

THE NAJADACEAE IN THE SOUTHEASTERN UNITED STATES ¹

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NAJADACEAE A. L. de Jussieu, Gen. Pl. 18. 1789, "Naiades," nom. cons.
(NAIAD FAMILY)

A monogeneric family of herbaceous submersed monocotyledons distinguished by subopposite serrulate leaves; axillary imperfect flowers, the staminate each consisting of one stamen and the ovulate each consisting of a single 1-ovuled gynoecium with a solitary, basal, anatropous ovule.

The Najadaceae are of somewhat uncertain taxonomic position. Some workers, e.g., Cronquist and Lawrence, have considered the family to be closely related to the Potamogetonaceae. Miki, however, suggested that it may be derived from the Hydrocharitaceae. The Najadaceae have been considered to consist of one genus, *Najas*, by Cronquist and Lawrence; four genera, *Najas*, *Potamogeton*, *Ruppia*, and *Zannichellia*, by Fassett and Eyles & Robertson; and five genera, *Najas*, *Potamogeton*, *Ruppia*, *Zannichellia*, and *Zostera*, by Gleason (in Gleason & Cronquist). After a recent study of the floral development of *Najas flexilis*, Posluszny & Sattler stated that it is advisable to keep the Najadaceae as a monogeneric family and to place it along with the Potamogetonaceae and Zannichelliaceae in one order. Their views are followed here.

1. *Najas* Linnaeus, Sp. Pl. 2: 1015. 1753; Gen. Pl. ed. 5. 445. 1754.

Plants glabrous, herbaceous, annual or rarely perennial, growing submersed in fresh or brackish waters, monoecious or dioecious. Stems slender, much branched, rooting at the lower nodes, sometimes armed with spinulose teeth on the internodes. Leaves subopposite or appearing whorled due to reduced internode length, sessile, each divided into blade and sheath; blade linear and flattened, 1-nerved, sometimes abaxially toothed on the

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The illustration was drawn by Karen S. Velmure under my direction from material collected by Ronald L. Stuckey in Ohio and by C. Barre Hellquist in Massachusetts.

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midrib, the margins usually serrulate with 5–100 teeth per side, the apex acute to acuminate, with 1–3 teeth per side, the teeth multicellular, formed by layers of cells decreasing in cell number distally and terminated by a large, sharp-tipped cell, or unicellular; sheaths variously shaped, each enclosing a pair of tiny hyaline scales, the margins usually spiny-toothed with 1–8[–15] teeth per side. Flowers imperfect, axillary, sessile or short pedunculate, solitary or clustered; perianth absent. Staminate flowers subtended by one or two clear to pale purple membranaceous envelopes [these rarely absent], each flower consisting of a single stamen; pedicel at first short, elongating at anthesis, pushing the anther through the outer envelope; anther sessile, 1- or 4-locular, dehiscing irregularly; pollen 3-celled, globose or ellipsoid, densely filled with starch, monocolpate, the wall with shallow reticulations, thin, not divided into exine and intine. Ovulate flowers sessile, an envelope absent [rarely present]; gynoecium ending in a short style with 3 or 4 branches; ovary 1-loculate, the wall delicate, 2 cell layers thick; ovule solitary, basal, anatropous, 2-integumented. Fruit 1-seeded, the gynoeceal wall 2 cells thick, closely enveloping the seed, which is released by decay of the wall. Seeds fusiform, the seed coat hard, brittle, 3- or several-cell-layered, areolate; areolae formed by two outer cell layers of the seed coat, irregularly arranged or in 15–40 [–50] rows, variously rectangularly shaped, the end walls often raised giving the seed coat a papillose appearance; endosperm absent; embryo elongate, without lateral enlargement of the cotyledon. TYPE SPECIES: *N. marina* L. (Name Greek and Latin, *Naias*, a water-nymph, a Naiad.) — BUSHY PONDWEED, NAIAD, WATER-NYMPH.

A nearly cosmopolitan genus of perhaps 40 species, divided into 2 subgenera, NAJAS, with only one species, and CAULINIA. Rendle divided subgenus CAULINIA into four sections based upon the presence or absence of the floral envelopes. In an investigation of the Asiatic and Malaysian species, De Wilde determined the presence of the envelopes to be too inconsistent to distinguish sections. The view of De Wilde is here accepted, and no sections are recognized. The genus is represented in the United States by eight species, at least some of which are widely distributed; six of them occur in our area.

Subgenus NAJAS (plants dioecious, seed coat several cell layers thick, internodes and abaxial surface of leaf blade spiny), represented by *N. marina*, is widespread in warm areas of the world, from Europe and Africa east to Japan, the Malaysian region, and Australia, and in North, Central, and South America. *Najas marina* L. (including *N. gracilis* (Morong) Small, *N. major* All.), spiny naiad, $2n = 12$, is a variable species occurring in the United States from North and South Dakota, Minnesota, Wisconsin, Michigan, Ohio, and New York, to Florida, Texas, Arizona, Utah, Nevada, and California. The species is found mostly in brackish or highly alkaline waters. It has been divided into numerous varieties based on minor differences in the size of leaves and the number of spines on the internodes. Such variations usually can be found within single populations and,

therefore, do not warrant taxonomic recognition. Viinikka, however, has observed two cytological races of the species, one with B chromosomes and one lacking them. He has indicated (pers. comm.) that these races correspond to differences in morphology. Specimens with large seeds and leaves (no size given) invariably lack accessory chromosomes, whereas plants with smaller seeds and leaves possess B chromosomes. He has not yet decided on appropriate categories for these apparent entities.

Subgenus *CAULINIA* (Willd.) Ascherson (Fl. Prov. Brandenburg 1: 670. 1864) (plants monoecious, testa three cell layers thick, internodes and abaxial surface of leaf blade spineless) consists of about 40 species, most of which occur in the Eastern Hemisphere. Five species are represented in our area. *Najas ancistrocarpa* Magnus (including *N. conferta* of authors) has a disjunct distribution in southeastern Asia and in the southeastern United States, where it is known from Leon and Santa Rosa counties, Florida, and from Decatur County, Georgia. The species is easily recognized by its crescent-shaped seeds with areolae longer than broad. *Najas Wrightiana* A. Br. is restricted in the United States to Collier County, Florida. It is easily separated from other species of *Najas* by its short (1–1.5 mm.), erect seeds with 5-angled areolae, the large teeth scattered along the margins of quite narrow leaves, and its bushy appearance produced by axillary tufts of leaves and very short internodes.

Najas minor All., $2n = 12$, is an Old World species that apparently invaded North America about 50 years ago. According to Meriläinen, it thrives in eutrophic waters and can tolerate pollution. With the gradual eutrophication of the waters of the eastern United States, the plant has spread from New York to Illinois, south to Florida, Mississippi, and Arkansas. *Najas minor* can be determined easily by its mature recurved leaves and by its seeds with areolae broader than long. The seeds are occasionally slightly curved but not as much as those of *N. ancistrocarpa*. *Najas minor* displays a seasonal dimorphism. Wentz & Stuckey have shown that young individuals have leaves erect to ascending, and not until late in the growing season does the characteristic recurved pattern develop. *Najas gracilima* (A. Br.) Magnus occurs in the United States from New Hampshire to Alabama, west to Minnesota and Missouri, and in California. The species can be distinguished by the style arising excentrically at the apex of the gynoeceal wall. Apparently intolerant of pollution, the plant has become exceedingly rare in some areas of the eastern United States.

Najas guadalupensis (Sprengel) Magnus is widely distributed throughout the country, except in the Rocky Mountain States. It can be distinguished from other North American species by seeds 1.2–2.5 mm. long, with (4- or) 6-angled areolae, and leaves with small, unicellular teeth. It is one of the many highly variable aquatic species, and has, therefore, been divided into several specific and infraspecific taxa. Clausen (1936), Oostroom, and Wentz & Haynes have discussed variability within this species and have suggested that it should probably be treated as several closely related taxa. Haynes & Wentz later recognized two varieties, both of which occur within our area. Varietas *guadalupensis* occurs throughout

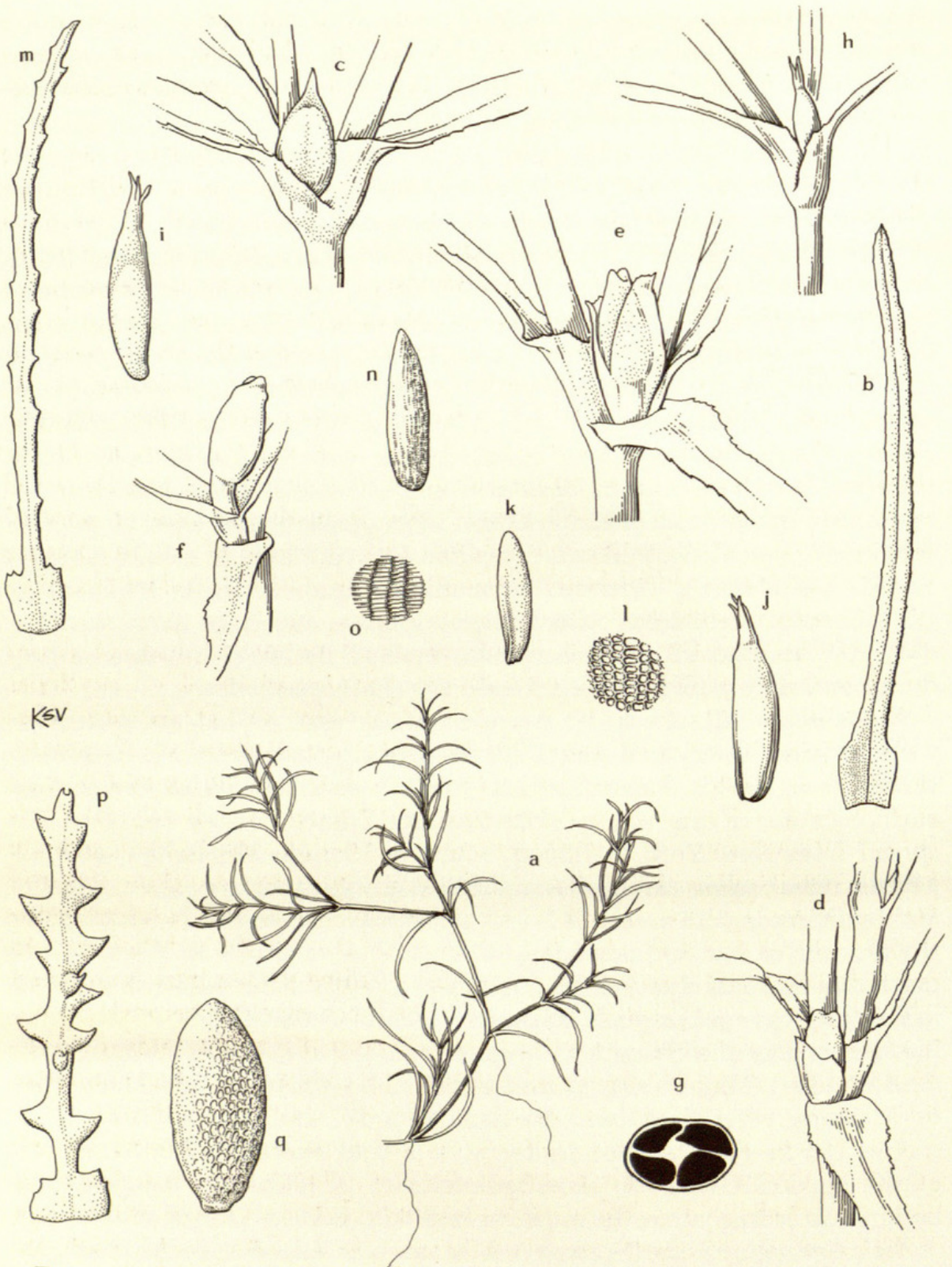


FIGURE 1. *Najas*. a-l, *N. guadalupensis*: a, habit of plant $\times \frac{1}{2}$; b, leaf, adaxial side, $\times 5$; c, young staminate flower, the outer envelope intact, $\times 6$; d, later stage, the outer envelope ruptured, stamen inclosed in inner envelope (two-lobed at tip), $\times 6$; e, staminate flower at anthesis, pollen shed through opening between two lobes of inner envelope, $\times 6$; f, still later stage, the outer envelope pulled back to show pedicel of staminate flower, $\times 6$; g, diagrammatic cross section of anther to show four locules, $\times 12$; h, carpellate flower, $\times 6$; i, carpellate flower, ovule showing through ovary wall, $\times 10$; j, fruit, $\times 10$; k, seed, $\times 10$; l, detail of seed coat, showing areolae, $\times 25$. m-o, *N. minor*: m, leaf, adaxial side, $\times 5$; n, seed, $\times 10$; o, detail of seed coat, $\times 25$. p, q, *N. marina*: p, leaf, abaxial side, $\times 3$; q, seed, $\times 10$.

the southeastern United States, while var. *floridana* Haynes & Wentz is restricted to Florida, southeastern Georgia, and Alabama. The varieties can be distinguished by the length of the seeds (var. *guadalupensis* 1.2–1.5 mm., and var. *floridana* 1.6–2.2 mm.).

The characters of the seeds of *Najas* are the most important ones for distinguishing the various taxa of the genus. Among the most distinctive characters are the arrangement of the areolae, either irregular (*N. marina*) or in rows (all other North American species of *Najas*); the shape of the areolae, longer than broad (*N. ancistrocarpa*, *N. marina*, *N. gracillima*) or broader than long (*N. minor*, *N. guadalupensis*), and 5-angled (*N. Wrightiana*); the length of the seeds; and the shape of the seeds, crescent-shaped (*N. ancistrocarpa*), fusiform (*N. gracillima*, *N. guadalupensis*, *N. Wrightiana*), slightly recurved (*N. minor*), or ovoid (*N. marina*). Of lesser importance for identification are the teeth along the margins of the leaf blades. These may be inconspicuous and composed of one large cell or conspicuous and formed of layers of cells decreasing in number outward and terminated by a large, sharp-tipped cell. Because of the importance of the seeds for the identification of *Najas*, care should be taken to collect seed-bearing specimens.

Sculthorpe has provided a review of the floral morphology of *Najas* which is controversial. The origin and significance of the floral envelopes have been of particular concern (see Miki, Rendle, and De Wilde). Posluszny & Sattler recently examined the floral development of *N. flexilis*, and their interpretations are presented here. Both staminate and ovulate flowers are produced terminally on an axillary shoot and, shortly after initiation, produce girdling primordia about their peripheries. In the staminate flower, the girdling primordium develops into an outer envelope two cell layers thick. Toward maturity, the distal portion of the outer envelope becomes elongated and stylelike, often with two or three branches. As the outer envelope is developing, a second girdling primordium is initiated which develops into the inner envelope. The inner envelope becomes closely appressed to the developing anther and is eventually almost indistinguishable from it except for its slightly protruding bilobed tip. The staminate flower develops a short stalk which usually elongates at anthesis.

The primordium of the ovulate flower develops into a two-cell-layered gynoecial wall which, near maturity, becomes elongated into a three- or four-lobed style. The floral apex is transformed into an ovule primordium as the apex is overgrown by the gynoecial wall. Two integuments are initiated, after which the ovule turns down, eventually becoming anatropous.

Posluszny & Sattler conclude that, since the ovule primordium is initiated in an exactly terminal position (a transformed floral apex) and not laterally on the gynoecial appendage, the carpel concept cannot be applied to the genus. According to them, the gynoecium of *Najas* is clearly acarpellate. They do not speculate whether this condition is primitive or derived.

Chase examined eight species of *Najas* and found that in all except *N.*

marina the seed coat is composed of three layers, with the inner layer somewhat membranaceous and compressed and the middle and outer layers quite stony. The outer layer, however, was observed to slough partly away in many species, this resulting in the pitting of the areolae of the testa. The outer layer does not slough away in species with a smooth seed coat, whereas some sloughing occurs in those with a rough one.

The genus is economically important in two respects. As a source of food for waterfowl, Martin & Uhler rank it eighth in importance in the United States and Canada, and Gaevskaya lists 18 species of animals that have been known to feed on it. In addition, populations of *Najas* have often been abundant enough in the southeastern United States to be regarded as weeds warranting the use of various methods of control.

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