing a horny mucro. Inflorescences cymose, each flower subtended by a bract. Calyx herbaceous, 5-parted, not accrescent, rupturing as the capsule expands. Corolla salverform or funnelform, 5-parted, red, pink, white [violet or yellow]. Stamens 5, equally inserted on the corolla tube or in the sinuses of the corolla, included or exserted. Style 1; stigmas 3; ovary 3-locular, each locule with 1-many ovules. Fruit a loculicidal capsule. TYPE SPECIES: *I. elegans* Michx. (= *I. rubra* (L.) Wherry). (Name from *Ipomoea* and Greek, *opsis*, aspect, in reference to the similarity of the corolla to that of species of *Ipomoea* of sect. *Quamoclit* Meissn.)

A genus of about 20 or more species in three sections, centered primarily in the Rocky Mountains and the adjacent plains, but extending west to the Pacific coast and east to the Carolinas and Florida, south to Texas and Mexico; one species in Argentina and Chile. A single species in our area, the biennial *Ipomopsis rubra* (L.) Wherry ($2n = 14$), occurring in sandy soil in fields and roadsides from Texas to Oklahoma, east to North Carolina and Florida, also escaped from cultivation and naturalized as far north as Illinois, Michigan, and Massachusetts.



Wilson, K A. 1960. "The genera of Hydrophyllaceae and Polemoniaceae in the southeastern United States." *Journal of the Arnold Arboretum* 41(2), 197–212.
<https://doi.org/10.5962/bhl.part.15230>.

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