

THE GENERA OF THE NYMPHAEACEAE AND  
CERATOPHYLLACEAE IN THE SOUTHEASTERN UNITED STATES

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THE TREATMENTS of the ranalian families Nymphaeaceae and Ceratophyllaceae presented here continue a series of studies toward a biologically oriented generic flora of the southeastern United States made possible by the interest and support of George R. Cooley and a grant from the National Science Foundation. The first paper in this series of generic treatments (The genera of the woody Ranales in the southeastern United States. Jour. Arnold Arb. 39: 296-346. 1958) includes a general explanation of the aims and scheme of this work. As noted there, the area covered in these studies is bounded by and includes North Carolina and Tennessee, Arkansas and Louisiana. The pattern of the descriptions, notes and references is the same as outlined and followed in the introductory paper. It may be called to attention again, however, that the descriptions are based upon the species which occur within this area, items in brackets being supplementary and not applying to our plants. The abbreviations of journals follow those of Schwarten and Rickett (Abbreviations of titles of serials cited by botanists. Bull. Torrey Bot. Club 76: 277-300. 1958). References which have not been checked are marked by an asterisk.

The illustration of *Nelumbo* by Dorothy H. Marsh is from living materials obtained through the enthusiastic assistance of Richard A. Eaton and Kenneth A. Wilson.

## NYMPHAEACEAE (WATER-LILY FAMILY)

Aquatic perennial [or annual] rhizomatous herbs, with alternate cordate to peltate floating or emersed leaves with involute vernation, and solitary, axillary, perfect, at least partially cyclic flowers. Plants usually with air-spaces, latex, vascular bundles without cambium or vessels, the leaf-tissues (especially) often with sclereids. Sepals 3-6[-12], green to petaloid, free or slightly united, hypogynous [in ours]. Petals 3-many, showy and colored, to stamen-like, free [in ours], hypogynous, or, with the stamens, inserted on the surface of the ovary, sometimes transitional to stamens. Stamens 3-200, extrorse or introrse; pollen more or less "monocotyledonoid," (monocolpate or derived types) or (in *Nelumbo*) 3-colpate. Gynoecium of [1]2-many carpels, free or united, superior to inferior. Ovules anatropous, many-2-1, pendulous from the top, the walls, or the abaxial suture of the carpels. Fruit a many-seeded berry, a nut, or 1-3 seeded, small and indehiscent. Seeds operculate (except *Nelumbo*), with or without an aril; embryo with thick and fleshy cotyledons, small and

with abundant perisperm and little endosperm or (in *Nelumbo*) large and lacking both. (Including Cabombaceae, Nelumbonaceae.)

A family of eight well-marked genera (five of which occur in our area), of very wide distribution in quiet fresh waters. The genera are linked together by the aquatic rhizomatous habit, the usually long-petioled simple leaves (with a strong tendency towards peltation), the solitary, long-peduncled flowers with at least partially cyclic arrangement of parts, the anatropous, pendulous parietal ovules, the presence of air spaces, the latex-producing habit, and the monocotyledonoid vascular bundles. In respect to other characteristics (e.g., pollen morphology, embryology, operculum and other features of seeds, seedlings, anatomy, floral structure, etc.) the relationships are reticulate. Although a large body of literature exists, many of these latter items have been investigated only partially and it is difficult to draw complete comparisons throughout the family. Various divergences occur between the genera, especially in respect to the structure of flower and fruit, these generally being associated with special mechanisms which function in connection with pollination and with the protection, dispersal, and survival of seeds. The structural features of all these plants need further study and interpretation in connection with their biology.

The treatment of Caspary, who regarded the family as composed of three well-marked subfamilies, is followed here. Some authors, however, split the group into three or even five families (in as many as three orders). These latter treatments seem unjustified, particularly in respect to the Cabomboideae (*Cabomba* and *Brasenia*) and to *Euryale*, *Victoria* and *Barclaya*, all of which clearly seem to be linked to *Nuphar* and *Nymphaea*. *Nelumbo*, the single genus of the Nelumboideae, is perhaps the most divergent member of the family, but even this genus may be regarded merely as being specialized in regard to leaves, dispersal mechanism, embryo and pollen. (See also *Brasenia* and *Nelumbo* below.)

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## KEY TO THE GENERA OF NYMPHAEACEAE

- A. Carpels united, either along their sides or along the outer margins by adnation to a cup-like "receptacle;" stigmas radiate; ovules numerous in each locule; stamens numerous, introrse; fruit an irregularly dehiscent berry, ripening in the water; leaves with a basal sinus. Subfam. NYMPHAEOIDEAE.
- B. Perianth wide-spreading, of 4 sepals and 12–32 showy white, pink, blue or yellow petals; carpels sunken in a cup-shaped fleshy receptacle or hypanthium on the outer surface of which petals and stamens are in-

- serted; carpels prolonged upward into slender incurved projections (carpellary styles); seeds arillate. . . . . 1. *Nymphaea*.
- B. Perianth subglobose, of 6 concave yellow (green- or red-tinged) sepals and numerous scale-like or stamen-like "petals" inserted with the numerous stamens on the receptacle beneath the ovary; carpels completely united, the stigmas radiate and sessile on a disc; seeds not arillate. . . . . 2. *Nuphar*.
- A. Carpels free (although in *Nelumbo* embedded in the receptacle); ovules solitary or 1-3 in each carpel; stamens hypogynous, few to many (3-36) and extrorse to slightly introrse, or very numerous and extrorse; fruits leathery or hard, indehiscent; leaves (at least the floating or emersed ones) peltate, lacking a basal sinus.
- C. Perianth of 6-8 segments, the flowers small; receptacle small, with 4-18 free, superior carpels; fruit small, 1-3 seeded; leaves all floating or submersed; plants more or less coated with mucilage. Subfam. CABOMBOIDEAE.
- D. Plants with dissected, opposite submersed leaves and small, peltate floating leaves; perianth petaloid, white or purple; stamens 3-6. . . . . 3. *Cabomba*.
- D. Plants with only undivided, alternate, peltate floating leaves; sepals persistent, the petals dull purple; stamens 18-36; plants heavily coated with mucilage. . . . . 4. *Brasenia*.
- C. Perianth of numerous segments, the flowers large and showy; receptacle large, top-shaped, with the many uniovulate carpels sunken separately in cavities in the upper side, only the stigmas protruding; receptacle enlarging greatly in fruit, the carpels maturing into nuts; stamens very numerous, extrorse, hypogynous; all leaves floating or emergent on strong petioles, centrally peltate, large, glaucous; plants lacking mucilage. Subfam. NELUMBONOIDEAE. . . . . 5. *Nelumbo*.

Subfam. NYMPHAEOIDEAE Casp.

1. *Nymphaea* L. Sp. Pl. 1: 510. 1753, partim, emend. J. E. Smith in Sibth. & Smith, Fl. Graec. Prodr. 1: 360. 1808-9, nom. cons.

Perennial rhizomatous aquatic herbs with floating ovate to orbicular leaves, cleft at the base, the submerged stipulate petiole inserted at the base of the deep sinus; aerial leaves exceptional; submersed leaves often present, filmy and delicate. Flowers solitary, showy, white (to pink), blue or yellow, borne either at the surface of the water or raised above it. Sepals 4, nearly free, one completely outside the others; petals 12-ca. 32, in whorls of 4, 8, 8 (in subg. BRACHYCERAS), or 4, 8, with the arrangement of petals within these not clear (in subg. NYMPHAEA), in this last the petals often transitional to stamens. Stamens numerous, 50-150, introrse, with or without an appendaged connective. Gynoecium of 7-25 carpels, apocarpous or syncarpous, in a circle abutting and adnate to a central prolongation of the floral axis and sunk in the cup-shaped fleshy receptacle (or hypanthium?), upon the outer surface of which petals and stamens are inserted, and produced above it as "carpellary styles;" upper surfaces of carpels stigmatic to form a broad, concave radiate stigma. Ovules numerous, anatropous, pendulous from the sides of the ovary

locules. Fruit an irregularly dehiscent spongy berry, ripening under water; seeds 1–many per carpel, hard, operculate, embedded in mucilage and each surrounded by a bell-shaped floating aril, embryo small, with 2 equal fleshy hemispherical cotyledons, embedded in a thin layer of endosperm and abundant perisperm. (*Castalia* Salisb., nom. rejic.) TYPE SPECIES: *N. alba* L. (From the Greek and Latin, *Nymphaea*, a water-lily, from *Nympha*, goddess of waters, meadows and forests.) — WATER-LILIES, POND-LILIES, WATER-NYMPHS.

A genus of about 35 species of very wide occurrence (lacking in New Zealand and the Pacific slope of North America) in quiet, fresh (rarely brackish) waters. Represented with us by three species in two of the five subgenera.

Subgenus BRACHYCERAS Casp., characterized by carpels free at the sides, thick, fleshy carpellary styles, and appendaged stamens, and including about 12 species of the tropics and subtropics, occurs in our area as *N. elegans* Hook., a pale-violet-flowered species of southern Florida, the West Indies and Mexico. The sepals and 4 outer petals persist, becoming turgid in fruit.

Subgenus NYMPHAEA (Subg. *Castalia* DC.) characterized by carpels united at the sides, ligulate carpellary styles, obscurely veined sepals, and outer stamens with petaloid filaments, includes about 7 species, all of the northern hemisphere. In our area the subgenus occurs as the yellow-flowered *N. mexicana* Zuccarini (*N. flava* Leitner),  $2n = 56$ , of Florida, southern Louisiana, Texas, and Mexico, one of the most restricted in range, and the white-flowered *N. odorata* Ait., a quite variable species. This latter occurs both as the typical form and the much larger var. *gigantea* Tricker (*Castalia lekophylla* Small). Some authors also recognize var. *stenopetala* Fern. and var. *minor* Sims. In view of this diversity and the two chromosome levels recorded for this species ( $2n = 56, 84$ ), further critical studies of *N. odorata* are needed. A perhaps parallel case is the complex *N. alba* L., of Europe, in which 84, 105, 112, and 160 chromosomes have been reported.

Flowers of all species are proterogynous. Some are self-fertile, others self-sterile. Our species are all day-flowering; at the latitude of Philadelphia Conard records the flowers of *N. mexicana* as open for each of 2 days from 10–11 A.M. to 3–4 P.M.; those of *N. odorata* open for 3 or 4 days from 6–7 A.M. to 12–1 P.M.; and those of *N. elegans* open from 7–8 A.M. to 12–1 P.M. When receptive, the stigmatic cup is filled with a sweetish, watery liquid. No nectar is secreted (although some species are very fragrant); insects visit the flowers for the abundant pollen.

Numerous hybridizations (particularly within subg. BRACHYCERAS and subg. LOTOS) since about 1850 have produced many showy horticultural plants. Crosses between members of subg. NYMPHAEA have resulted in hardy forms (all sterile) with white, yellow, pink, orange or red flowers. Natural hybrids occur within this subgenus where two or more species grow in the same pond. All attempts to cross species of different subgenera

have failed; within a subgenus interspecific hybrids may be either sterile or fertile. Recorded chromosome numbers range from 28 to 224. The chromosomes of plants used in hybridization work apparently have not been determined. One of the smallest-flowered species (*N. tetragona* Georgi) and one of the largest-flowered (*N. gigantea* Hook.) are both high polyploids ( $2n = 120$  and  $224$ , respectively)!

*Nymphaea mexicana* spreads rapidly by runners and produces on geotropic shoots hibernating bodies or "brood bodies" which consist of a cluster of fleshy roots more or less resembling a "hand" of bananas. Rich in starch, these brood bodies are an important duck food. *Nymphoides aquatica* (Walt.) Kuntze (Gentianaceae) produces similar clusters of fleshy roots at the base of the inflorescence; the two are often confused.

The nomenclatural confusion centering around the application of the name *Nymphaea* to this genus or to that now known as *Nuphar* J. E. Smith has resulted in the conservation of both of these names in the sense in which they are used here.

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2. **Nuphar** J. E. Smith in Sibth. & Smith, Fl. Graec. Prodr. 1: 361. 1808-1809, nom. cons.

Perennial aquatic herbs with stout, creeping rootstocks, emersed, floating or submersed narrowly lanceolate to orbicular entire leaves with a deep sinus at the base; submersed leaves thin and delicate. Sepals usually 6[5-12], the 3 outer greenish to yellowish, the inner yellow, tinged with red or green. "Petals" numerous, linear to oblong, thick, stamen-like or scale-like, bearing a nectary on the outer surface and inserted with the very numerous introrse stamens on the receptacle under the ovary. Gynoecium of 5-23[-30] carpels, resembling that of *Papaver*, with a stigmatic disc, each carpel with a stigmatic ray; ovary multilocular, with numerous ovules on the inner walls. Fruit an ovoid to columnar berry, dehiscing irregularly by the swelling of a gelatinous covering of the seeds; seeds usually ovoid, yellow to brown, opening by a small operculum, lacking an aril. Embryo with 2 fleshy cotyledons. Pollen monocolpate, oblate-sphaeroidal, spiny.  $2n = 34$ . (*Nymphaea* L. partim, emend. Salisb. and *Nymphozanthus* L. C. Rich., nom. rejic.) TYPE SPECIES: *N. luteum* (L.) Sibth. & Smith. (The name from Greek *nouphar*, the flowers of a medicinal plant mentioned by Dioscorides, perhaps *N. luteum*.) — SPATTERDOCK, COW-LILY, YELLOW POND-LILY.

Perhaps 19 species in North America, two in Europe and several poorly known in eastern Asia; probably about 14 in our area, but some of these not well understood. The group is taxonomically difficult, especially from herbarium materials, in which the features of the plants are not well re-

tained. Ecological and ontogenetic variations add to the difficulty. Entire populations need study; specimens should be preserved in liquid and carefully pressed flowers and adequate notes made in the field. Taxonomic characters used in the group include habit; shape and pubescence of leaf-blades; cross-sectional shape of petioles; presence or absence of submersed leaves and their shape; number of sepals and color, shape and size of "petals;" shape of pistil; lobing, rays and color of stigmatic disc; shape and coloration of fruit; and color, size and indument of seeds. Special efforts should be made to press open flowers carefully and to record variation in numbers of stigmatic rays; at least some discs should be pressed separately and longitudinal sections of pistils and fruits are valuable.

All of the chromosome counts made thus far indicate a genus with a uniform chromosome number of  $2n = 34$ . Largely sterile hybrids are known between the European *N. pumilum* and *N. luteum*, between *N. advena* and *N. sagittifolium*, and between *N. variegatum* and *N. microphyllum* (of the northern U. S. and Canada). (This last also exists in a fertile form, *N. × rubrodiscum* Morong.) Where *N. advena* and *N. variegatum* overlap in range (e.g., southern Michigan) intermediate plants are known, but these have not been studied in detail. The existence of hybrids of this kind has led to the treatment of the European and American representatives of the genus as a single variable species with 9 subspecies. Most entities appear to be definite units which maintain themselves both ecologically and geographically, however.

The flowers are proterogynous and are visited by pollen-collecting insects (sweat bees, flies and beetles) which work over the introrse anthers exposed by the recurving of the filaments as anthesis proceeds. The fruit ripens generally below the surface of the water, splitting irregularly, the carpels tending to separate and float as decay of the berry occurs.

As in *Nymphaea*, long known for the occurrence of sclereids in blades and petioles, bizarre stellate sclereids occur at the intersections of vertical diaphragms in the petioles. Both genera have been the subject of numerous anatomical and physiological investigations, a great many of which have dealt with the European *Nuphar luteum* and *Nymphaea alba*.

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Subfam. CABOMBOIDEAE Casp.

3. *Cabomba* Aubl. *Hist. Pl. Guiane Franç.* 1: 321, *t.* 124. 1775.

Strictly aquatic herbs with opposite submersed leaves and sometimes a few alternate floating leaves. Roots adventitious from the nodes. Sub-

mersed leaves petiolate, the blade divided into 5–7 parts at the summit of the petiole, each part divided dichotomously and trichotomously several times into many long, narrow segments. Floating leaves (when present) peltate, small, narrow and tapered to both ends, or narrow and forked [or resembling miniature leaves of *Brasenia*]. Flowers borne singly on long axillary peduncles, the perianth white or purple [or yellow], sepals 3 and petals 3, slightly united near the base. Petals clawed, the blade often auriculate. Stamens 3–6, extrorse, the pollen 1-sulcate. Carpels [1]2–4, free, elongate, with small terminal stigmas; ovules usually 3, one on the adaxial, one on the abaxial suture and one on the wall near either. Fruit indehiscent; seeds 3, pendulous, operculate, covered with elongated processes; embryo as in *Nymphaea*, small. TYPE SPECIES: *C. aquatica* Aubl. (The name presumably a barbaric one.) — FANWORT, WATER-SHIELD.

Seven species of warm and temperate regions of the New World. Two species, *C. caroliniana* Gray ( $2n = 24$ ) and *C. pulcherrima* (Harper) Fassett, in our area. *Cabomba caroliniana*, with yellow-based white petals rounded at the summit, ranges from south-central Texas to southern Florida, northward to Kentucky, southern Michigan and along the Atlantic coast to New York, Connecticut, and southeastern Massachusetts. Often used as an aquarium plant, this species appears to be adventive north of Virginia. *Cabomba pulcherrima*, with purple, emarginate perianth segments, occurs at low altitudes from southwestern South Carolina to southwestern Georgia and adjacent Florida. The terminal divisions of the leaves of both species have spatulate tips.

As an aquarium plant *Cabomba* is most likely to be confused with *Limnophila* (*Ambulia*) *heterophylla* Benth. (Scrophulariaceae), which has sessile ternate leaves with the segments pinnately divided.

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#### 4. *Brasenia* Schreb. Gen. Pl. ed. 8. 1: 372. 1789.

Aquatic herbs with floating, alternate, long-petioled, elliptic, centrally peltate leaves and small, solitary, axillary dull-purplish flowers. Rhizome small, bearing leaves and axillary runners which creep on the surface of mud, root at the nodes, and produce leafy branches and other runners.

Submersed leaves present, at least in seedlings. Submersed parts of plant heavily covered with a mucilaginous jelly. Sepals 3–4, colored within, persistent. Petals 3–4, linear, sessile. Stamens 18–36, the filaments filiform, and anthers slightly introrse; pollen 1-sulcate. Carpels 4–18, free, oblong-ovate, the ovules 2 in each, anatropous, pendulous from the abaxial suture. Fruit clavate, indehiscent, with 1 or 2 small, dull, grayish white, operculate seeds. TYPE SPECIES: *B. Schreberi* Gmel. (Origin of name not explained by Schreber.) — WATER-SHIELD, WATER-TARGET, PURPLE BONNET, PURPLE WEN-DOCK.

A single species widely but sporadically distributed in ponds and slow streams in the West Indies, Mexico and Central America, Florida to Texas, north to Prince Edward Island, southern Quebec, southern Ontario, and Minnesota; also Idaho, California to British Columbia and Alaska; eastern Asia, Australia and Africa.

This curious plant with centrally peltate leaves is clearly linked to *Cabomba* through leaves, floral structures, and pollen morphology. Both plants are sometimes treated as a separate family, the Cabombaceae. Seeds, seedling ontogeny, pollen morphology and embryology, as well as structural features, do not bear out such a segregation, however. It may be noted that in *Brasenia* the mode of seed germination and the early seedling stages are essentially the same as in *Nymphaea* and *Nuphar*. The first leaf is awl-like, the second narrowly oblong with the petiole at the margin at the lower end. Subsequent leaves are eccentrically peltate, then centrally peltate, a total of 6–9 submersed leaves being produced before the first characteristic floating leaves.

The submersed parts of the plant are notable for the extremely heavy covering of mucilaginous jelly, the secretion of numerous ephemeral glandular hairs (found also, but to a lesser degree, in the other genera, with the exception of *Nelumbo*). Specimens should be prepared with waxed paper, for the leaves become quite brittle in drying and adhere firmly to newsprint.

Dianthesis has been reported in *Brasenia* in Japan by Tokura (cf. H. L. Mason, Fl. Marshes Calif. 491. 1957). The proterogynous flowers are raised above the water and are open for the first time from about 6 to 9 A.M., are then drawn into the water to reappear the following morning when the pollen is shed, and finally are withdrawn again. (Cf. dianthesis in *Persea* [Lauraceae]).

In the southern part of our range the plant is evergreen, but at least in the northern United States it produces in autumn winter buds which absciss from the parent plant and overwinter at the bottom of the pond. These reddish, translucent bodies consist of the thickened stem-tip with dwarf leaves with thickened petioles and the characteristic gelatinous covering. Dispersal is effected not only by the winter buds but by the fruiting peduncles which become detached and float.

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## Subfam. NELUMBONOIDEAE Casp.

5. *Nelumbo* Adans. Fam. Pl. 2: 76. 1763.

Aquatic herbs with fibrous roots borne at the nodes of slender horizontal vegetative rhizomes and thickened storage rhizomes, and with large, dimorphic (floating and emersed) peltate leaves and large yellow or pink flowers borne on stout peduncles well above water. Perianth of ca. 14-26 petaloid tepals, the outer 2-5 persistent (and thus calyx-like), the inner caducous in 2-4 days. Stamens ca. 200, with a conspicuous fleshy terminal appendage, extrorse, spirally inserted; pollen tricolpate. Carpels usually 12-28 (9-39), borne singly in cavities in the pithy obconical receptacle, basally attached, flask-shaped, the ovary oblong-cylindric, completely immersed, the style short, neck-like, the stigma circular, centrally depressed; ovule solitary in each carpel, anatropous, pendulous from the top of the locule. Carpels becoming in fruit acorn-like very hard-walled nuts in the greatly enlarged receptacle. Embryo with only a rudimentary primary root, filling the fruit with two large fleshy cotyledons which inclose in a delicate stipule-like sheath a green plumule with two peltate involutely folded leaves and two rudimentary leaves. Seedling floating upon germination; all roots adventitious.  $2n = 16$ . (*Nelumbium* Juss.) TYPE SPECIES: *N. nucifera* Gaertn. (Name derived from the Ceylonese name for *N. nucifera*.) — YELLOW LOTUS, YELLOW NELUMBO, GREAT YELLOW LILY, POND-NUTS, WATER-NUT, WATER-CHINQUAPIN, WONKAPIN, YONKAPIN, YOCKERNUT, DUCK ACORNS, RATTLE-BOX, ALLIGATOR BUTTONS.

Two species, *N. lutea* (Willd.) Pers. (West Indies, Central America, Florida to Texas, and locally northward to southern New England, New York, southern Ontario, Minnesota and Iowa) and *N. nucifera* Gaertn. (China to Australia, India and Persia and introduced and established

locally through cultivation in the United States). The former species has sulfur-yellow to white flowers and nearly spherical fruits, the latter pink to white flowers and somewhat larger ellipsoidal fruits.

*Nelumbo lutea* is one of our showiest and most interesting native plants. The greatly enlarged top-shaped receptacle with numerous separate carpels is a unique dispersal mechanism. The petals fall after 2–4 days leaving the

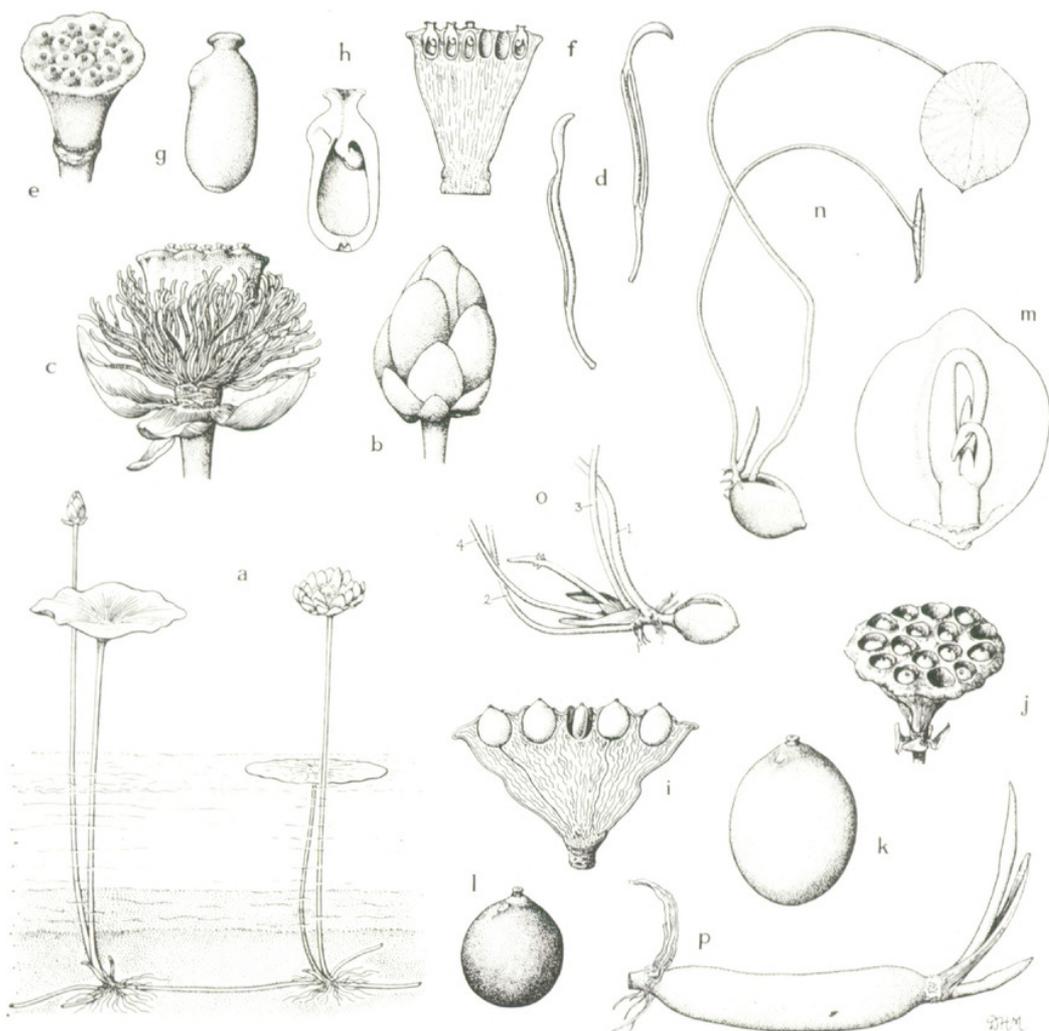


FIG. 1. *Nelumbo*. a–p, *N. lutea*: a, habit,  $\times 1/20$ ; b, flower-bud,  $\times 1/4$ ; c, flower with petals removed, sepals persistent,  $\times 1/2$ ; d, stamens — note extrorse dehiscence, appendages,  $\times 1$ ; e, receptacle at anthesis, the stigmas of carpels protruding,  $\times 1/2$ ; f, receptacle and carpels, vertical section,  $\times 1/2$ ; g, carpel at anthesis,  $\times 2$ ; h, carpel, vertical section, with pendulous anatropous ovule,  $\times 2$ ; i, receptacle with nearly mature green fruit, vertical section,  $\times 1/4$ ; j, dry receptacle with mature fruit,  $\times 1/4$ ; k, green fruit at maximum size,  $\times 1$ ; l, mature fruit, the ovary wall sclerified,  $\times 1$ ; m, embryo from mature but green fruit, one cotyledon removed — note absence of hypocotyl and radicle,  $\times 2$ ; n, seedling with two leaves — note eccentric peltation, involute veneration, adventitious roots,  $\times 1/2$ ; o, seedling with four leaves (only bases of petioles numbered in sequence shown), the fruit coat removed — note distribution of roots, beginning of rhizome,  $\times 1/2$ ; p, tuber (a single swollen internode) with terminal bud and leaf-bud to right,  $\times 1/4$ ; f, i, semi-diagrammatic.

outermost 4-5 tepals which persist into fruit. Within a few days the peduncle bends just below the receptacle, tilting it first to about 45 degrees and later to an almost horizontal position. As the fruits near maturity the receptacle is returned to an upright position, but later is bent downward through 180 degrees. The dry receptacle breaks off, falls into the water and floats with the cavities downward. The individual fruits shrink greatly ( $\frac{1}{2}$ - $\frac{2}{3}$  their volume) in ripening and the ovary wall becomes very hard and impermeable. Germination of fully ripened fruit may thus be greatly delayed. (*Nelumbo* seeds are the longest lived of any known; roughly 1000-year-old seeds of *N. nucifera* from peat beds in the Pulantien basin of southern Manchuria have germinated consistently.) The fruits strongly resemble those of the chinquapin, *Castanea pumila*, in appearance and the very edible cotyledons (the green plumule is bitter) taste much like those of the same plant.

The plant grows best in organic soil in water up to 6(8) feet deep and spreads as much as 50 feet radially each year by slender runners with internodes up to 5 feet long, the longest of any plant in our flora. It may thus under favorable conditions cover acres crowding out other aquatic vegetation and becoming a pest. The roots are entirely adventitious in 6 groups at the nodes, where lateral branching also occurs. In autumn one or two nodes at the growing tip develop into enlarged banana-like tubers 8-28 cm. long, the overwintering structures from which growth proceeds the following spring. The tubers of both species are highly edible: *N. lutea* was planted by the American Indians for both seeds and tubers and *N. nucifera* is widely cultivated in Asia for the same items.

Although a unique plant, *Nelumbo* appears to be related to the other Nymphaeaceae, differing from them primarily in the seed-dispersal mechanism, the more fully developed embryo (an enlarged and somewhat more specialized version of that of *Nymphaea* and *Nuphar*), the elimination of all submersed leaves, the more completely peltate leaves, and the tricolpate pollen. It is notable that in the leaves there are usually about 25 main veins, all but one of which branch dichotomously, this last being simple. Seedling leaves are apiculate at the end of the simple vein and are eccentrically peltate in the opposite direction, indications of the derived and specialized nature of the centrally peltate leaves which have proceeded to an evolutionary level beyond *Brasenia* (q.v.). Leaf vernation is involute as in the other genera. *Nelumbo* is placed by some in a separate family (Nelumbonaceae Dumort., 1829; Nelumbiaceae Lindl., 1836), or even in a separate order, but it seems better for the present to retain the genus in the Nymphaeaceae in the status accorded it by Caspary.

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#### CERATOPHYLLACEAE (HORNWORT FAMILY)

The family includes only a single small genus, *Ceratophyllum* L., of nearly cosmopolitan distribution, the plants growing entirely submerged in quiet, fresh waters. The group is easily recognized by the rather brittle and rough, whorled, dichotomously dissected leaves, the minute imperfect flowers, each solitary in the axil of one leaf of a whorl, the equally solitary branching, and the complete lack of roots.

*Ceratophyllum* was first placed near the Nymphaeaceae in 1837 by Asa Gray, largely on the basis of comparisons drawn with *Nelumbo* [itself highly specialized but mostly along other lines], the chief points being the simple, one-seeded ovaries, the pendulous orthotropous, exalbuminous seeds, the large and fleshy cotyledons, and the unusually developed plumule. Unfortunately, the most strongly emphasized evidence, the ovule, is not orthotropous in *Nelumbo*, *Brasenia* and *Cabomba*, but anatropous. However, Strasburger and others have maintained the same position for the Ceratophyllaceae, citing the convex receptacle, the numerous extrorse stamens, the superior ovary with the single pendulous parietal ovule, and the details of embryogeny (which seem to agree well with Nymphaeaceae). It may be noted that the stamens of *Ceratophyllum* seem to be spirally (not cyclicly) arranged, that the orthotropous ovule has but a single integument (instead of the two usual in Ranales) and that the pollen has lost all features which might be used as an indication of the relationships of the genus

#### 1. *Ceratophyllum* L. Sp. Pl. 2: 922. 1753; Gen. Pl. ed. 5. 428. 1754.

Aquatic herbs with whorled dissected leaves; monoecious, with minute, sessile, axillary flowers lacking a perianth but with an 8-12-cleft involucre

in place of a calyx. Plants entirely submerged, branching, a single branch produced at a node. Roots lacking (even in the embryo) but leafy branches sometimes modified as "rhizoids." Leaves 6–10 at a node, rather rigid, 1–4-dichotomously dissected, with two rows of minute teeth along the upper side of the ultimate segments, tipped by two bristles, usually with a purplish hair of tannin-filled cells between. Flowers usually solitary in the axil of one leaf of a whorl. Staminate flowers with an involucre of 8–12 segments, slightly united at the base, each tipped with a purplish hair, with a convex receptacle and 10–20 extrorse, 4-locular stamens with large, sessile, often 2-cuspidate anthers; pollen large, nearly smooth, thin-walled, acolpate. Pistillate flower of a solitary pistil with involucre, the style filiform, oblique, the stigma a lateral pocket, the ovary ovate, 1-locular, with a single orthotropous 1-integumented suspended ovule; embryo sac development normal (*Polygonum* type). Fruit an achene tipped by the indurated persistent style [or its base] and often with additional basal or marginal spines. Seeds filling the fruit, nucellar tissue forming the only seed coat, with a large embryo with 2 ovate cotyledons, a well-developed plumule of several nodes with simple or forked leaves, and lacking a hypocotyl and radicle; endosperm scant or lacking. TYPE SPECIES: *C. demersum* L. (The name from Greek, *keras*, a horn, and *phyllon*, leaf, in reference to the stiff, divided leaves.) — HORNWORT, COONTAIL.

Six or more species, three of which occur in our area: *C. demersum* L., of very wide distribution, from Canada to Argentina and also in Europe, Asia, Africa, and perhaps Australia; *C. echinatum* Gray, distributed from Quebec to Michigan and south to Florida and eastern Mexico; and *C. floridanum* Fassett, known only from the Florida Keys.

The genus is almost completely adapted to an aquatic life. The plants lack cuticle, stomata and roots (even in the embryo, the anchoring function being taken over by leafy branches which grow into the mud); both xylem and phloem are reduced, mechanical cells are lacking, and about a third of the plant is occupied by air spaces. The greatly reduced flowers are borne abundantly and pollination is entirely subaquatic. Fruits develop only if water temperatures are maintained above 80°F (cf. Guppy), a phenomenon which may account for the scarcity of fruiting collections in herbaria. The plants may vegetate indefinitely, however, even under ice in winter; vegetative reproduction occurs by fragmentation.

Species of *Ceratophyllum* are highly variable and are difficult taxonomically. The principal taxonomic characters used are those of fruits and leaves, the fruits being unarmed, or with either long or short spines at the base and the apex or along the margin, the leaves varying in the amount of forking, width of segments, degree of tapering at base, coarseness and distribution of the teeth. The female flowers are so reduced as to be useless in classification, but stamens need further examination, particularly in connection with their terminal cusps and hairs. Chromosome numbers reported from European plants include 24 in *C. demersum* and 40 and 72 in *C. submersum* L. These, combined with the wide range of morphological

characteristics, suggest that much more needs to be done toward an understanding of the biosystematics of the genus.

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