

THE GENERA OF MENYANTHACEAE IN THE SOUTHEASTERN UNITED STATES¹

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MENYANTHACEAE Dumortier, Anal. Fam. Pl. 20, 25. 1829,
"Menyanthideae."

Marsh, wetland, or aquatic perennial [or annual] herbs with alternate, simple or 3-foliolate, exstipulate leaves with sheathing petiole bases. Inflorescences various, monopodial or sympodial. Flowers regular (actinomorphic), perfect and often distylous, to imperfect. Calyx of 5 free or united sepals. Corolla sympetalous, 5-lobed, the lobes valvate or induplicate-valvate in bud, often with the margins and sometimes the inner surface fringed or bearded. Stamens 5, epipetalous, alternate with the corolla lobes, the anthers versatile, sagittate at base. Nectaries usually present at base of ovary. Gynoecium syncarpous, 2-carpellate, the calyx and corolla adnate to the lower part; style single, the stigma 2-lobed; ovary 1-locular, with numerous ovules on 2 (or 3) parietal placentae. Fruit a 2–4-valved capsule, or $\pm$ fleshy and irregularly dehiscent or indehiscent. Seeds numerous to few, usually smooth (or variously ornamented), with copious endosperm and a cylindrical embryo. (Tribe Menyantheae Griseb.) TYPE GENUS: *Menyanthes* L.

A small family of five genera and about 45 species: *Menyanthes* L., *Fauria* Franchet (*Nephrophyllidium* Gilg), and *Liparophyllum* J. D. Hooker, each with a single species; *Villarsia* Ventenat, with 12 species in Australia and one in South Africa; and *Nymphoides* Séguier, with about 30 species in Africa, Australia, tropical America, eastern North America, and Europe. *Menyanthes tri-*

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I am indebted to Dr. Norton Miller for his editorial and bibliographic help, and to Dr. Robert Ornduff, who has kindly read the manuscript and offered several suggestions and additional references. The illustration was prepared by the late Dorothy H. Marsh in 1957, long before Dr. Ornduff showed that *Nymphoides cordata* is dioecious. The living material came from Bateman's Pond in Concord, Massachusetts, where only the staminate plant occurs, and the other materials came from specimens in the Gray Herbarium from Florida (e, f, *Godfrey* 55096 & *Kral*), South Carolina (g, *Godfrey* & *Tryon* 405), and New York (h, *Muenschner* 3541).

foliata L. is circumboreal in distribution. *Fauria Crista-galli* (Menzies ex Hooker) Makino is bicentric, with subsp. *Crista-galli*, $2n = 102$, in western North America (coastal Washington and British Columbia, northward to the Gulf of Alaska) and subsp. *japonica* (Franchet) Gillett, $2n = 68$, in eastern Asia (southern Kuril Islands, the Japanese islands of Hokkaido and Honshu, and southern Korea). *Liparophyllum Gunnii* J. D. Hooker is restricted to Tasmania and New Zealand.

Variously recognized as a tribe of the Gentianaceae (Grisebach, Benthams & Hooker), as a subfamily (Gilg, Rendle), or as a family (Cronquist, Hutchinson, Lindsay, Takhtajan, Thorne, Wagenitz), the Menyanthaceae differ from the Gentianaceae in their marsh or aquatic habitat; alternate, petiolate leaves; collateral vascular bundles; valvate or induplicate-valvate aestivation of the corolla lobes; fused lateral corolla traces and $\pm$ bilaterally symmetrical vascular plan in the flowers; tenuinucellar ovules with a single integument and integumentary tapetum; cellular endosperm development; and chemistry (loganin present, gentiopicroin and L-(+)-bornesitol absent). The Menyanthaceae are generally agreed to be related to the Gentianaceae but were placed in the Polemoniales by Cook and in the Solanales by Cronquist.

Nilsson has distinguished two pollen types in the family: the *Menyanthes* type (*Menyanthes*, *Fauria*), with "3-colporate, generally subprolate to prolate, striate to rugulose" grains; and the *Villarsia* type (*Villarsia*, *Nymphoides*, *Liparophyllum*), with "3-colporate, generally oblate to suboblate, parasyncolpate, striate, rugulose, spinulose, verrucose or $\pm$ smooth" grains. He found that pollen morphology supports an alliance of Menyanthaceae with Gentianaceae, *Menyanthes* and *Fauria* having pollen "similar to such genera as *Gentiana*, *Crawfurdia*, etc."

Heterostyly and associated self-incompatibility occur in *Fauria*, *Menyanthes*, *Nymphoides*, and *Villarsia*. *Liparophyllum* is monomorphic and self-compatible (Ornduff, 1982). Both homostylous self-compatible and heterostylous self-incompatible species occur in *Villarsia* (Ornduff, 1974), and dioecious species occur in *Nymphoides* (Ornduff, 1966). Gynodioecy has been recorded in *N. cristatum* (Vasudevan Nair). In heterostylous species pollen grains from short-styled flowers are larger than those from long-styled ones.

The family is of little economic consequence. *Menyanthes* has been used rarely in medicine. Several species of *Nymphoides* (especially *N. peltata*) are grown to a limited extent as ornamental, floating-leaved aquatics.

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KEY TO THE GENERA OF MENYANTHACEAE IN THE
SOUTHEASTERN UNITED STATES

General characters: *Marsh or aquatic herbs with simple or compound alternate leaves; corolla regular, sympetalous, the 5 stamens alternate with the 5 lobes; gynoeceium syncarpous, 2-carpellate, adnate at the base to the perianth, the ovary 1-locular with 2 parietal placentae; fruit a dehiscent or indehiscent capsule.*

- Leaves 3-foliate, emersed; palustrine herbs with a creeping rhizome; inflorescences racemose, emersed; corolla lobes valvate in bud; petals bearded on the inner surface; fruits borne above water, dehiscent, 2-valved. 1. *Menyanthes*.
Leaves simple, cordate to reniform, floating or submersed; aquatic herbs; inflorescences cymose, the flowers opening singly above water; corolla lobes induplicate-valvate in bud; petals not bearded on the inner surface; fruits ripening under water, indehiscent or opening irregularly. 2. *Nymphoides*.

1. **Menyanthes** Linnaeus, Sp. Pl. 1: 145. 1753; Gen. Pl. ed. 5. 71. 1754.

Glabrous perennial aquatic herbs with creeping sympodial rhizomes bearing adventitious roots and a cluster of leaves at the apex; leaves and flowers emergent from water. Leaves alternate, ternate, petiolate, with large, membranaceous, sheathing bases. Inflorescences racemose on a leafless scape from the terminal bud of the rhizome. Flowers distylous (heterostylous, dimorphic), each subtended by a small bract. Calyx 5-lobed, synsepalous, the lobes partly recurved. Corolla deeply 5-lobed, pink outside, [pink to] white inside, the tube short, adnate to base of ovary, the lobes 3-veined, valvate in bud, the inside of lobes bearded with white fimbriae. Stamens at sinuses of lobes, the anthers basifixed, introrse. Style terminal, the stigma 2-lobed; ovary globular, the placentae parietal. Fruit a 2-valved loculicidal capsule, opening along lateral sutures, with numerous (ca. 20) seeds. Seeds light brown, shining, elliptical, slightly compressed, with abundant endosperm and a cylindrical embryo. LECTOTYPE SPECIES: *M. trifoliata* L.; typified by the transfer from *Menyanthes* to *Villarsia* of two of the three Linnaean species (Ventenat, Choix de Plantes, pl. 9. 1803); see also Britton & Brown, Illus. Fl. No. U. S. Canada. ed. 2. 3: 17. 1913. (Name used by Theophrastus, from Greek *menyein*, disclosing, and *anthos*, flower; later applied to this genus with flowers expanding in succession in the raceme.) — BOG BEAN, BUCK BEAN.

The single species, *Menyanthes trifoliata*, $2n = 54$, is circumpolar in distribution in cold bogs, boggy meadows, fens, and shallow waters of pond margins, mainly between lat. 40°N and the Arctic Circle. It occurs in most of Europe but is rare in the Mediterranean region (Tutin), and it is distributed eastward to eastern Central Asia, Siberia, the Himalayas, Tibet, western China and Manchuria, Korea, Sakhalin, and Japan (Hokkaido, Honshu, and northern Kyushu) (Hara). In North America it is found from Greenland, Labrador, and

Newfoundland, west to Alaska, and south to the limit of the Wisconsin glaciation, with scattered, often disjunct localities in the eastern United States in New Jersey, Delaware, and Pennsylvania, northern Virginia (Madison and Augusta counties), eastern West Virginia (Pocahontas County), northwestern-most North Carolina (Watauga County), Ohio, Indiana, Illinois, Missouri (Reynolds County, in the southeastern Ozarks), and Nebraska. In the western United States it occurs mostly at higher altitudes south to Colorado, Montana, Wyoming, Nevada, California (in the Sierra Nevada), and southern Oregon.

Fernald segregated the eastern American representatives from the European plants as a weakly defined geographical variety (var. *minor* Raf.) on the basis of corolla size, color, and bearding of the upper surface of the lobes.

The species is distylous (or possibly monomorphic in some localities; see Avebury), but collectors seldom indicate whether both long- and short-styled forms are present in a given population. Long-styled plants of var. *trifoliata* have smaller pollen grains than short-styled ones (see Nilsson, Fossel & Vorwohl), but the situation is inconsistent in var. *minor* (Nilsson).

According to Guppy, seeds of *Menyanthes* float for two months. Ravn noted the buoyant seed coat. Ridley recorded that the seeds have been found in the excreta of reindeer, and in the crops of the European wild duck and the American mallard duck. Hochreutiner, who fed the seeds to three species of fish, found that nearly all germinated after passage (1–3 days) through the digestive tract.

On the basis of morphology, *Menyanthes* is presumably most closely related to *Fauria*, a relationship supported by pollen morphology.

The dried leaves of *Menyanthes* have been used as a substitute for hops in brewing. The very bitter juice has been used as a remedy for bowel trouble and dyspepsia; in large doses the effect is purgative and emetic. It has also been used as a tonic, an astringent, an antirheumatic, and a febrifuge.

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2. **Nymphoides** J. F. Séguier, Pl. Veron. (Stirp. Agro Veron. Reper.) **3**: 121. 1754.

Perennial rhizomatous herbs with floating, rounded to cordate leaves (superficially resembling miniature leaves of *Nymphaea* or *Nuphar*). Flowers borne in cymose, umbellike clusters (in our indigenous species at the summit of a slender, petiolelike internode with the petiole of the single floating leaf an apparent continuation of the stem), often with clusters of spurlike or “banana-like” tuberous adventitious roots. Plants [homostylous,] heterostylous (distylous), or dioecious (our indigenous species). Flowers emergent, the corollas white or yellow, delicate, 5-lobed, bearing 5 glandular, staminodelike tufts or fringes of trichomes near the base, 1 opposite each lobe; lobes induplicate-valvate in bud. In heterostylous species (e.g., *N. peltata*) flowers with styles either long and with well-developed 2-lobed stigmas and anthers borne below the level of the stigma on short filaments, or short and with smaller stigmas and anthers borne above the stigmatic level on long filaments; anthers dehiscing introrsely; pollen of long-styled flowers smaller than that of short-styled ones. In dioecious species gynoecium of staminate flowers lacking a style, the stigmas undeveloped, the ovules as large as those of carpellate flowers but nonfunc-

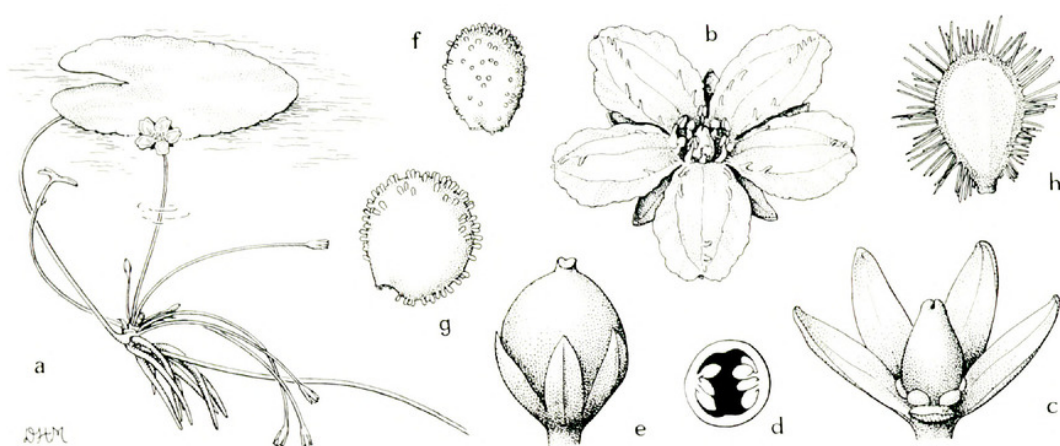


FIGURE 1. **Nymphoides**. a–f, *N. cordata*: a, floating leaf, inflorescence with spurlike adventitious roots, and small branch with unexpanded leaf and inflorescence, $\times \frac{1}{2}$; b, staminate flower, showing staminodiumlike appendages at base of petals and stamens alternating with petals, $\times 3$; c, staminate flower, corolla removed to show sterile gynoeceum and 4 of 5 nectar glands at base of ovary, $\times 6$; d, cross section of ovary of staminate flower showing nonfunctional ovules, $\times 8$; e, fruit, $\times 4$; f, seed, $\times 10$. g, *N. aquatica*: seed, $\times 10$. h, *N. peltata*: seed, $\times 4$.

tional; in carpellate flowers the style short, the stigmas well developed, fleshy. Five nectar glands present at base of ovary opposite base of corolla lobes. Fruits maturing under water, small, indehiscent or irregularly dehiscent with small, plump, nearly smooth to papillate seeds, or (in *N. peltata*) the capsules larger, resembling those of *Frasera*, the seeds larger, flat, their margins coarsely ciliate. (*Limnanthemum* S. G. Gmelin.) TYPE SPECIES: *Nymphoides aquis innatans* Tournefort = *N. peltata* (S. G. Gmelin) Kuntze. (Name from Greek, *nymphaia*, and *eidos*, resemblance, from the similarity of the leaves of *N. peltata* to those of the water lily, *Nymphaea*.) — FLOATING-HEART.

A genus of 30–35 species of floating-leaved aquatics, primarily of the tropics, best represented in the Old World (13 species in Africa and Madagascar, 12 species in Australia), with about five species in tropical America and two indigenous to eastern North America. *Nymphoides peltata*, the single Eurasian species, is often cultivated as an ornamental plant and is sporadically naturalized in the United States.

Nymphoides cordata (Ell.) Fern. (*N. lacunosa* sensu Fernald), $2n = 36$, is distributed in quiet “soft” (noncalcareous) waters from Louisiana and western Florida, northward on the Coastal Plain to New England, Nova Scotia, and Newfoundland, southwestern Quebec, and Ontario. It has thin, cordate-ovate floating leaves that are nearly smooth beneath and not densely dark pitted, capsules to 1.5 times the length of the calyx, and small seeds with a smooth to papillate surface. *Nymphoides aquatica* (J. F. Gmelin) Kuntze, banana floating-heart, $2n = 36$, a larger, coarser plant with ovate to reniform leaves with the lower surface usually thickened and densely dark pitted, the petiole and stem densely covered with dark glands, a capsule much larger than the calyx, and larger seeds with a tuberculate or papillate surface, is found on the Coastal

Plain from southern Florida west to eastern Texas, and north to Delaware and southern New Jersey. The corollas of *N. aquatica* are almost twice as large as those of *N. cordata*. However, corollas press so poorly (waxed paper or facial- or toilet-tissue should be used) that they are seldom adequately preserved in herbarium specimens of either these or other members of the genus.

Nymphoides peltata (*Limnanthemum peltatum* S. G. Gmelin, *L. Nymphoides* (L.) Hoffmans. & Link), yellow floating-heart, $2n = 54$, is indigenous to most of Europe north to Sweden and north-central Russia and is distributed eastward through the Caucasus to Iran, India, Taiwan, Mongolia, Manchuria, southern Siberia, Korea, and Japan. It is sporadically naturalized in the United States in New England, New York, New Jersey, Pennsylvania, Maryland, Ohio, Indiana, Illinois, Missouri, Arkansas, Mississippi, Louisiana, Oklahoma, Texas, Arizona, and Washington (see Stuckey). It is the best-studied species of the genus (see references). Sometimes forming dense stands in quiet waters, it overwinters by short-shoots that form new leaves and long-shoots in the spring. The flowering stems develop from a leaf axil of a long-shoot, and the flowers are produced sympodially in cymose, umbellike inflorescences. Each golden-yellow flower (ca. 3.5 cm across) lasts a single day, as in other species. The corolla absorbs ultraviolet light centrally and reflects it peripherally (Van der Velde & Van der Heijden), as do the yellow flowers of the Australian *N. geminata* (R. Br.) Kuntze (see Ornduff & Mosquin). Distyly is coupled with a weak self-incompatibility system. Van der Velde & Van der Heijden recorded 43 species of insects (mostly Apidae, Syrphidae, and Ephydriidae) as visitors to the flowers in the Netherlands. Megagametophyte development is of the Polygonum type. The capsules mature under water one to two months after flowering, then burst open at the base. The flesh becomes soft and decays. The seeds float and are dispersed over the water surface by wind; they also adhere to water birds.

In both of our white-flowered indigenous species, the long, slender first internode of the inflorescence (see Goebel) is often misinterpreted as the long petiole of a floating leaf. Actually, each elongated stem bears a single floating leaf and is terminated by a flower; the cymose inflorescence develops sympodially as in *Nymphoides peltata* and is supported near the surface of the water by the floating leaf-blade (see FIGURE 1). In both species, fleshy spurlike (*N. cordata*) or somewhat banana-shaped (*N. aquatica*) adventitious roots are produced on either side of the inflorescence. These clusters function as overwintering vegetative reproductive structures. Both species are dioecious (Ornduff, 1966); collectors should note the occurrence of staminate and carpellate plants. The ultraviolet reflectance patterns have not been studied, but in the similarly white-flowered *N. indica* (L.) Kuntze the corolla absorbs ultraviolet light uniformly (Ornduff & Mosquin).

The genus includes diploids, tetraploids, and hexaploids ($2n = 18, 36, 54$). The American species studied thus far are tetraploids, and Ornduff (1969) found that the white-flowered tropical American tetraploids generally known as *Nymphoides Humboldtiana* (HBK.) Kuntze are conspecific with the Old World white-flowered diploid *N. indica*. Both homostylous self-compatibility and distylous self-incompatibility, as well as dioecism, occur in the genus. Ornduff

(1970) concluded that "dioecism has evolved at least two and perhaps three times in *Nymphoides*" and that it is "evident that tetraploidy has arisen independently in the genus more than once."

Nymphoides is closely related to *Villarsia* Vent., which has about 12 species in Australia and one in South Africa. In comparing the Australian members of the two genera, Aston (1969, 1973) pointed out that in *Nymphoides* the plants are true aquatics, the flowers are in nonpaniculate inflorescences, the pedicels bend downward after flowering, and the fruits ripen under water and are indehiscent or break up irregularly. In *Villarsia* the plants are mostly wetland herbs with erect paniculate (rarely condensed and capitate) inflorescences, the capsules are not carried under water for ripening, and the fruits are usually valvate capsules.

Nymphoides peltata, *N. aquatica*, and *N. indica* (including *N. Humboldtiana*) are cultivated in the United States to limited degrees for their attractive flowers and floating leaves. The somewhat bananalike adventitious roots from the inflorescences of *N. aquatica* are sold as an aquarium oddity, underwater banana plant.

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