

THE GENERA OF GERANIACEAE IN THE SOUTHEASTERN UNITED STATES¹

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GERANIACEAE A. L. de Jussieu, Gen. Pl. 268. 1789, "Gerania," nom. cons.

(GERANIUM FAMILY)

Annual, biennial or perennial herbs [infrequently shrubs to trees; stems sometimes succulent] with simple and often glandular trichomes; underground stems, rhizomes [enlarged tubers and roots] frequently produced. Leaves opposite or alternate, palmately or pinnately lobed or compound [rarely simple and entire], palmately veined, stipulate, the petioles sometimes persistent. Inflorescences terminal or axillary, variable but basically cymose and sometimes condensed into umbels [rarely solitary], bracteate. Flowers perfect [or imperfect] and regular to slightly [or distinctly] irregular, 5-merous [rarely some parts fewer by abortion]. Sepals mostly distinct, persistent, imbricate. Petals distinct, often emarginate, imbricate, or convolute in aestivation [rarely absent]. Androecium obdiplostemonous [or of 5 bundles of three stamens], the stamens all fertile or some reduced to staminodia or scales; filaments connate at the base or distinct; anthers versatile, 2-locular at anthesis, opening lengthwise; nectar glands usually alternating with the petals. Gynoecium of 5 carpels united to an elongated columella, styles united to the columella, forming a beak on the ovary and fruit [or almost absent], 5-fid at the apex; stigmas distinct, ligulate to clavate [or filiform], ovary superior, 5-lobed, 5-loculate, the ovules 2 in each locule, anatropous to campylotropous, superposed and

¹ Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant GB-6459X, principal investigator, Carroll E. Wood, Jr.). This treatment follows the format established in the first paper in the series (Jour. Arnold Arb. 39: 296-346. 1958). The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants in this area, with additional information from extraterritorial taxa in brackets. References I have not seen are marked by an asterisk.

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pendulous from axile placentae. Fruit a schizocarp, usually dehiscing elastically into 5 one-seeded mericarps that separate from the persistent columella with a part of the style forming an awn on the apex of the mericarp, the awn hygroscopic, becoming revolute or spiralled. Seeds without endosperm; embryo curved, with plicate to convolute incumbent cotyledons, often green. Embryo sac development of the *Polygonum* type, embryo development of the Asterad to Onagrad types. (Geranieae of Engler & Prantl, Knuth, and Scholz.) TYPE GENUS: *Geranium* L.

Five genera and about 700 species widely distributed in temperate and subtropical regions of both hemispheres; essentially restricted to high altitudes in the tropics. *Geranium* and *Erodium*, with both indigenous and naturalized species, represent the family in North America. A number of species of *Pelargonium* L'Hérit. ex Aiton, the horticultural "geraniums," a predominantly South African genus of about 250 species, are commonly cultivated in our area but are not naturalized although several are ephemeral escapes in California. *Sarcocaulon* (DC.) Sweet (six species) is South African, and *Monsonia* L. (about 30 species) occurs both north and south of the Sahara Desert in Africa and eastward to India.

These five genera comprise the Geranieae of Engler & Prantl, Knuth, and Scholz, and the Geraniaceae of Airy Shaw (in Willis), a very natural group with two ovules per carpel and the carpels in fruit separating into one-seeded mericarps, each with a curved or curled awn. The Biebersteiniaceae, Dirachmaceae, Ledocarpaceae, and Vivianiaceae, which differ in the number of ovules per carpel and in fruit structure, are often included in the Geraniaceae, but the taxonomic affinities of these families need further study. The Biebersteiniaceae have recently been placed with the Rosaceae (Bortenschlager), the Dirachmaceae in the Tiliales (Hutchinson), and questionably related to the Greyiaceae (Airy Shaw), the Ledocarpaceae in the Malpighiales (Hutchinson), and the Vivianiaceae in the Pittosporales (Hutchinson) or in the Centrospermae (Bortenschlager). There is rather general agreement that the Geraniaceae, sensu stricto, the Oxalidaceae, and the Tropaeolaceae belong together in a single order.

The schizocarp of the Geraniaceae is rather complex, and differing and inconsistently applied terminology has created confusion. At the base of the fruit are five mericarps (cocci, carpel bodies) which reflect the five lobes (locules) of the ovary. Arising immediately above is an elongated and more or less cylindrical rostrum (stylar column, beak), the apex of which abruptly tapers into the stylar beak, a narrow cylinder five-fid at the apex. Passing through the center of the fruit from the receptacle to the tip of the rostrum is a persistent columella (central column, stylar column, or rostrum), which has been said variously to be receptacular, ovarian, or stylar in origin. At maturity the fruits dehisce elastically or even explosively with the mericarps and awns separating from the columella. The awns, evidently strips of stylar material that before dehiscence form vertical bands on the rostrum, are hygroscopic and at dehiscence become revolute or spiralled, usually remaining attached to the mericarps

and either remaining affixed to the apex of the rostrum or not. The seeds are either ejected from the mericarps or retained within them.

Reported chromosome numbers are *Sarcocaulon Burmannii*, $2n = 44$; *Monsonia senegalensis*, $2n = 24$, *M. longipes*, $2n = 38$; *Pelargonium*, $2n = 9$ (haploid sporophyte), 14, 16, 18, 20, 22, 32, 36, 38, 44, 45, 54, 56, 60, 66, 72, 77, 81, 88, and 90, with 18 and 22 occurring most frequently; *Erodium*, $2n = 18, 20, 27, 30, 36, 40, 48, 54$ (56?), 60; and *Geranium*, $2n = 18, 20, 22, 24, 26, 28, 32, 34, 36, 38, 42, 48, 50, 52, 56, 64, 68, 84, 128$.

Pollen grains of the Geraniaceae are 3-colpate or 3-colporate with striate to reticulate exine sculpturing. Bortenschlager recognized seven distinct pollen types based on aperture type and sculpturing patterns. Most species of *Erodium* lack supratectate processes, while most of those of *Geranium* have mono- or dimorphic processes, although the pollen of certain species in both genera is indistinguishable. *Monsonia* and *Sarcocaulon* are palynologically identical, and *Pelargonium* has several distinct pollen types.

The studies of Konrad Sprengel, who first observed insect pollination scientifically and proposed the theory of cross-pollination, began with observations on *Geranium sylvaticum*. Since that time the pollination of numerous species of *Geranium*, *Erodium*, and *Pelargonium* has been investigated. The petals of most species are usually some light to dark shade of red to blue with the more intensely colored veins forming nectar guide lines that converge toward the center of the flower. Some species also have darker-colored spots toward the base of one or more petals, and in *Erodium* and *Pelargonium* there is a trend toward irregular corollas. A nectar-secreting spur of the uppermost sepal is adnate to the pedicel in *Pelargonium* species, and each of the five sepals of *Monsonia parvifolia* has a small spur. Species of the other genera have five nectar glands alternating with the petals. In some species the odor of the flower is evidently more important than corolla markings in the attraction of insects. Hymenoptera, and to a lesser degree, Lepidoptera, Diptera, and Coleoptera, are important pollinators; some large-flowered *Pelargonium* species of South Africa are visited by sun birds (Nectariniidae).

Numerous chemical substances have been identified in the Geraniaceae. Tannins have been reported in *Geranium*, *Pelargonium*, *Monsonia*, and *Erodium* and are especially abundant in the subterranean parts of perennial *Geranium* species. Gallic and ellagic acids are known from *Erodium cicutarium* and several species of *Geranium*, including *G. maculatum*, and catechins have been isolated from *G. pratense* and *G. palustre*. Essential oils occur in the glandular trichomes of a few *Geranium* species and in many *Pelargonium* species and hybrids. Most *Pelargonium* species accumulate tartaric acid, but those of *Geranium* and *Erodium* do not. The bark of xerophytic species of *Sarcocaulon* is rich in aromatic resins and waxes. The numerous species, hybrids, and cultivars of *Pelargonium*, the widely grown ornamental garden "geraniums," account for the principal economic importance of the family. In addition to the commonly cultivated pelargoniums, several species of *Geranium* and *Erodium* are grown for their

interesting appearance or showy flowers. Geranium oil used in perfumery, often as a substitute, extender, or adulterant for more expensive essences such as attar of roses, is extracted from several species of *Pelargonium*, particularly *P. graveolens* and *P. odoratissimum*. Extracts from various species of *Geranium* are used as astringents and aphrodisiacs and for tanning and dyeing, while extracts from *Monsonia ovata* and *Pelargonium antidysentericum* are used for the treatment of dysentery. *Erodium cicutarium* and some other species are important forage crops, but sometimes become rampant weeds.

REFERENCES:

- ANDREWS, H. C. Geraniums: or, A monograph of the genus *Geranium*: containing coloured figures of all the known species and numerous beautiful varieties, drawn, engraved, described, and coloured, from the living plants. 2 vols. 124 pls. London. 1805. [Mostly *Pelargonium* spp.]
- BAILLON, H. Géraniacées. Hist. Pl. 5: 1-41. 1874. [English transl. M. M. HARTOG, The natural history of plants. 5: 1-41. London. 1878.]
- BENTHAM, G., & J. D. HOOKER. Geraniaceae. Gen. Pl. 1: 269-278. 1862. [Treatment by BENTHAM; family divided into 7 tribes.]
- BOLKHOVSKIKH, Z., V. GRIF, T. MATVEJEVA, & O. ZAKHARYEVA. Chromosome numbers of flowering plants. Ed. by A. A. FEDOROV. (Russian and English prefaces.) 926 pp. Leningrad. 1969. [Geraniaceae, 331-333.]
- BORTENSCHLAGER, S. Vorläufige Mitteilungen zur Pollenmorphologie in der Familie der Geraniaceen und ihre systematische Bedeutung. Grana Palynol. 7: 400-468. 1967. [Comprehensive sampling of 241 taxa in 9 genera; 4 segregate families recognized.]
- BROUWER, W., & A. STÄHLIN. Handbuch der Samenkunde. Introd. + 656 pp. Frankfurt am Main. 1955. [Geraniaceae, 200-204.]
- BRUNIES, S. Anatomie der Geraniaceenblätter in Beziehung zur Systematik der Familie. 40 pp. Breslau. 1900.*
- CANDOLLE, A. P. DE. Geraniaceae. Prodr. 1: 637-682. 1824.
- CAROLIN, R. C. The genus *Pelargonium* L'Hér. ex Ait. in Australia. Proc. Linn. Soc. New S. Wales 86: 280-294. 1962. [Taxonomic treatment; notes and diagrams on habit types.]
- . Geraniaceae. In: C. G. G. J. VAN STEENIS, ed., Fl. Males. I. 6: 445-449. 1964. [Includes summary of phytochemistry by R. Hegnauer.]
- CAROTHERS, Z. B., JR. The comparative stem anatomy of some shrubby members of the Geraniaceae. 192 pp. 1958. Ph.D. thesis, The University of Michigan.* [Cf. Diss. Abstr. 19(8): 1904, 1905. 1959; species of *Balbisia*, *Biebersteinia*, *Geranium*, *Monsonia*, *Pelargonium*, *Rhynchotheca*, *Viviania*, and *Wendtia* examined.]
- . Observations on the procambium and primary phloem of *Pelargonium domesticum*. Am. Jour. Bot. 46: 397-404. 1959. [The "pericycle" fibers in the family actually are protophloem fibers.]
- CHRTEK, J. *Geraniopsis* eine neue Gattung der Familie Geraniaceae. Novit. Bot. Univ. Carolinae Pragensis 1967: 9. 1967. [*G. trilopha* (Boissier) Chrtek, *G. yemensis* (Deflers) Chrtek.]
- CLIFFORD, D. Pelargoniums, including the popular 'Geranium.' ed. 2. xx + 350 pp. 15 colored pls. 83 figs. Blandford Press. 1970. [Horticultural information, brief descriptions of 219 spp. and 850 cultivars.]

- DAKER, M. G. Chromosome numbers of *Pelargonium* species and cultivars. Jour. Roy. Hort. Soc. **94**: 346–353. 1969. [47 spp. or named hybrids in 13 sects. and 50 cultivars.]
- DAVIS, G. L. Systematic embryology of the angiosperms. x + 528 pp. New York. 1966. [Geraniaceae, 127; references.]
- DAVIS, P. H. Geraniaceae. Fl. Turkey **2**: 450–488. 1967. [Includes 33 *Geranium* spp. in 5 “groups” and 20 *Erodium* spp. in 2 sects.]
- DAWSON, M. L. The floral morphology of the Polemoniaceae. Am. Jour. Bot. **23**: 501–511. 1936. [Includes *Geranium maculatum* and *Erodium cicutarium*; discussion of 3 theories of obdiplostemony in family.]
- ERDTMAN, G. Pollen morphology and plant taxonomy. Angiosperms. Corrected reprint and new addendum. xiv + 552 pp. New York. 1966. [Geraniaceae, 186–189; references.]
- FEARN, B. Some succulent Geraniaceae. Natl. Cact. Succ. Jour. **23**: 15–18. 1968. [*Geranium*, *Pelargonium*, *Sarcocaulon*; photographs.]
- GAGNEPAIN, F. Contribution à l'étude du pollen des Géraniacées. Bull. Soc. Hist. Nat. Autun **16**: 83–97. 1903. [*Geranium*, *Erodium*, *Pelargonium*.]
- GAMS, H. Geraniaceae. In: G. HEGI, Illus. Fl. Mittel-Europa **4**(3): 1656–1725. pls. 173, 174. 1924.
- GAUGER, W. Ergebnisse einer zytologischen Untersuchung der Familie der Geraniaceae. I. Planta **26**: 529–531. 1937. [*Geranium*, 23 spp.; *Pelargonium*, 29 spp.; *Erodium*, 10 spp.; *Sarcocaulon Burmannii*.]
- HANKS, L. T., & J. K. SMALL. Geraniaceae. N. Am. Fl. **25**(1): 3–24. 1907.
- HANNIG, E. Über den Mechanismus der Sekretausscheidung bei den Drüsenhaaren von *Pelargonium*. Zeitschr. Bot. **23**: 1004–1014. 1930.
- HARNEY, P. M. A chromatographic study of species presumed ancestral to *Pelargonium* × *hortum* Bailey. Canad. Jour. Genet. Cytol. **8**: 780–787. 1966.
- HEGNAUER, R. Chemotaxonomie der Pflanzen. Band 4. Dicotyledoneae: Daphniphyllaceae-Lythraceae. 551 pp. Basel & Stuttgart. 1966. [Geraniaceae, 193–201; references.]
- HEIMSCH, C., JR. Comparative anatomy of the secondary xylem in the “Gruinales” and “Terebinthales,” of Wettstein with reference to taxonomic grouping. Lilloa **8**: 83–198. pls. 1–17. 1942. [Geraniaceae, 98–100; wood structure parallels in certain respects that of Oxalidaceae.]
- HESS, H. E., E. LANDOLT, & R. HIRZEL. Flora der Schweiz. Vol. 2. 965 pp. Basel & Stuttgart. 1970. [Geraniaceae, 615–632; illustrations and useful comments.]
- HOFMEISTER, W. Über den Bau des Pistills der Geraniaceen. Flora **47**: 401–410. 1864.
- HUTCHINSON, J. Evolution and phylogeny of flowering plants. Dicotyledons: facts and theory. xxvi + 717 pp. 2 charts. London & New York. 1969. [Geraniales, 641–647.]
- JÄNNICKE, W. Beiträge zur vergleichenden Anatomie der Geraniaceae. Abh. Senckenberg. Naturf. Ges. **14**(3): 1–24. 1886.*
- KENDA, G. Das Hypoderm der Geraniaceen-Kelchblätter. Phytion Austria **6**: 207–210. 1956. [*Geranium*, *Erodium*, *Pelargonium*.]
- KERS, L. E. *Monsonia parvifolia* Schinz (Geraniaceae), a species with concealed spurs. Bot. Not. **124**: 208–212. 1971. [Each of the five sepals has a small, sac-like spur.]
- KLOTZSCH, J. F. Bemerkungen zu den Geraniaceen und deren Verwandtschaften. Linnaea **10**: 425–439. 1836.

- KNUTH, P. Handbook of flower pollination. Vol. 2. (Transl. J. R. A. DAVIS.) viii + 703 pp. Oxford. 1908. [Geraniaceae, 218–232. In German ed. cf. 2(1): 227–242.]
- KNUTH, R. Geraniaceae. Pflanzenreich IV. 129(Heft 53): 1–640. 1912. [11 genera in 5 tribes; comprehensive treatment of all known species.]
- . *Pelargonium* oil. Am. Jour. Pharm. 93: 302–315. 1921.*
- . Geraniaceae. Nat. Pflanzenfam. ed. 2. 19a: 43–66. 1931.
- KOKWARO, J. O. The family “Geraniaceae” in North-East tropical Africa. Webbia 25: 623–669. 1971. [*Erodium*, *Geranium*, *Monsonia*, *Pelargonium*.]
- . Geraniaceae. Fl. Trop. E. Afr. 24 pp. 1971.
- KOMAROV, V. A., ed. Geraniaceae. Fl. URSS. (In Russian.) 14: 1–76. 1949. [*Geranium* and *Pelargonium* by E. G. BOBROV, *Erodium* and *Biebersteinia* by A. I. VVEDENSKIJI; also see vi–viii for classification scheme.]
- KUGLER, H. Blütenökologie. ed. 2. xi + 347 pp. Stuttgart. 1970. [*Erodium*, *Geranium*, *Pelargonium*; includes photograph of *G. pratense* taken with ultraviolet light.]
- KUTSCHERA, L. Wurzelatlas mitteleuropäischer Ackerunkräuter und Kulturpflanzen. xvi + 575 pp. Frankfurt am Main. 1960. [Geraniaceae, 372–378; drawings of root systems of *Geranium pusillum*, *G. molle*, *Erodium cicutarium*.]
- LABBE, A. Sur l’“éperon” de la fleur de *Pelargonium*. Bull. Soc. Bot. France 111: 321–324. 1964. [Ontogeny and anatomy of the spur in *P. zonale*.]
- LEGAULT, A. Recherches anatomiques sur l’appareil végétatif des Géraniacées. Thèses Fac. Sci. Paris. 245 pp. 4 pls. Lille. 1908. [*Geranium*, *Erodium*, *Pelargonium*, and *Monsonia*. See also Compt. Rend. Acad. Sci. Paris 147: 382–384. 1908; *Geranium* and *Erodium*.]
- L’HÉRITIER DE BRUTELLE, C. L. Geraniologia, seu Erodii, Pelargonii, Geranii, Monsoniae et Grieli historia iconibus illustrata. 1 p. pls. 1–44. Paris. 1787–1788 [1792]. [Text unpublished, names validated by Aiton, Hortus Kewensis. Vol. 2. 1789.]
- LUBBOCK, J. A contribution to our knowledge of seedlings. Vol. 1. viii + 608 pp. London & New York. 1892. [Geraniaceae, 294–316.]
- MARLOTH, R. Geraniaceae. Fl. S. Africa 2: 83–91. pls. 30–32. 1925. [Photographs and colored plates of *Monsonia*, *Sarcocaulon*, *Pelargonium* and *Geranium*.]
- MERXMÜLLER, H. Die stammsukkulente Pelargonien des Lüderitz-Distriktes (Südwestafrika). Mitt. Bot. Staatssam. München 5: 229–245. 1964.
- MIRIMANOFF, A. Remarques sur les glandes extra-staminales de quelques Géraniacées. Bull. Soc. Bot. Genève II. 32: 195, 196. 1941. [*Geranium*, *Erodium*, *Pelargonium*; histochemical study of the secretory tissues.]
- MOINET-SIMON, L. Considérations sur l’inflorescence du *Pelargonium zonale* Ait. Mém. Soc. Bot. France 1964: 125–134. 1964. [The determinate umbel has resulted from condensation of biparous or uniparous cymes.]
- MOORE, H. E., JR. Pelargoniums in cultivation. Bailey 3: 5–25, 41–46, 70–97. 1955. [Evaluation of names for species and hybrids grown in the U.S.; keys, illustrations.]
- MOSEBACH, G. Die Fruchtsstielschwellung der Oxalidaceen und Geraniaceen. Jahrb. Wiss. Bot. 79: 353–384. 1934. [Includes *Geranium dissectum* and comments on *Geranium*, *Erodium*, and *Pelargonium* spp.]
- MÜLLER, H. The fertilisation of flowers. (Transl. D. W. THOMPSON.) xii + 669 pp. London. 1883. [Geraniaceae, 149–160.]

- MÜLLER, T., J. R. LAUNDON, & L. F. BOWDEN. Geraniaceae. In: A. W. EXELL, A. FERNANDES, & H. WILD, *Fl. Zambesiaca* 2: 130–149. 1963. [*Geranium*, 7 spp.; *Monsonia*, 4; *Pelargonium*, 8.]
- MURLEY, M. A seed key to fourteen species of Geraniaceae. *Proc. Iowa Acad. Sci.* 51: 241–246. 1944 [1945]. [Includes 2 pls. of seeds and mericarps.]
- NARAYANA, H. S., & P. K. AROPA. Floral anatomy of *Monsonia senegalensis* Guill. and Perr. *Curr. Sci. Bangalore* 32: 184, 185. 1963.
- NEUBAUER, H. F. Über Blattgrund und Stammknoten von Pelargonien. *Österr. Bot. Zeitschr.* 119: 141–153. 1971. [English summary.]
- OLTMANN, O. Pollenmorphologische-systematische Untersuchungen Innerhalb der Geraniales. 183 pp. *pls. Lehre*. 1971.*
- REICHE, K. F. Geraniaceae. *Nat. Pflanzenfam. III.* 4: 1–14. 1889. (Supplement by A. ENGLER.)
- RICKETT, H. W. Wildflowers of the United States. Vol. 2. The Southeastern States. Part 1. x + 322 pp. *pls. 1–116*. New York. 1966. [Geraniaceae, 296–299, *pl. 107*.]
- SAUER, H. Blüte und Frucht der Oxalidaceen, Linaceen, Geraniaceen, Tropelaceen und Balsaminaceen. Vergleichendentwicklungsgeschichtliche Untersuchungen. *Planta* 19: 417–481. 1 *pl.* 1933. [Floral and fruit anatomy of *Geranium sylvaticum*, *Erodium cicutarium*, *Pelargonium zonale*.]
- SCHÖNBECK-TEMESY, E. Geraniaceae. In: K. H. RECHINGER, *Fl. Iranica* 69: 1–67. *pls. 1–8*. 1970. [5 genera, 54 spp.]
- SCHOLZ, H. Geraniaceae. In: H. MELCHIOR, *Engler's Syllabus der Pflanzenfamilien*. ed. 12. 2: 248–250. 1964.
- SCHÜRHOFF, P. N. Zytologische Untersuchungen in der Reihe der Geraniales. *Jahrb. Wiss. Bot.* 63: 707–759. 1924. [Geraniaceae, 708–714; development of pollen, embryo sac, and embryo.]
- SCHWIEKER, F. Untersuchungen über die Postflorationsbewegungen einiger Geraniaceen. *Bot. Arch.* 6: 206–230. 1924. [*Geranium*, *Erodium*.]
- SØRENSEN, W. Sur la structure du fruit de nos Géraniacées comment il se comporte au moment de la maturité. *Danske Vidensk. Selsk. Forh.* 1911(Meddel.): 99–137. 1 *pl.* 1911. [*Erodium*, *Geranium*, *Pelargonium*.]
- STAFFORD, H. A. Distribution of tartaric acid in the Geraniaceae. *Am. Jour. Bot.* 48: 699–701. 1961. [*Geranium*, *Erodium*, *Pelargonium*.]
- SWEET, R. Geraniaceae. The natural order of Gerania, illustrated by coloured figures and descriptions; comprising the numerous and beautiful mul-varieties cultivated in the gardens of Great Britain, with directions for their treatment. 5 vols. 500 *pls.* London. 1820–1830.
- THURNHILL, J. W., R. K. MATTA, & W. H. WOOD. Examining three-dimensional microstructures with the scanning electron microscope. *Grana Palynol.* 6: 1–6. *pls. 1–3*. 1965. [*Pl. 1*, Nutmeg variety of *Pelargonium*, one of the first published SEM photomicrographs of pollen.]
- TRELEASE, W. A study of North American Geraniaceae. *Mem. Boston Soc. Nat. Hist.* 4: 71–104. *pls. 9–12*. 1888.
- WANGERIN, W. Geraniaceae. In: O. VON KIRCHNER, E. LOEW, & C. SCHRÖTER, *Lebensgeschichte der Blütenpfl. Mitteleuropas* 3(3): 1–147. 1926. [Extensive references to early literature.]
- WARBURG, E. F. Taxonomy and relationship in the Geraniales in the light of their cytology. *New Phytol.* 37: 130–159, 189–210. 1938. [Geraniaceae, 138–159, 189–195; chromosome counts sometimes inaccurate.]
- WEBB, D. A., ed. Geraniaceae. In: T. G. TUTIN, V. H. HEYWOOD, *et al.*, eds.,

Fl. Europaea 2: 193–204. 1968. [*Geranium* by D. A. WEBB & I. K. FERGUSON; *Erodium* by D. A. WEBB & A. O. CHATER; *Biebersteinia* by D. A. WEBB.]

WILLIS, J. C. A dictionary of the flowering plants and ferns. ed. 7. (Revised by H. K. AIRY SHAW.) xxii + 1214 pp. + liii pp. (Key to the families of flowering plants.) Cambridge, England. 1966. [Geraniaceae, 473.]

ZANKER, J. Untersuchungen über die Geraniaceen. *Planta* 9: 681–717. 1930. [Includes studies on inflorescences and embryos of *Geranium*, *Erodium*, and *Pelargonium*.]

KEY TO THE GENERA OF GERANIACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *annual to perennial herbs with palmately or pinnately lobed to dissected, stipulate leaves; inflorescences terminal or appearing axillary, basically cymose, sometimes condensed into determinate umbels; flowers 5-merous, perfect, regular to slightly irregular, sepals mostly distinct, imbricate; petals distinct, imbricate or convolute; androecium obdiplostemonous, all stamens fertile or some reduced to staminodia or scales; gynoecium 5-carpellate with an elongated central columella, the ovary superior, ovules 2 per carpel, only one maturing; fruit a beaked schizocarp dehiscing into 5 mericarps with a strip of stylar tissue forming a hygroscopic awn on each; embryo curved, endosperm absent.*

Leaves palmately lobed; all stamens with anthers (except in *G. pusillum*); ultimate peduncles with 2 flowers; mericarps rounded at base, ejecting the seed; awn of mericarp revolute, glabrous or puberulent on the inner surface. 1. *Geranium*.

Leaves pinnately lobed or dissected; only the inner 5 stamens with anthers; peduncles terminating in a several-flowered umbel; mericarps pointed at the base, retaining the seed; awn of mericarp spiraling, pubescent on the inner surface. 2. *Erodium*.

1. *Geranium* Linnaeus, Sp. Pl. 2: 676. 1753; Gen. Pl. ed. 5. 306. 1754.

Annual to perennial herbs [rarely shrubs to small trees]; stems of two kinds, herbaceous and leafy flowering stems with $\pm$ swollen nodes, and thickened, condensed, often potentially perennial, basal stems or rhizomes underground or at ground level; roots branched or unbranched taproots or numerous adventitious roots originating from the condensed stems or rhizomes. Leaves mostly circular in outline, palmately lobed [infrequently dissected, entire or pinnate], the lobes variously toothed or incised; basal leaves long-petiolate, the petioles often $\pm$ persistent; cauline leaves opposite or alternate (especially in the inflorescence), $\pm$ similar to basal leaves but usually smaller and with shorter petioles. Inflorescences basically cymose, the ultimate peduncles [1]2-flowered and [2]4-bracteate, usually terminal but by continued and sympodial branching within the inflorescences often appearing axillary. Flowers perfect [rarely imperfect], regular. Sepals 5, with obtuse to caudate apices. Petals 5, pubescent at least basally, frequently emarginate at apex, white to some shade of pink or red-purple [blue to blackish-purple], the veins more intensely colored, reticulately veined throughout or only apically. Stamens 10, in two

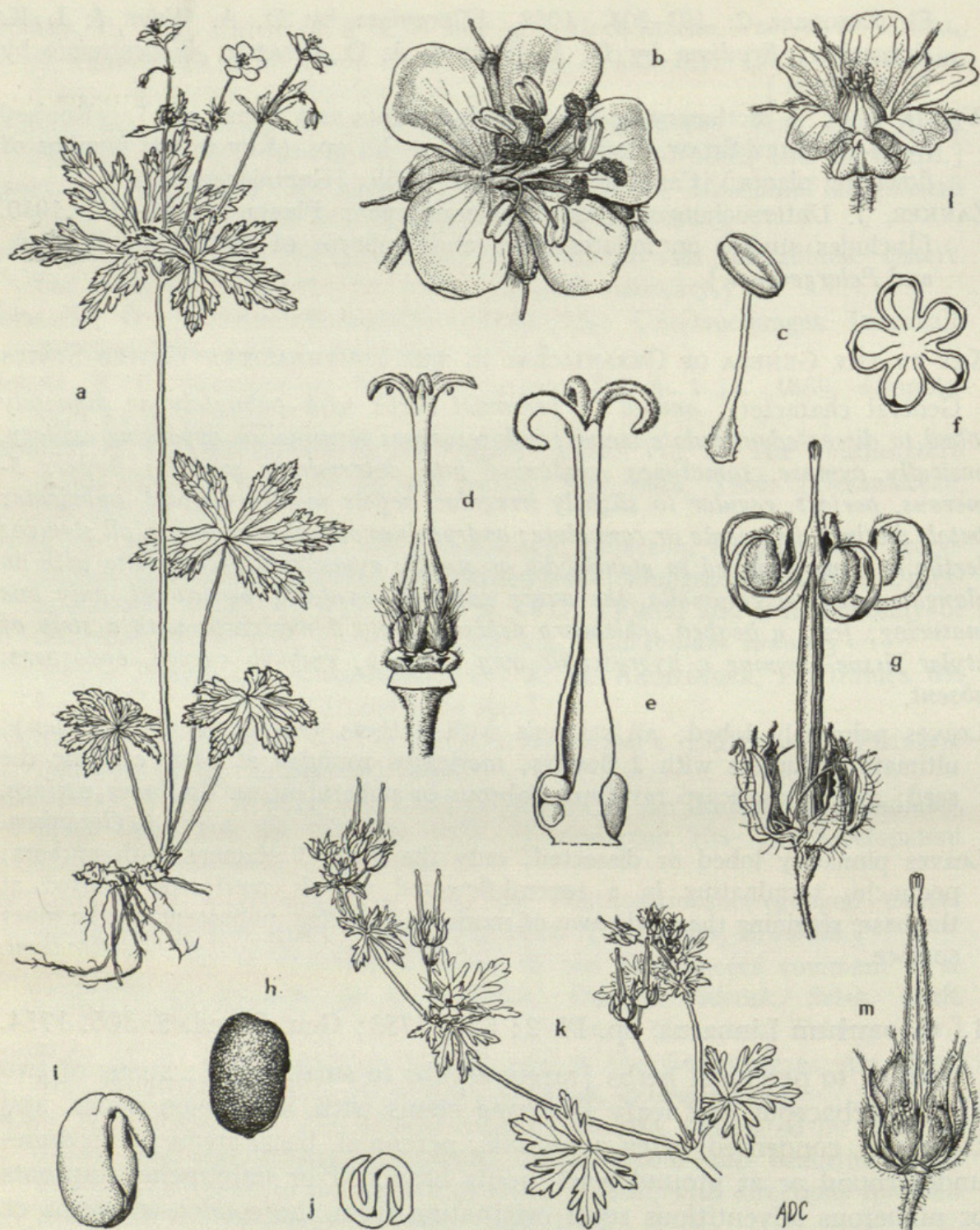


FIGURE 1. *Geranium*. a-j, *G. maculatum*: a, flowering plant showing erect annual shoot and perennial underground rhizome, $\times \frac{1}{4}$; b, flower at anthesis — note inner whorl of dehiscing stamens and still closed stigmas, $\times 1\frac{1}{2}$; c, stamen of outer whorl, $\times 4$; d, gynoecium with nectar glands on receptacle below pubescent ovary, sepals, petals, and stamens removed (petal attachment points triangular, stamen attachment points open circles), $\times 4$; e, semidiagrammatic vertical section of same to show placentation, $\times 6$; f, diagrammatic cross section of ovary with two superposed ovules in each locule, $\times 8$; g, dehiscent fruit showing mericarps attached to recurved hygroscopic awns, $\times 2$; h, seed, $\times 5$; i, embryo, $\times 5$; j, cross section of embryo to show folding of cotyledons, $\times 5$. k-m, *G. carolinianum*: k, tip of flowering and fruiting branch showing one sympodially branched inflorescence, $\times \frac{1}{2}$; l, flower with receptive stigmas, anthers mostly fallen, $\times 3$; m, mature fruit before dehiscence (one sepal recurved) — note persistent filaments and connivent stigmas, $\times 2$.

whorls, the outer whorl opposite the petals and maturing after the inner antesepalous whorl; filaments often of two lengths, basally connate, all bearing anthers (except in *G. pusillum*); nectar glands 5, alternating with petals, occurring on receptacular area between sepals and the inner whorl of stamens. Ovary frequently pubescent. Schizocarp elastically or explosively septicidal from base upwards, awns usually remaining attached to top of columella; mericarps rounded at base, each with a persistent awn, these glabrous or puberulent on the adaxial surface, recurving abaxially. Seeds mostly ejected from mericarps, the seed coat reticulate to smooth. Cotyledons long petiolate, transversely elliptic and somewhat asymmetrical when expanded, emarginate at apex and cordate at base, entire or slightly 3-lobed. (Including *Robertiella* Hanks in Hanks & Small.) LECTOTYPE SPECIES: *Geranium sylvaticum* L.; see L. T. Hanks & J. K. Small, N. Am. Fl. 25: 4. 1907. (Name from Greek *geranion*, a crane, in allusion to the beaklike fruit; used by Dioscorides, see Gunther.) — CRANE'S-BILL, WILD GERANIUM.

A genus of 250–300 species widely distributed in temperate, montane, and subpolar regions of both hemispheres, extending into the tropics only in the mountains. Some species have amphiatlantic or subantarctic distributions. Major centers of diversification are the mountains of Europe, the Mediterranean region, the Cordilleras of South, Central, and western North America, and Hawaii. About 20 species are native and 12 naturalized in the continental United States; six of these (including four introduced) occur in our area.

The genus was divided by Knuth into 30 often unnatural sections based on longevity, habit, floral size, distribution, and the morphology of the rhizome, leaf, and inflorescence. Subsequent authors have rearranged the species into “series” or “groups” (Moore, Davis), have rejected Knuth's system without attempting a formal division of the genus (most authors of floras), or have accepted provisionally Knuth's sectional names, while admitting the inadequacy of his system (Carolin).

The only perennial species of *Geranium* in our area, *G. maculatum* L., is of common occurrence in diverse plant communities, especially of the eastern deciduous forests, but also in fields, meadows, forest openings, thickets, along stream banks, and along the edges of cleared land, from Maine and southern Ontario to southeastern Manitoba, northeastern South Dakota and north-central Nebraska, south to central Georgia and eastern Oklahoma. The occasional white-flowered individuals are sometimes separated from the typical rose-purple-flowered plants as forma *albiflorum* (Raf.) House. Placed by Knuth in his sect. *Sylvatica* (= sect. GERANIUM), *G. maculatum* with simple or branched horizontal rhizomes, was closely allied by Jones & Jones to three other species with unbranched, more or less vertical or oblique rhizomes: *G. pratense* L., $2n = 28$ (Eurasia, occasionally adventive in the northeastern United States), *G. erianthum* DC., $2n = 28, 30$ (northern Japan to Alaska and British Columbia), and *G. oreganum* T. J. Howell (northwestern United States). This group is

characterized by large flowers, only basally pubescent petals, short stigmas, and erect fruiting pedicels (sometimes recurved in *G. pratense*).

The six remaining species in our area have been placed in sect. COLUMBINA Koch (mostly small-flowered annuals with fine roots, leaves round to almost reniform in outline, calyx open or scarcely adpressed to the mature fruit). Carolin, in his treatment of the Malesian species, states that species grouped around *Geranium carolinianum* in North America have some links with "a complex group — containing Knuth's sections *Chilensia*, *Australiensia*, and fragments of *Striata* and *Columbinum* — extending from India, through Malesia, temperate Australia, New Zealand, and the Subantarctic islands, to southern America,"

Geranium carolinianum L. (including *G. Langloisii* Greene), $2n = 52$, is indigenous throughout temperate North America, mostly in dry disturbed habitats. Distinguished from other species in the area by its awned sepals, pedicels less than twice as long as the sepals, and mature carpels hirsute with long antrorse trichomes, plants of this species are quite variable, particularly in density of pubescence and structure of the inflorescence. Plants with the upper internodes greatly shortened and the flowers in compact, many-flowered, determinate umbels are sometimes separated as var. *confertiflorum* Fernald, confined mostly to the northeastern United States but occurring also in the mountains of North Carolina. Until recently known only from south and central Texas, *G. texanum* (Trelease) Heller, with circular-ovate sepals and an eglandular rostrum, has recently been collected in Louisiana by J. W. Thieret. *Geranium Bicknellii* (including *G. longipes* Goodding non DC., *G. nemorale* Suksdorf; trans-Canada and northeastern United States), and *G. sphaerospermum* Fernald (questionably distinct from *G. carolinianum*; northern states and adjacent Canada) are closely related to *G. carolinianum*.

Possibly native in the western United States, but more likely an early introduction from Europe, *Geranium dissectum* L. (including *G. laxum* Hanks in Hanks & Small), $2n = 22$, is locally naturalized and abundant in disturbed habitats in the eastern United States from Massachusetts to Michigan south to Georgia and Texas. It is distinguished from the very similar *G. carolinianum* by the pubescent but not long hirsute mericarps and more strongly reticulate seeds.

Three introduced European species of this section are found locally in disturbed habitats in the eastern United States. *Geranium columbinum* L., $2n = 18$ (indumentum eglandular, pedicels twice as long as the awned sepals, mericarps glabrous) occurs from New York west to the Dakotas and south to North Carolina and Georgia; it is also reported from one county in Washington and along the Columbia River in Oregon. Widespread in the Pacific Northwest, *G. pusillum* L., $2n = 26$ (sepals acute, several filaments without anthers, fruit rostrum very short, mericarps pubescent) is infrequent eastward to Massachusetts and south to North Carolina, Oklahoma, and Utah. *Geranium molle* L., $2n = 26$ (sepals acute, all stamens fertile, fruit rostrum short, mericarps obliquely wrinkled — or smooth in forma *Preuschoffii* Abromeit), ranges from Newfoundland

to British Columbia and the Pacific States and south to North Carolina, Tennessee, and Illinois.

Geranium Robertianum L., Herb Robert, $2n = 64$ (32, 54?, 56), of sect. ROBERTIANA Boiss., the only species of the genus in North America with completely palmately compound leaves with the middle segment prominently petiolulate, occurs to the north of our area, extending as far south and west as Virginia, West Virginia, Ohio, Indiana, Illinois, and Nebraska. Amphiatlantic in distribution, this species is common throughout Europe, and it has been introduced into many regions of the world, including the Pacific United States.

The prevalent somatic chromosome number, especially in the perennial species, is 28. There are evidently two chromosomal races of *Geranium phaeum* L., $2n = 14$ and 28. A polyploid series based on 14 exists, with reports of $2n = 42$ (2 species), 56 (numerous species), and 84 (*G. sanguineum* L.). Other base numbers are found, particularly in the annual species, the most frequent being $2n = 26$ and 52; aneuploidy and polyploidy are fairly common. *Geranium Robertianum* has been reported as $2n = 32$, 56 (54?), 64, with the last the most frequent; further studies are needed to determine the scope of chromosomal variation in this species. The closely related *G. purpureum* Vill. is consistently $2n = 32$. *Geranium anemonifolium* L'Hérit. ex Aiton, a species from Madeira and the Canary Islands allied to *G. Robertianum*, evidently has two races, $2n = 68$ and 128 (the highest number known in the genus).

Hybridization between *Geranium* species is infrequent, occurring mostly between closely related species. Documented hybrids involving species indigenous to North America are thus far unknown, but the species in the western United States have not been closely examined in this respect. Naturally occurring hybrids have been found between two European species of sect. COLUMBINA with different base chromosome numbers, *G. bohemicum* L., $2n = 28$, and *G. lanuginosum* Lamarck, $2n = 48$, the hybrid chromosome number being $2n = 38$. The seeds of these two species do not readily germinate without exposure to heat and plants often appear in areas after forest fires.

The pollen of *Geranium* species is 3-colporate with round to lologate ora and short colpi. The exine is semitectate with the infrategillar bacula circular in cross section. More or less uniform suprattegillar structures are found in the majority of species, with strongly dimorphic processes occurring in many circum-Pacific species, including *G. Richardsonii* of the western United States, and *G. Hernandezii* of Mexico. The pollen of a few species lacks suprattegillar processes and has a striate-reticulate exine like most species of *Erodium*.

Numerous large-flowered species of *Geranium*, such as *G. maculatum*, *G. palustre*, and *G. pratense*, are strongly proterandrous and mostly cross-pollinated. As the flowers open, the outer whorl of stamens curves out and downward while the inner whorl remains erect, the anthers soon dehiscent (see FIGURE 1b). The outer whorl then becomes erect, the anthers dehisce, and the filaments again recurve, as do those of the inner

whorl. After this the anthers frequently become detached from the filaments, and the lobes of the style open, exposing the stigmatic surfaces. In the smaller-flowered species, such as *G. carolinianum*, that attract few insects, there is a tendency for homogamy with increased probability for self-pollination. Some species of *Geranium* and *Erodium* have both perfect flowers and smaller and functionally carpellate ones that are usually gynodioecious in distribution. (Gynomonoecism, androdioecism, andromonoecism, and true dioecism are rare in the Geraniaceae.)

There have been several detailed studies of intraspecific variation in European *Geranium* species. *Geranium Robertianum* and the closely related *G. purpureum* (sometimes treated as a subspecies of the former) were studied genecologically by Böcher and by Baker. Böcher & Lewis investigated variations in leaf and petal morphology, height, habit, time and length of the flowering period, longevity, pubescence, and flower color in 36 strains of *G. sanguineum* from nine European countries. The polymorphic breeding system of *G. sylvaticum* has been investigated numerous times, most recently by Putrament (1962) and Vaarama & Jääskeläinen (1967). Except for Martin's study of *G. maculatum* and Russell's brief account of *G. Richardsonii*, detailed studies of variability in North American species are lacking but would probably be quite informative.

Most species of *Geranium*, including all in North America, have two types of stems. The above-ground floriferous and annual stems are the more prominent. This kind of stem and the basal leaves arise from a thickened and condensed basal stem (caulorrhiza, caudex) which is usually at or below ground level, and may be horizontal and forming a rhizome, oblique, or vertical. In many species this basal stem is the perennating organ, but some form of basal stem is present even in annual species. A taproot and/or numerous adventitious roots arise from the basal stem.

In some species the schizocarp dehisces explosively with such force that the seeds are thrown out of the mericarps and travel laterally for several hundred centimeters. Observations made by C. E. Wood, Jr. (personal communication), on *Geranium maculatum* indicate that when undisturbed the fruit opens over a short period with the mericarps separating from the columella and the adaxial side, where the dehiscence suture is located, becoming oriented away from the axis due to the revolting awns. At this point the seeds are forcibly ejected from the mericarps due to the drying and subsequent contraction of the carpel wall. The awns become even more revolute after dehiscence (see FIGURE 1g). Martin, in her study of this species found that the fruits would dehisce explosively if subjected to a slight mechanical stimulation; this violent dehiscence evidently occurs spontaneously in nature with the awns and/or mericarps becoming detached from the fruit.

Some species of *Geranium* are commonly grown as ornamentals. The most frequently encountered species in eastern North America are *G. sanguineum* L., $2n = 84$, which has several varieties and named cultivars, and *G. grandiflorum* Edgew.

REFERENCES:

- Under family references see BOLKHOVSKIKH *et al.*, BORTENSCHLAGER, BROUWER & STÄHLIN, CAROTHERS, P. H. DAVIS, DAWSON, GAMS, HANKS & SMALL, HESS *et al.*, KENDA, P. KNUTH, R. KNUTH (1912, 1931), KOMAROV, KUGLER, LEGAULT, LUBBOCK, MIRIMANOFF, MOSEBACH, H. MÜLLER, MURLEY, RICKETT, SAUER, SCHWIEKER, SØRENSEN, STAFFORD, WANGERIN, WEBB, and ZANKER.
- BAKER, H. G. *Geranium purpureum* Vill. and *G. Robertianum* L. in the British flora. I. *Geranium purpureum*. *Watsonia* 3: 160–167. 1955; II. *Geranium Robertianum*. *Ibid.* 270–279. 1956.
- . Genecological studies in *Geranium* (section *Robertiana*). General consideration and the races of *G. purpureum* Vill. *New Phytol.* 56: 172–192. *pls.* 2, 3. 1957.
- BARTON, W. P. C. Vegetable materia medica of the United States; or medical botany. Vol. 1. 273 pp. *pls.* 1–24. Philadelphia. 1817. [*G. maculatum*, 149–159, *pl.* 13.]
- BASTIN, E. S. Structure of *Geranium maculatum*. *Am. Jour. Pharm.* 66: 516–522. 1894. [Includes anatomical details of rhizomes, roots, starch grains.]
- BATE-SMITH, E. C., & P. RIBÉREAU-GAYON. Leuco-anthocyanins in seeds. *Qual. Pl. Mater. Veg.* 5: 189–198. 1959. [*G. ibericum*, *G. pratense*, *G. sylvaticum*.]
- BLARINGHEM, L. Hérité en mosaïque du *Geranium pratense* L. var. *album striatum*. *Compt. Rend. Acad. Sci. Paris* 198: 2044–2047. 1934.
- BÖCHER, T. W. Cytogenetic and biological studies in *Geranium Robertianum* L. *Danske Vidensk. Selsk. Biol. Medd.* 20(8): 1–29. 1947. [Includes cultivation and intraspecific hybridization studies.]
- & K. LARSEN. Experimental and cytological studies on plant species. IV. Further studies in short-lived herbs. *Danske Vidensk. Selsk. Biol. Skrifter* 10(2): 1–24. 1958. [*G. molle*, 19, 20.]
- & M. C. LEWIS. Experimental and cytological studies on plant species. VII. *Geranium sanguineum*. *Ibid.* 11(5): 1–25. *pls.* 1, 2. 1962. [Variation patterns for 7 characters.]
- CAROLIN, R. C. The genus *Geranium* L. in the southwestern Pacific area. *Proc. Linn. Soc. New S. Wales* 89: 326–361. *pls.* 6, 7. 1964. [Morphological notes, taxonomic treatment, plates of seeds and pedicel indumentum.]
- CLEMENTS, F. E., & F. L. LONG. Experimental pollination. An outline of the ecology of flowers and insects. vii + 274 pp. *pls.* 1–17. Washington, D.C. 1923. [*G. caespitosum*, 39–45, *pl.* 7; *Geranium*, 105–110; list of pollinators, 257.]
- DAHLGREN, K. V. O. Chromosomes in *Geranium bohemicum* and *G. lanuginosum* with some notes on the hybrid. *Hereditas* 38: 314–320. 1952. [Seeds of these species do not germinate without exposure to heat.]
- DOROGANEVSKAYA, E. A. On the vicarious species of *Geranium* L. in the basin of the Chon-Kyzyl-Su River. (In Russian; English summary.) *Bot. Zhur.* 47: 1292–1300. 1962. [Effect of ecological conditions at various altitudes on chemical composition of *G. collinum* and *G. saxatile*.]
- DUNCAN, W. H. Preliminary reports on the flora of Georgia. 4. Notes on the distribution of flowering plants including species new to the state. *Castanea* 15: 145–159. 1950. [*G. columbinum*, 154, possibly native.]
- EASTWOOD, A. The fertilization of Geraniums. *Zoë* 2: 112. 1891. [*G. Fremontii*, *G. Richardsonii*, *G. caespitosum*, descriptions of pollination.]

- FERNALD, M. L. *Geranium carolinianum* and allies of northeastern North America. *Rhodora* 37: 295–301. *pls.* 371–374. 1935. [9 spp. recognized.]
- FOSBERG, F. R. The Hawaiian *Geraniums*. *Occas. Pap. Bishop Mus.* 12(16): 1–19. 1936. [4 spp. of the anomalous sect. *NEUROPHYILLODES*.]
- GILLOT, P., & A. M. MORISOT. Sur la composition glucidique du géranium des prés (*Geranium pratense* L.). *Assoc. Franç. Avanc. Sci. Compt. Rend.* 55: 415–418. 1931.
- GSTIRNER, F., & K. H. LISKEN. Über Inhaltsstoffe des Rhizoms von *Geranium pratense* L. *Arch. Pharm.* 295: 823–833. 1962. [Eight crystalline substances isolated from solutions, and several other compounds identified by chromatography.]
- GUNTHER, R. T. The Greek herbal of Dioscorides. xii + 701 pp. Frontisp. Oxford. 1934. [*Geranion*, 361, 362.]
- HARA, H. Contributions to the study of variations in the Japanese plants closely related to those of Europe or N. America. I. *Jour. Fac. Sci. Univ. Tokyo Bot.* 6: 29–96. 1952. [*G. Robertianum*, 81.]
- JACKSON, W. What is *Geranium anemonefolium*? *Heredity* 6: 279. 1952. [$2n = 68, 128$.]
- JOHNSON, W. C. *Trillium cernuum* L. and *Geranium maculatum* L.: New for South Dakota. *Rhodora* 72: 554. 1970 [1971]. [Sisseton Co.]
- JONES, G. N., & F. F. JONES. A revision of the perennial species of *Geranium* of the United States and Canada. *Rhodora* 45: 5–26; 32–53. 1943. [18 spp.]
- KNUTH, R. Über die geographische Verbreitung und die Anpassungserscheinungen der Gattung *Geranium* im Verhältnis zu ihrer systematischen Gliederung. *Bot. Jahrb.* 32: 190–230. 1903.
- LEIFERTOVÁ, I. Zur Chemotaxonomie der Gattung *Geranium* — freie Saccharide und Aminosäuren. *Preslia* 40: 357–361. 1968.
- & H. BUČKOVÁ. Zur Chemotaxonomie der Gerbstoff-Merkmale bei der Gattung *Geranium*. Der Gerbstoffgehalt bei der *G. sanguineum* L. III. (In Czechoslovakian; German abstr.) *Preslia* 40: 60–63. 1968.
- , ——— & E. EISENREICHOVÁ. Zur Chemotaxonomie der Gattung *Geranium* — die Stetigkeit der Gerbstoffe bei der Art *Geranium pyrenaicum* L. (In Czechoslovakian; German abstr.) *Preslia* 42: 267–269. 1970.
- , ——— & L. NATHEROVÁ. Zur Chemotaxonomie der Gerbstoff-Merkmale in der Gattung *Geranium*. (In Czechoslovakian; German abstr.) *Preslia* 37: 413–418. 1965. [9 spp.]
- LEWIS, M. C. Genecological differentiation and adaptive significance of leaf structure in relation to xeric environments. XI. *Int. Bot. Congr. Abstr.* p. 128. 1969. [Energy budgets determined for *G. sanguineum* leaves of different degrees of dissection.]
- LUNDMAN, B. Some notes on the regional variation of flower colour by *Geranium silvaticum* L. (In Swedish; English summary.) *Sv. Bot. Tidskr.* 42: 153–157. 1948.
- MACBRYDE, B. Geraniaceae. In: R. E. WOODSON, JR., & R. W. SCHERY. *Flora of Panama*. *Ann. Missouri Bot. Gard.* 54: 201–205. 1967. [*Geranium* only.]
- MARTIN, M. C. An ecological life history of *Geranium maculatum*. *Am. Midl. Nat.* 73: 111–149. 1965. [Morphology, geographical variation.]
- MILLSPAUGH, C. F. *Geranium maculatum*. *American medicinal plants* 1(32): [2 pp.]. *pl.* 32. 1887.
- MOORE, H. E., JR. A revision of the genus *Geranium* in Mexico and Central

- America. Contr. Gray Herb. **146**: 1-108. *pls. 1-5*. 1943. [43 spp.; for corrections cf. Gent. Herb. **8**: 250-257. 1951.]
- MUNESADA, T., N. MURAKAMI, M. NISHIMOTO, & K. MATSUMOTO. Anatomical characters of a *Geranium* herb, *G. carolinianum* L. (In Japanese; English summary.) Jour. Jap. Bot. **35**: 187-190. 1960. [Naturalized in Japan.]
- NAGL, W. Über Endopolyploidie, Restitutionskernbildung und Kernstrukturen im Suspensor von Angiospermen und einer Gymnosperme. Österr. Bot. Zeitschr. **109**: 431-494. 1967. [*G. phaeum*, 448-452.]
- NEGER, F. W. Über Blätter mit der Funktion von Stützorganen. Flora **92**: 371-379. 1903. [Includes *G. Robertianum*.]
- NEGODI, G. Su di un modo di rappresentazione grafica degli sviluppi quantitativi di organi fiorali: antogrammi quantitativi. Appunti sull'architettura floreale di *Geranium nepalense* Sweet. Atti Soc. Nat. Mat. Modena **65**: 81-87. 1934.
- POHLHEIM, F., & H. J. TILlich. Verbänderung (Fasciation) bei *Geranium pratense* L. und ihre Vererbungsweise. Flora B. **158**: 580-593. 1969. [Single recessive-gene fasciation of the stem.]
- PUTRAMENT, A. Some observations on male sterility in *Geranium sylvaticum* L. var. *alpestre* Schur. Acta Soc. Bot. Polon. **31**: 723-736. 1962. [Cytological observations and breeding experiments.]
- RAINIO, A. J. Über die Intersexualität bei *Geranium pratense* L. und ihre Entstehung durch Bastardierung. I. Ann. Bot. Soc. Zool.-Bot. Fenn. **8**(4): 1-28. *1 pl.* 1937.
- ROBERTSON, C. Flowers and insects. III. Bot. Gaz. **14**: 297-304. 1889. [*G. maculatum*, 299, 300; flower agrees with *G. palustre* & *G. pratense*; list of pollinators.]; XI. *Ibid.* **18**: 267-274. 1893. [*G. carolinianum*, 272; flowers imperfectly proterandrous; list of pollinators.]
- RUSSELL, N. H. Quantitative studies in angiosperm taxonomy. X. *Valeriana*. XI. *Geranium*. XII. *Mimulus*. Castanea **29**: 138-150. 1964. [*G. Richardsonii*, 143-146; 26 characters show plant to plant variation.]
- SANSOME, F. W. Some experiments with *Geranium* species. Jour. Genet. **33**: 359-363. 1936. [*G. Endressii*, *G. striatum*; *G. sanguineum*, *G. sanguineum* var. *album*, *G. lancastriense*; inheritance in hybrid crosses.]
- SHAW, R. J. A cytotaxonomic study of the genus *Geranium* in the Wasatch region of Idaho and Utah. Madroño **11**: 297-304. *pl. 6*. 1952. [*G. carolinianum*, *G. pusillum*, *G. nervosum*, *G. Richardsonii*.]
- SOUÈGES, R. Embryogénie des Géraniacées. Développement de l'embryon chez le *Geranium molle* L. Compt. Rend. Acad. Sci. Paris **177**: 556-558. 1923.
- VAARAMA, A., & O. JÄÄSKELÄINEN. Studies on gynodioecism in the Finnish populations of *Geranium sylvaticum* L. Ann. Acad. Sci. Fenn. A. IV. Biol. **108**: 1-40. 1967. [Also history of the study of floral biology in the genus.]
- VISIULINA, O. D. On the morphology and nomenclature of *Geranium sanguineum* L. (In Ukrainian; English summary.) Jour. Inst. Bot. Acad. Sci. RSS Ukr. **12**: 137-140. 1935.*

2. *Erodium* L'Héritier ex Aiton, Hortus Kew. **2**: 414. 1789.

Annual or biennial herbs [sometimes perennial, caespitose or shrubby], at first acaulescent rosette plants, later with several $\pm$ jointed elongate, simple or branched stems often arising and radiating from generally unbranched taproots. Leaves longer than broad, pinnately compound [or lobed; rarely simple or palmate], the leaflets toothed, lobed or subdivided,

sessile or shortly petiolulate; basal and cauline leaves similar, the latter opposite [or all alternate] and tending to be more strongly lobed, divided, or subdivided. Inflorescences determinate umbels, arising from the rosette and/or from nodes of elongated stems; ultimate peduncles several flowered [infrequently with 1 or 2 flowers]. Flowers perfect [rarely imperfect, the plants dioecious], regular to slightly irregular. Sepals 5, often mucronate or aristate. Petals 5, glabrous, equal or the two upper smaller [rarely absent], pink to violet, purple [white, blue or lilac, very rarely yellow or deep red], the veins typically more intensely colored, sometimes with a dark or blackish spot near the base of the two upper [or all] petals. Fertile stamens 5, the outer antepetalous whorl reduced to staminodia [or scales]; filament bases sometimes with two lateral teeth. Ovary pubescent. Schizocarp dehiscing mostly from apex downwards, the mericarps and awns becoming completely detached from the columella; mericarps tapering toward base; awns persistent on mericarps [or deciduous], pubescent on adaxial surface, lower portion spirally coiling when freed from columella. Seed smooth, retained within mericarp. LECTOTYPE SPECIES: *E. crassifolium* L'Hérit. ex Aiton = *E. hirtum* (Forsk.) Willd. non Jacq.; see L. T. HANKS & J. K. SMALL, N. Am. Fl. 25: 21. 1907. (Name from Greek *erodios*, heron, in comparison of the shape of the fruit to a heron's bill.) — HERON'S-BILL, STORK'S-BILL, ALFILERIA, FILAREE, PIN-CLOVER.

A genus of 60 to 80 species centered in Mediterranean Europe, North Africa, and the Middle East; species have been introduced into most temperate regions of the world. Two sections are usually recognized, *ERODIUM* (§ *Plumosa* Boissier) (mericarp awns quickly deciduous and plumose on the adaxial surfaces with long silvery or yellowish trichomes) and *BARBADA* Boissier (awns persistent on mericarps, trichomes on adaxial surfaces short, adpressed, and reddish). The latter section was subdivided by Knuth into ten subsections based on leaf morphology, habit, rostrum length, petal size and shape, and density of indumentum.

In the United States at least ten species, all belonging to sect. *BARBATA*, have been reported, several being ephemeral escapes. Two introduced species, *Erodium cicutarium* (L.) L'Hérit. ex Aiton and *E. moschatum* (L.) L'Hérit. ex Aiton, both belonging to subsect. *CICUTARIA*, a taxonomically difficult group centered in the southwestern Mediterranean region, occur in our area. Both are also naturalized in the West, as are *E. Botrys* Bertol., $2n = 40$ (southern Europe and the Mediterranean region) and *E. brachycarpum* (Godr.) Thell. (including *E. obtusiplicatum* (Maire, Weiller & Wilczek) J. T. Howell and *E. Botrys* f. *montanum* Brumh.; North Africa), $2n = 40$. Apparently the western *E. macrophyllum* Hooker & Arnott (*E. californicum* Greene; related to *E. malacoides* (L.) L'Hérit. ex Aiton of southern Europe) and *E. texanum* Gray, $2n = 20$, placed by Knuth in subsect. *GUTTATA*, otherwise Mediterranean in distribution, are indigenous.

Erodium cicutarium, characterized by its eglandular apical mericarp pits, aristate sepals, sessile leaflets divided more than half-way to the midrib, and toothless anther-bearing filaments, is found in fields, roadsides, and waste places throughout most of the United States. It probably occurs sporadically in all states in our range but is poorly represented in herbaria. A very plastic species, particularly in habit, size, leaf shape, indumentum, and fruit morphology, *E. cicutarium* has had a tortuous nomenclatural history with numerous segregate species, subspecies, and varieties described and several classification schemes proposed (see Litar-dièrè in Briquet, Andreas, Rottgardt, Larsen, Tutin *et al.*, and Guitton-neau). In Europe there are several chromosomal races with the predomi-nant number being $2n = 40$, but $2n = 20$ is common and $2n = 36$, 48 and 54(56?) also occur; hexaploid populations, $2n = 60$, have been segre-gated as *E. danicum* K. Larsen. At least three morphological entities occur in Europe: a mostly tetraploid "field" type, a tetraploid "dune" type, and a mostly diploid "dune" type. The plants in the United States evidently correspond to the "field" type, *E. cicutarium* subsp. *cutarium*, and the only chromosome number reported from this country is $2n = 40$. This species is also naturalized in Australia, Java, East Africa, and prob-ably in most other temperate regions of the world.

Erodium moschatum, $2n = 20$, characterized by its glandular apical mericarp pits, acute to mucronate sepals, shortly petiolate leaflets divided less than half-way to the midrib, and anther-bearing filaments with two lateral teeth, is common in California and has been reported as an infre-quent adventive in waste places and roadsides in northern Florida and the northeastern United States. It is also naturalized in East and South Africa and Australia.

The awn of the mericarp is pubescent inside and has a dextrorsely spiraled coiled portion, the spirillum, and an arching terminal portion, the flagellum. The awns are hygroscopic, the spirals loosening when moist and becoming tighter when dried. In nature, varying weather conditions cause the awns to coil and uncoil repeatedly, and this action evidently forces the seeds into the soil. The awns have been used to make hygrom-eters. The seed is usually retained within the tapering mericarps. At the apex of the mericarp are two flattened areas referred to as pits (foveae, foveoles) which are subdivided in some species by one or more ridges, giving the impression of furrows below the pits.

The base chromosome number in the genus is $x = 10$, with $2n = 20$ the most frequently reported number. Tetraploids are common, hexaploids have been recorded in three subsections, and one octoploid is known. Aneuploidy occurs in *E. cicutarium* (see above) and all reports for species in subsect. ABSINTHIOIDEA are $2n = 18$. Most, if not all, species in this latter subsection are dioecious (see Davis & Roberts; illustration in Stefani, *et al.*).

The pollen of *Erodium* species is 3-colporate and most species lack suprattegillar processes with the exine striate-reticulate. Three subtypes based on sculpturing patterns were distinguished by Bortenschlager. A

few species, including *E. texanum*, have strongly dimorphic supratragillar processes, like the pollen found in most *Geranium* species.

In the Southwest several species, particularly *E. cicutarium*, are important spring and winter range forage plants for domestic and game animals. Some species are also grown as ornamentals in rock gardens. *Erodium cicutarium* can be an aggressive weed, competing vigorously with crops such as alfalfa.

REFERENCES:

- Under family references see BOLKHOVSKIKH *et al.*, BORTENSCHLAGER, BROUWER & STÄHLIN, P. H. DAVIS, DAWSON, GAMS, HANKS & SMALL, HESS *et al.*, KENDA, P. KNUTH, R. KNUTH (1912, 1931), KOMAROV, KUGLER, KUTSCHERA, LEGAULT, L'HÉRITIER, LUBBOCK, MIRIMANOFF, MOSEBACH, H. MÜLLER, MURLEY, RICKETT, SAUER, SCHWIEKER, SØRENSEN, STAFFORD, WANGERIN, WEBB, and ZANKER.
- ANDREAS, C. H. De inheemsche *Erodia* van Nederland. (In Dutch; English summary.) Nederl. Kruidk. Arch. 54: 138–229. *pl.* 1. 1947. [Field, morphological, cytological and hybridization study with emphasis on *E. cicutarium* and its relatives.]
- BRUGGEMAN, C. J. M. Overzicht der in Nederland gevonden inheemse en adventieve *Erodium*-soorten. (In Dutch; English summary.) Gorteria 2: 49–55. 1964. [10 spp.; illustrations.]
- BRUMHARD, P. Monographische Übersicht der Gattung *Erodium*. 59 pp. Inaug. Diss. Breslau. 1905. (Also see Repert. Sp. Nov. 2: 116–119. 1906.)
- CAROLIN, R. C. Notes on the genus *Erodium* L'Hér. in Australia. Proc. Linn. Soc. New S. Wales 88: 313–319. 1964. [Introduced spp.; for endemic spp. see *Ibid.* 83: 92–100. 1958.]
- DAVIS, P. H., & J. ROBERTS. Materials for a flora of Turkey I. Geraniaceae. Notes Bot. Gard. Edinburgh 22: 9–27. 1955. [Includes comments on dioecism in subsect. ABSINTHIOIDEA.]
- DAYTON, W. A. Alfileria (filaree) "seed." Rhodora 39: 233–235. 1937. [Includes key to mature carpels of 5 spp.]
- EIJK, J. L. VAN. Phytochemical investigation of *Erodium cicutarium*. (In Dutch; English summary.) Pharm. Weekbl. 17: 581–587. 1957.*
- FINN, O. B. The brace and bit plant. Sci. Am. 139: 426, 427. 1928.*
- GUITTONNEAU, G. Contribution à l'étude caryologique [caryosystématique] du genre *Erodium* L'Hér. I. Bull. Soc. Bot. France 111: 1–4. 1964; II. *Ibid.* 112: 25–32. 1 *pl.* 1965; III. *Ibid.* 113: 3–11. 1966; IV. *Ibid.* 114: 32–41. 1967.
- . Sur la répartition de l'*Erodium brachycarpum* (Godr.) Thell. [= *E. obtusiplicatum* (Maire, Weiller et Wilczek) Howell] dans le bassin méditerranéen. *Ibid.* 113: 66–68. 1966.
- . Note sur le texte de la Geraniologia de L'Héritier. *Ibid.* 114: 42–45. 1967.
- . Contribution à l'étude biosystématique du genre *Erodium* L'Hér. dans le bassin méditerranéen occidental. Thèse Fac. Sci. Orsay Univ. Paris. 253 pp. 23 *pls.* in 2 vols. Orsay. 1970.
- HANSTEIN, J. Ueber die Einbohrung der Geraniaceen-Früchte in den Boden. Bot. Zeit. 27: 528, 529. 1869. [Seed dispersal mechanism in *E. gruinum*; for partial English transl. see I. Sprague & G. L. Goodale, Wild Flowers of America, Vol. 1: 17, 18. 1882.]

- HARDIN, J. W. Some notes on weeds of North Carolina. *Castanea* 24: 22, 23. 1959. [*E. cicutarium* has completely destroyed alfalfa crops in the Piedmont.]
- IRVING, W. The heronsbill family. *Garden London* 87: 329-331. 1923. [15 perennial spp. listed for rock garden cultivation.]
- JARRETT, M. P. Arizona's Wildflowers. *Arizona Highways* 47(8): 10-39. 1971. [*E. cicutarium*, *E. texanum*, 31; colored photographs, 19.]
- LARSEN, K. Cytological and experimental studies on the genus *Erodium* with special references to the collective species *E. cicutarium* (L.) L'Hér. *Danske Vidensk. Selsk. Biol. Medd.* 23(6): 1-25. 1958.
- LITARDIÈRE, R. DE. *Erodium*. In: J. BRIQUET, *Prodr. Fl. Corse* 2(2): 15-36. 1935.
- MARTIN, P. S., & C. M. DREW. Scanning electron photomicrographs of southwestern pollen grains. *Jour. Arizona Acad. Sci.* 5: 146-176. 1969. [*E. cicutarium*, pl. 38, p. 164.]
- PRESTON, C. E. Two instructive seedlings. *Bot. Gaz.* 33: 150-154. 1902. [*E. cicutarium*, phylogeny of trichomes.]
- RAMALEY, F. The trichome structures of *Erodium cicutarium*. *Bot. Gaz.* 34: 140-142. 1902. [Disputes Preston's findings.]
- ROTTGARDT, K. Morphologische, cytologische und physiologische Untersuchungen von Ökotypen in Schleswig-Holstein. *Beitr. Biol. Pflanzen* 32: 225-278. 1956. [*E. cicutarium* vars. *immaculatum* and *pimpinellifolium*, 228-243.]
- SHAW, W. R. Hygrometer made with *Erodium* awns. *Bot. Gaz.* 24: 372. 1897.
- SIEGERT, A. *Erodium corsicum* Léman, ein weiteres Beispiel für Blattstioldornen, zugleich ein Beitrag zur Kenntnis der Blattstioldornen überhaupt. *Beitr. Biol. Pflanzen* 46: 461-480. 1970. [Thorns are modified petioles.]
- SOUÈGES, R. Embryogénie des Géraniacées. Développement de l'embryon chez l'*Erodium cicutarium* L'Hérit. *Compt. Rend. Acad. Sci. Paris* 176: 1565-1567. 1923.
- STEFANI, C. DE, C. J. F. MAJOR, & W. BARBEY. Samos. 99 pp. pls. 1-14. Lausanne. 1891. [Pl. 2 illustrates staminate and pistillate flowers of *E. Vatteri*.]
- VIERHAPPER, F. Beiträge zur Kenntnis der Flora Griechenlands 2. *Verh. Zool.-Bot. Ges. Wien* 69: 102-156. 1919. [*Erodium*, 112-155.]
- WAGNON, K. A., & H. H. BISWELL. Two types of broad-leaf *Erodium* in California. *Madroño* 7: 118-125. 1943. [*E. botrys* and *E. botrys* f. *montanum*.]

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Robertson, Kenneth Ray. 1972. "The genera of Geraniaceae in the southeastern United States." *Journal of the Arnold Arboretum* 53(2), 182–201.
<https://doi.org/10.5962/p.58026>.

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