A GENERIC TREATMENT OF ALISMATIDAE IN THE NEOTROPICS WITH SPECIAL REFERENCE TO BRAZIL (*)

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RESUMO

A subclasse Alismatidae nos neotrópicos é composta de nove famílias com 22 gêneros das quais nove ocorrem na bacia amazônica e cinco no Brasil extra-amazônico. Apenas duas famílias não estão presentes no Brasil e mais duas ausentes da Amazônia brasileira. Este trabalho apresenta descrições detalhadas das famílias e gêneros, além de comentários sobre distribuição geográfica dos gêneros. As famílias estão organizadas na sequência sistemática que nós aceitamos. Os gêneros de cada família estão organizados em ordem alfabética sem significado sistemático. Fornecemos desenhos de pelo menos um gênero para cada família. Referências importantes -- tais como revisões genéricas, levantamentos da literatura, ou monografias de áreas neotropicais -- estão relacionadas no início de cada tratamento a nível de família. As excelentes coleções do Projeto Flora Amazônica foram de importância decisiva para nosso trabalho; sem elas não poderíamos fazer um tratamento genérico completo para toda a região neotrópica.

The Alismatidae in the Neotropics consists of nine families with 22 genera, of which nine occur in the Amazonian drainage and five genera occur in extra-Amazonian Brazil. Only two families are not present in Brazil and two additional in Amazonian Brazil. The present study was undertaken as a part of the authors' work with Brazilian and other neotropical plants. The excellent collections from the Projeto Flora expeditions to the Amazon region have been of decisive importance, without which a complete generic treatment for the whole region would not have been possible.

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In the treatment that follows, detailed descriptions are presented for families and genera, as well as comments on generic distributions. The families are arranged in the systematic sequence we accept. The genera within the families are arranged alphabetically, with no attempt to illustrate relationships. At least one genus per family is illustrated, and, for genera that occur in Amazonia, at least one species is illustrated. Important references, such as generic revisions, literature surveys, or neotropical treatments, are given at the beginning of each family treatment. All cited references are included in the References section.

The subclass consists mostly of aquatic or subaquatic plants, which nearly all have trinucleate pollen and lack endosperm in the mature seed. The development of the young endosperm mostly is of the helobial pattern.

The subclass is usually considered to be among the most primitive group of monocots (Cronquist 1968) and has been considered to closely approach the Nymphaeales and possibly to have originated from some Nymphaeales ancestor. Dahlgren and Clifford (1982), however, question this closeness and suggest that the "primitive characters" of the Alismatidae which give the impression of similarity to Nymphaeales actually are derived and result from a parallel adaptation to the aquatic habitat.

The Alismatidae as treated here has been widely accepted for some time. It has been recognized as the order Helobiae by Lawrence (1950), the super order Alismatiflorae by Dahlgren and Clifford (1982), and the subclass Alismatidae by Cronquist (1968, 1981). Although our treatment of the Alismatidae does not follow any one classification system, we agree with Dahlgren and Clifford that the Triuridales should be omitted from the taxon. The order Triuridales differs from the Alismatidae by having achlorophyllous terrestrial saprophytes with endospermous seeds, absence of parietal cells, and periclinal division in the epidermis of the nucellus. Cronquist (1968) states: "Any phyletic connection between the Triuridales and the other orders of the Alismatidae must presumably antedate the loss of endosperm by the other orders". This seems to imply that although there is a relationship between the Triuridales and the orders of the Alismatidae, there are enough differences to separate the Triuridales into another taxon. Dahlgren and Clifford (1982) note the order is distantly related to the Alismatidae, but the closeness of the relationship is uncertain.

For the neotropical genera of Alismatidae, the classification of Cronquist (1981) and Dahlgren and Clifford (1982) are remarkably similar. Cronquist differs from Dahlgren and Clifford, in separating the Alismataceae and Limnocharitaceae and separating the Potamogetonaceae and Ruppiaceae. We are herein following Cronquist in separating the Alismataceae and Limnocharitaceae and Dahlgren and Clifford in combining the Potamogetonaceae and Ruppiaceae.
KEY TO FAMILIES OF NEOTROPICAL ALISMATIDAE

1. Ovary compound; flower epigynous..............................................Hydrocharitaceae

1. Ovary simple; flower hypogynous..................................................2

2. Flowers 10-many, arranged along one side of a flattened spadix...........Zosteraceae

2. Flowers 1-many, variously arranged but without a spadix..................3

3. Perianth parts absent or, if present, of similar segments...................4

3. Perianth parts present, separated into sepals and petals....................8

4. Flowers all imperfect........................................................................5

4. Flowers either all perfect or both perfect and imperfect on same plant....7

5. Stigma funnel-shaped; leaves whorled, opposite, and alternate on same plant..................................................Zannichelliaceae

5. Stigma linear; leaves opposite or alternate, but only one arrangement on any one plant...........................................................6

6. Leaves opposite, serrate; seeds areolate.........................................Najadaceae

6. Leaves alternate, entire or possibly with one or two teeth at apex; seeds ridged or smooth but without areolae.........................................Cymodoceaceae

7. Plants emergent; leaves basal.........................................................Juncaginaceae

7. Plants submersed or submersed and floating; leaves cauline..............Potamogetonaceae

8. Ovules several to many; placentation laminar; fruits dehiscent........Lymnocharitaceae

8. Ovules 1-2; placentation basal or marginal; fruits indehiscent............Alismataceae

ALISMATAEAE Ventenat

References: Bogin, C. Revision of the genus Sagittaria (Alismataceae). Mem. New York Bot. Gard. 9: 179-233 (1955). -- Fassett, N.C. Echinodorus in the American tropics. Rhodora 57:133-156, 174-212 (1955). -- Haynes, R.R. Alismataeae. Flora de Veracruz 37:1-20 (1984). -- Holm-Nielsen, L.B. The identity of Alisma boliviana Rusby (Alismataeae). Brittonia 31:276-278 (1979). -- Micheli, M. Alismataeae. In A.&C. DC. Monogr. Phan. 3:29-83 (1881). -- Rataj, K. Revizion of the genus Sagittaria II. Annot. Zool. Bot. 78:1-61 (1972). -- Revizion of the genus Echinodorus Rich. Ceskosl. Akad. Ved. 156 pp., Prague (1975). -- Alismataeae of Brazil. Acta Amazonica 8:1-53 (1978). -- Alismataeae. Flora de Venezuela 11(2):43-84 (1982). -- Rogers, G.K. The genera of Alismataeae in the Southeastern United States. J. Arnold Arbor. 64:383-420 (1983). -- Small, J.K. Alismataeae. North Amer. Fl. 17:43-62 (1909).

A generic treatment ...
Plants herbaceous, with milky juice, monoecious or monoclinous, annuals or perennials, glabrous to stellate pubescent, submersed, floating-leaved, or emergent, of fresh or brackish waters. Roots fibrous, few to many, septate or aseptate, at base of stem or lower nodes. Stems short, erect, corn-like, often with rhizomes, the rhizomes occasionally terminated by tubers, the internodes without teeth, the apices without turions. Leaves basal, sessile or petiolate; petiole terete to triangular, mostly 2 or more times length of blade, with sheathing base, the sheath without auricles; blade linear, lanceolate, ovate to rhomboid, with or without pellucid markings of dots or lines, the margins entire or undulate, the apex obtuse, acute, or acuminate, the base with or without basal lobes, if without basal lobes, then attenuate, if with basal lobes, then truncate, cordate, sagittate, or hastate, the venation reticulate, with parallel primary veins from base of blade to apex and reticulate secondary veins. Inflorescences scapose, mostly erect, rarely floating, verticillate, forming racemes or the verticels branching to form panicles, rarely umbellate, without a subtending spathe, bracteolate, the bracts whorled, linear, delicate to coarse, smooth to papillose, entire, obtuse to acute. Flowers hypogynous, perfect or imperfect, subsessile to long pedicellate; perianth actinomorphic; of 6 separate segments in 2 series, the outer 3 sepal-like, green, persistent, erect and enclosing flower and fruit or spreading to reflexed, the inner 3 petal-like, delicate, deciduous, androecium of 6, 9, or many free stamens, if 6 then in pairs alternating with the petals, if 9 then in 2 whorls with outer whorl of 6 and inner whorl of 3, if many then spiralling, the anthers 2-loculed, elongate, basifixed or versatile, dehiscing by longitudinal slits, the pollen 5-aperturate, globose, separate; gynoecium of 6-many free carpels, the carpels in 1 whorl or spiralled, 1-loculed, each with 1 or rarely 2 anatropous ovules, the placenta basal, the styles terminal or lateral, the stigma linear. Fruits achenes or rarely follicles, mostly numerous. Seeds 1-few, U-shaped; endosperm helobial in development, absent in mature seeds. Type genus: *Alisma* Linnaeus.

A family of 10 genera of which *Echinodorus* and *Sagittaria* occur in the neotropics and in Amazonia. *Echinodorus* has a distributional and possible evolutionary center in the neotropics.

**Key to the Genera**

1. Flowers all perfect; fruits terete, mostly ribbed with glands between the ribs......

................................................................. *Echinodorus*

1. Flowers, at least the lower, imperfect; fruits flattened, without ribs, often with one curved wing and one or two glands................................. *Sagittaria*

**Echinodorus** Rich. ex Engelm. in A. Gray

*Manual* 460 (1848). Type: *Echinodorus rostratus* (Nutt.) Engelm. (=*Alisma rostrata* Nutt.).



Haynes & Holm-Nielsen
Fig. 1. A-F. Echinodorus paniculatus. A, habit; B, enlargement of leaf section showing no pellucid markings; C, young inflorescence; D, flower; E, achene without any facial glands; F, seed. G-L. Echinodorus bracteatus var. bracteatus. G, habit; H, enlargement of leaf section showing short pellucid lines; I, top of inflorescence showing bracts; J, flower; K, achene with one facial gland; L, seed. (A-D from Holm-Nielsen, et al. 2760, AAU; E-F from Holm-Nielsen, et al. 22959, AAU; G-H, K-L from Holm-Nielsen, et al. 7154, AAU; I from Holm-Nielsen, et al. 22975, AAU; J from Holm-Nielsen, et al. 22976, AAU.)
Helianthium (Engelm. ex J.D. Hook.) J.G. Smith in Britton, Manual Fl. N. States, ed. 2, 54 (1905). Type: Helianthium tenellum (Mart.) Britton ex J.G. Smith. (=Alisma tenellum Mart.)

Plants monochinuous, annual or perennial, emersed, in fresh water. Roots aseptate. Leaves erect, emersed or submersed; emersed leaves petiolate, the petiole mostly triangular, rarely terete, often with aerenchymous tissue, the blade linear to broadly ovate, the pellucid markings present as dots or lines, or absent, the margins entire or undulate, the apex acute to acuminate, the base truncate to cordate; submersed leaves mostly sessile phylloides, the blades mostly linear to rarely ovate, the pellucid markings present as dots or lines, or absent, the margins entire or undulate, the apex acute to acuminate. Inflorescence erect, emersed, racemose or paniculate, rarely umbelliform, the bracts coarse, smooth to papillose, obtuse to acute. Flowers perfect, subsessile to pedicellate; pedicels often elongating after anthesis, ascending to recurved; sepals herbaceous to coriaceous, reflexed to spreading; petals white, larger than sepals; androecium of 9-many stamens, the anthers versatile or basifixed, the filaments glabrous; gynoecium of many carpels, the carpels spiralled, 1-ovuled, the styles terminal or lateral, persistent. Achenes terete, often longitudinally costate and glandular.

A predominantly neotropical genus of approximately 50 species. All but one species occurs in the neotropics, although two others occur in temperate and subtemperate North America. Rataj's treatment (1978) of the genus for Brazil included 38 species. Fifteen of these occur in Amazonia.

The genus has been divided into two subgenera, Echinodorus and Helianthium, by Fassett (1955). The subgenera can be separated by subgenus Echinodorus having versatile anthers and many more than 20 carpels, whereas subgenus Helianthium has basifixed anthers and 20 or fewer carpels.

Characteristics other than anther attachment and carpel number that are important in the taxonomy of Echinodorus are stamen number, fruit beak length and gland number and arrangement, leaf shape, and presence and shape of pellucid markings in the leaf. When viewing a leaf for pellucid markings, it is best to place the specimen in front of a strong desk lamp and examine the leaves with a hand lens. This usually can be done with light passing through the herbarium sheet, if the light intensity is strong enough and the sheet is not too thick. If pellucid markings are present, they will appear as light areas in the leaf tissue (see Fig. 1, B and H) which form dots, lines or an interconnecting network of lines separate from the venation pattern.

_Sagittaria_ Linnaeus

Sp. Pl. 2:993 (1753). Gen. Pl. ed. 5. 429 (1754). Type: _Sagittaria sagittifolia_ L.

_Lophotocarpus_ Th. Durand, Index Gen. Phan. x (1888). Type: _Lophotocarpus_ guy-
Fig. 2. A-B. Sagittaria latifolia. A, habit; B, achene. C-E. Sagittaria guyanensis C, habit; D, transection of flower showing perfect flower; E, achene. F. Sagittaria sprucei. F, habit indicating the inflated scape with sessile to subses-sile flowers. (A from Holm-Nielsen & Jeppesen 106, AAU; B from Haynes 7093, UNA, collected in Guatemala; C-D from Haynes 8630, UNA; E from Haynes 8592, UNA; F from Asplund 14019, S.)

A generic treatment ...
Plants monoecious or rarely dioecious, perennial or rarely annual, submersed, floating-leaved, or emersed in fresh or brackish waters. Roots septate. Stems often with rhizomes, the rhizomes occasionally terminated by tubers, the tubers brown, smooth. Leaves submersed, floating, or emersed, entire, sessile or petiolate, the petioles terete to triangular, the blades present or absent, with or without basal lobes, without pellucid markings. Inflorescence erect, emersed or floating, rarely submersed, racemose or paniculate, rarely umbelliform, the bracts coarse or delicate, smooth to papillose, obtuse to acute, the staminate flowers above, the carpellate below. Flowers mostly imperfect, rarely the lower perfect, pedicellate; pedicels elongating after anthesis, ascending to recurved; sepals herbaceous to coriaceous, often sculptured, reflexed in staminate flowers, reflexed to appressed in carpellate flowers; petals white or rarely with a pink spot or tinge; androecium of 7-many stamens, the filaments linear to dilated, glabrous to pubescent, the anthers basifixed, linear to orbicular; gynoecium of many carpels, the carpels spirally arranged, 1-ovuled. Achenes compressed, numerous, often laterally winged, glandular, dorsally with a conspicuous wing.

A predominantly Western Hemisphere genus of approximately 20 species. Bogin (1955) combined Sagittaria and Lophotocarpus, recognizing 2 subgenera, subgenus Sagittaria and subgenus Lophotocarpus. The two subgenera can be separated by subgenus Sagittaria having ascending to reflexed sepals and mostly spreading to ascending pedicels in fruit, and all flowers imperfect, whereas subgenus Lophotocarpus has appressed sepals and recurved pedicels in fruit, and the flowers perfect.

Approximately 12 species occur in the neotropics, Rataj (1978) recognized seven species from Brazil. Four species, Sagittaria guyanensis, S. sprucei, S. rhombifolia and S. lancifolia, occur in Amazonia.

LIMNOCHARITACEAE Takhtajan ex Cronquist

References: Buchenau, F. Butomaceae. In Engl., Pflanzenr. IV. 16:1-12 (1906).
-- Micheli, M. Butomaceae. In A. & C. de Candolle, Monogr. Phan. 3:84-93 (1881).
-- Pederson, T.M. New species of Hydrocleis, Scirpus, and Stellaria. Bot. Tidsskr. 57: 38-46 (1961). -- Richard, M.L.C. Proposition d'une nouvelle famille de plantes: Les Butomées (Butomaceae). Mêm. Mus. Nat. Hist. Paris 1:364-374 (1815). -- Seubert, M. Butomaceae. In Martius, Fl. Bras. 3(1):113-118 (1847).

Plants herbaceous, with milky juice, monoclinous, perennials, glabrous, growing emergent, submersed, or floating-leaved, in fresh waters. Roots fibrous, few to many, aseptate, from a stout rhizome or stolon. Stems fleshy, erect, unbranched, the internodes without spinulose teeth, the tips without turions or tubers. Leaves basal or alternate, petiolate; petioles terete to triangular, mostly 3 or more times length of blade, with sheathing base, the sheath without auricles, the infravaginal scales ab-
sent; blades orbicular to lanceolate, without pellucid markings, the margins entire, the apex obtuse to round-acute, the base cordate to attenuate, the venation reticulate, with parallel primary veins from base of blade to apex and reticulate secondary veins. Inflorescence scapose, erect to floating, terminal, an involucrate umbel, without subtending spathe, the involucre of few to several bracts, the bracts ovate, membranous, acuminate. Flowers hypogynous, perfect, pedicellate; perianth actinomorphic, of 6 separate segments in 2 series, the outer 3 sepal-like, persistent, mostly erect and enclosing flower and fruit, the inner 3 petal-like, usually delicate, deciduous, androecium of 6-many stamens, separate, the anthers 2-loculed, basifixed, dehiscing by longitudinal slits, the pollen 3-7 aperturate, globose, separate; gynoecium of 3-many separate or basally coherent carpels, the carpels 1-loculed, each with numerous anatropous ovules, the placentation laminar the styles short or absent, the stigma linear. Fruit a follicle, dehiscing adaxially. Seeds numerous, glandular pubescent or costate, U-shaped; endosperm helobial in development, absent in the mature seed. Type: Limnocharis Humboldt & Bonpland.

A family of three genera, two of which, Limnocharis and Hydrocleys, occur in the neotropics. The family is considered to be among the primitive monocots by the presence of many separate carpels, many stamens, and laminar placentaion. There has been considerable confusion as to the systematic position of the genera here accepted to constitute the Limnocharitaceae. Lawrence (1951) and Hutchinson (1959) have combined these genera with Butomus to form an enlarged family Butomaceae, Dahlgren and Clifford (1982) and Pichon (1946) combined these genera with the Alismataceae leaving the Butomaceae as monotypic with Butomus, and Cronquist (1968) has separated the three families. We are following Cronquist and separating the Limnocharitaceae from the Butomaceae by the Limnocharitaceae possessing lactiferous ducts, leaves with petioles and expanded blades, caduceous petals, campylotropus ovules, and seeds with curved embryos, whereas these characteristics are absent in the Butomaceae. The Limnocharitaceae can be separated from the Alismataceae in having numerous ovules per carpel with laminar placentaion and dehiscent fruits, whereas the Alismataceae have 1-few ovules per carpel with basal placentaion and indehiscent fruits.

Key to the Genera

1. Carpels 3-8, linear-lanceolate, blades about as broad as long; styles present.......  
   ...................................................................................................................... Hydrocleys

1. Carpels numerous, semicircular; blades much longer than broad; styles absent.......  
   ...................................................................................................................... Limnocharis

Hydrocleys Richard

Mém. Mus. Nat. Hist. 1:368 (1815). Type: Hydrocleys commersoni Rich.

Vespuccia Parl., Nuov. Gen. Sp. Monocot. 55 (1854). Type: Vespuccia humboldtii Parl., nom. illeg. (=Stratiotes nymphoides Willd. =Hydrocleys nymphoides (Willd.)

A generic treatment ...
Fig. 3. A-D. *Hydrocleys nymphoides.* A, habit; B, longitudinal section of flower illustrating two series of stamens and many staminodia; C, fruit, the one on the right opened to illustrate the laminar placentation; D, seed with glandular pubescence. E-F. *Hydrocleys modesta.* E, habit illustrating submersed linear and floating elliptical leaves, flowers with petals as long as or slightly longer than sepals; F, seed with glandular pubescence. (A-D from living material cultivated at the AAU green houses; E-F from Macedo 2271, S, collected in Brazil.)
Plants submersed, with floating leaves. Stems short; stolons often present, terete. Leaves basal, floating or submersed, the submersed sessile phyllodia, the floating long-petiolate, the petioles terete, septate, with a sheathing base, the blade orbicular to oblong-lanceolate, the apex mucronate to obtuse, the base rounded to cordate. Inflorescence of few to numerous flowers, terminating a long septate scape, occasionally proliferating with leaves and stolons, the scapes few to many peduncles terete, septate; bracts elliptic to lanceolate, delicate, separate, shorter than pedicel subtended. Flowers long pedicellate, the pedicels cylindric, terete; sepals green, coriaceous, erect, lanceolate, with or without a midvein, the apex cucullate; petals yellow to white, delicate, oblong-ovate to orbicular, fugacious, erect to spreading, longer than to shorter than sepals; stamens 6-many, in 1-several series, the outer often sterile, the filaments linear or lanceolate, flattened, the anthers linear; carpels 3-8, terete, linear-lanceolate, basally scarcely cohering, attenuate into the style, the style curved inward, papillose at apex. Fruits more or less terete, linear-lanceolate, membranous, without dorsal furrows, dehiscing along the inner margins. Seeds numerous, sparsely to densely glandular pubescent.

A genus of five species, all native to Central and South America. Four species are known from Brazil, two of these Hydrocleys nymphoides and H. parviflora, occur in Amazonia.

Limnocharis Humboldt & Bonpland

Pl. Aequinoct. 1:116 (1808). Type: Limnocharis emarginata Humb. & Bonpl., non. illeg. (=Alisma flava L. = L. flava (L.) Buchenau).

Plants emersed. Stems short, rhizomatous; stolons occasional, erect. Leaves basal, emersed, long petiolate; petiole triangular, aseptate, often with aerenchyma; blade lanceolate to oval, the apex acute to round, the base acute to cordate. Inflorescences of 1-many flowers, terminating an elongate, aseptate scape, occasionally proliferating, the scapes to ca. 10 in number; peduncles shorter than to equal the length of petioles; bracts separate, delicate throughout, shorter than pedicel subtended. Flowers long pedicellate, the pedicels somewhat dilated, often winged, often inflated, trigonous; sepals green, broadly ovate, obtuse, appressed; petals yellow, fugacious, ovate to suborbicular, longer than the sepals; stamens many, the outer ones often sterile, the filaments linear, flattened, the anthers linear; carpels 15-20, laterally compressed, verticillate, scarcely coherent at base, the style absent, the stigma extrose. Fruits laterally compressed, semicircular, scarcely coherent, membranous, dorsally furrowed, dehiscent internally. Seeds numerous, transversely multicostate.

A neotropical genus of two species, Limnocharis flava and L. laforesti; both species occur in Amazonia. One species, L. flava, has been introduced into the Asian tropics.

A generic treatment ...
Fig. 4. **Limnocharis flava.** A, habit illustrating the inflated peduncles and triangular, winged pedicels; B, inflorescence; C, longitudinal section of flower with two circles of stamens and two circles of staminodia; D, fruit with seeds dropping out; E, seed. F-K. **Limnocharis laforesti.** F-G, habit illustrating typical short non-inflated peduncles and short pedicels; H, inflorescence; I, longitudinal section of flower illustrating one circle of stamens and no staminodia; J, fruit; K, seed. (A-B, D-E from Holm-Nielsen 22991, AAU; C from Holm-Nielsen, et al. 2883, AAU; F-G from Spruce 6452, K; H from Haynes 8338, UNA; I-K from Davidse 3820, UNA.)
Wilder (1974) notes that the ultimate bud of the inflorescence of *Limnocharis flava* always develops into a vegetative bud. This vegetative bud produces a vegetative component. When the inflorescence is mature and the fruits have fallen, the peduncle of the inflorescence falls to the side. A new vegetative shoot will arise from the vegetative component of the mature inflorescence. This vegetative shoot will grow into a new erect plant.

**HYDROCHARITACEAE** A.L. Jussieu

References: Ancibor, E. Systematic anatomy of vegetative organs of the Hydrocharitaceae. J. Linn. Soc., Bot. 78:237-266 (and microfiche) (1979). -- Cook, C.D.K. Pollination mechanisms in the Hydrocharitaceae. pp. 1-15 In J.J. Symons, et al. Studies on Aquatic Vascular Plants. Brussels (1982). -- Cook, C.D.K. & R. Lüönd. A revision of the genus *Hydrida* (Hydrocharitaceae). Aquatic Bot. 13:485-504 (1982). -- Cook, C.D.K. and K. Urm-König. A revision of the genus *Limnobium* including *Hydromystria* (Hydrocharitaceae). Aquatic Bot. 17:1-27 (1983). -- A revision of the genus *Egeria* (Hydrocharitaceae). Aquatic Bot. 19:73-96 (1984). -- A revision of the genus *Ottelia* (Hydrocharitaceae). 2. The species of Eurasia, Australasia and America. Aquatic Bot. 20:131-177 (1984). -- Díaz-Miranda, D., D. Philcox, and P. Denny. Taxonomic clarification of *Limnobium* Rich. and *Hydromystria* G.F.W. Meyer (Hydrocharitaceae). J. Linn. Soc., Bot. 83:311-323 (1981). -- Hartog, C. den. The Sea-grasses of the World. North-Holland Publ. Co., Amsterdam 275 pp + 31 pl. (1970). -- Hunziker, A.T. *Hydromystria laevigata* (Hydrocharitaceae) en el centro de Argentina. Lorentzia 4:5-8 (1981). -- Observaciones biológicas y taxonomicas sobre *Hydromystria laevigata* (Hydrocharitaceae). Taxon 31:472-477 (1982). -- Kaul, R.B. Floral morphology and phylogeny in the Hydrocharitaceae. Phytomorphology 18:13-35 (1968). -- Lowden, R.M. An approach to the taxonomy of *Valisneria* L. (Hydrocharitaceae). Aquatic Bot. 13:269-298 (1982). -- St. John, H. Monograph of the genus *Elodea* (Hydrocharitaceae). Pt. 1. Res. Stud. State Coll. Wash. 30: 19-44 (1962). -- Pt. 2. Caldasia 9:95-113 (1964). -- Pt. 3. Darwiniana 12:639-652 (1963). -- Pt. 4. Rhodora 67:1-35, 155-180 (1965).

Plants herbaceous, without milky juice, monoecious, dioecious, or monocrinous, annual or perennial, glabrous or pubescent, entirely submersed, or with both submersed and floating leaves, or with submersed stolons and emergent leaves, in fresh, brackish, or marine waters. Roots fibrous, few to many, aseptate, at nodes or bases of stems. Stems either rhizomatous, creeping with an abbreviated erect axis at the nodes, or erect, leafy, elongate, without teeth or tubers, and rarely with turions. Leaves basal, alternate, opposite, or whorled, entire or serrate, sessile or petiolate, 1-many-veined, the stipules sometimes present, forming a tubular sheath around the stem, the venation parallel, connected by perpendicular or ascending cross-veins, the infravaginal scales membranous. Inflorescence axillary, terminal, or scapose, solitary or cymose.
subtended by a spathe consisting of a bifid bract or a pair of opposite bracts, the spathe often persistent, sessile or peduncled, often ridged or winged. Flowers epigynous, imperfect and often with rudiments of the opposite sex or perfect, actinomorphic or rarely slightly zygomorphic; perianth separate, rarely 3, mostly 6, then differentiated into sepals and petals, the sepals mostly green, valvate, persistent, the petals mostly colored, imbricate or convolute, deciduous; androecium with stamens absent or 2-many in 1 or more whorls, the inner often staminodial, the anthers basifixed, 2-loculed, dehiscing by parallel vertical slits, the filaments slender, rarely absent, the pollen spherical, rarely adnate into slender chains; gynoecium with carpels 0 or 2-6, united, the ovary linear, lanceolate, or ovate, unilocular, the ovules numerous, bitegmic, anatropous, the placentation parietal or the parietal zones ill-defined and placentation then laminar, the style filiform, the stigmas equal the carpels. Fruit berry-like, submersed, linear, lanceolate or ovate, opening by decay of the pericarp. Seeds many, fusiform, elliptic, ovate, or globose; testa smooth, papillose, or spiny; embryo straight; endosperm helobial in development, absent in mature seed.

A family of about 16 genera and 100 species, indigenous primarily in waters of the tropical and subtropical regions of the world. Eight genera, Egeria, Elodea, Halophila, Hydrilla, Limmobium, Ottelia, Thalassia, and Vallisneria, occur in the neotropics. Two of these genera, Halophila and Thalassia, are marine spermatophytes; the remainder occur in fresh to slightly brackish water. Limmobium and Elodea occur in Amazonia.

The Hydrocharitaceae are most closely related to the Butomaceae by the modified laminar placentation and lack of lactiferous ducts. The family is unique among the Alismatidae in having united carpels and an inferior ovary.

Key to Neotropical Genera of Hydrocharitaceae

1. Plants of marine habitat; pollen grains adhering in moniliform chains..............2
1. Plants of fresh or slightly brackish waters; pollen grains separate..................3
2. Leaf-bearing branches arising from rhizome at each internode; styles 3-5; fruit smooth or ridged, not echinate, dehiscing by pericarp decay......................Halophila
2. Leaf-bearing branches arising from rhizome at distances of several internodes; styles 6-8; fruit echinate, dehiscing into 6-8 irregular valves......................Thalassia
3. Stems elongate (greater than 3 cm), erect; leaves cauleine, whorled..............4
3. Stems short (less than 2 cm), or if elongate, then stoloniferous; leaves basal.....6
4. Leaves with prickles along lower surface of midrib; infravaginal scales fringed with orange-brown marginal hairs..........................................................Hydrilla
4. Leaves without prickles along lower surface of midrib; infravaginal scales entire, or if fringed, the marginal hairs clear, not orange-brown..............Egeria
5. Whorls with 5 or more leaves per node.................................................Egeria
5. Whorls with 3-4 leaves per node..................................................Elodea
6. Stems stoloniferous, floating on surface or suspended in water; leaves with aerenchyma along lower surface; peduncle mostly short (less than 5 cm)..........Limnobium
6. Stems short, rooted in substrate; leaves without aerenchyma along lower surface; peduncle mostly elongate (more than 5 cm)...........................................7
7. Leaves petiolate; spathe winged or ribbed.........................................Ottelia
7. Leaves sessile; spathe without wings or ribs......................................Vallisneria

Egeria Planch.

Ann. Sci. Nat. Bot. ser. 3. 11: 79. 1849. Type: Egeria densa Planch.

Plant dioecious, perennial, glabrous, submersed, in fresh waters, propagated by seeds or stem fragments. Roots smooth, without root hairs, slender, pale, from lower nodes. Stems erect, branched or unbranched. Leaves whorled, 1-veined, serrate, the midrib without dorsal prickles. Inflorescences axillary, solitary; staminate spathes sessile, funnelform to broadly tubular, 2-4-flowered; carpellate spathes cylindric, split half-way down one side, 1-flowered. Flowers imperfect; staminate flowers projected to surface of water by slender elongate hypanthium base, the sepals 3, herbaceous, green, the petals 3, membranous, white, ca. 3 times size of sepals, the stamens 9, distinct, the anthers loculicidal, the filaments glandular papillose above, the nectary canal central, small, 3-lobed; carpellate flowers projected to surface of water by slender elongate hypanthium base, the sepals 3, herbaceous, green, the petals 3, membranous, white, ca. 2 times as long as sepals, the staminodia 3, the ovary unilocular, the ovules numerous, the placentation parietal, the stigma 3-lobed, the lobes linear. Fruits cylindric, many seeded. Seeds rare, fusiform, beaked, the testa mucilaginous.

A genus of 2 species, Egeria densa and E. najas, which are native to the neotropics. Both species occur in Brazil but neither one is known from Amazonia. One species, E. densa, has been introduced into the United States of America and Europe where, at least in the USA, it has become a problem weed.

The two species can be separated by Egeria densa generally being a larger plant. For example, the leaves of E. densa are 1.7 mm or more wide whereas those of E. najas are less than 1.4 mm wide. Also, filaments of E. densa are clavate, whereas those of E. najas are linear.

Elodea Michx.

Fl. Bor.-amer. 1:20 (1803). Type: Elodea canadensis Michx.

Anacharis Rich., Mém. Cl. Sci. Math. Inst. Natl. France 12(2):7,61 (1814). Type: Anacharis callitrichoides Rich.

Apalanche Planch., Ann. Mag. Nat. Hist. 11. 1:87 (1848). Type: Not designated.

A generic treatment ...
Fig. 5. A-I. Limnobium laevigatum. A, habit sketch with emersed and floating leaves; B, enlargement of aerenchyma on lower surface of floating leaf; C, staminate flower; D, longitudinal section of staminate flower showing fusion of filaments; E, carpellate flower; F, longitudinal section of carpellate flower; G, fruit; H, seed with echinate testa; I, embryo. J-N. Elodea granatensis. J, habit sketch with attached flower and attached fruit; K, enlargement of node showing the number of leaves per whorl and fruit; L, flower; M, seed; N, embryo. (A-F from Holm-Nielsen & Jeppesen 92, AAU; G-I from Haynes 8286, UNA; J-K, M-N from Clark 6567, AAU; L from Brandbyge, et al. 36149, AAU).
Elodea Rich., Mém. Cl. Sci. Math. Inst. Natl. France 12(2):7, 61 (1814). Type: Elodea guyanensis Rich.

Diplandra Bertero, Mercurio Chileno 13:612 (1829). Type: Diplandra potamogeton Bertero.

Philotria Raf., Amer. Monthly Mag. & Crit. Rev. 2:175 (1818). Type. Same as Elodea Michx.

Udora Nutt., Gen. N. Amer. Pl. 2:242 (1818). Type: Same as Elodea Michx.

Plants dioecious or monoclinous, perennial, glabrous, submersed, in fresh waters, propagated by seeds, stem fragments or turions. Roots smooth, slender, pale, unbranched. Stems erect, rooting at lower nodes, branched or unbranched. Leaves whorled or rarely opposite, sessile, linear to linear-lanceolate, 1-veined, serrate, the midrib without a dorsal prickle, the whorls with 3-7 leaves. Inflorescences axillary, solitary; spathes perfect or imperfect, sessile, usually narrowed toward base, cylindric to elliptic-spatulate, 1-flowered. Flowers perfect or imperfect, usually projected to surface of water by the elongating hypanthium base; sepals 3, herbaceous, green; petals 3, membranous, white to pale blue, elliptic, clawed; stamens 3-9, or reduced to 3 staminodia, the anthers oblong to ellipsoid, the filaments subulate to lanceolate, separate or the 3 inner united halfway to apex; carpels 3, the locules 1, the placentation parietal, the styles 3, the stigmas 3, bifid. Fruit ovoid to lance-ellipsoid, beaked; seeds 3-8, cylindric to fusiform, glabrous to hirsute.

A Western Hemisphere genus of 13-14 species separated into two subgenera, Elodea and Apalanthe. The subgenera can be separated by subgenus Elodea having imperfect flowers, the stamine flowers with 6-9 stamens, and some filaments united. Subgenus Apalanthe has perfect flowers with three stamens, these having separate filaments. Two species, representing both subgenera, occur in the neotropics. One species, E. granatensis, occurs in Brazil, including Amazonia.

The taxonomy of Elodea is based on differences in floral structure. Without flowers, therefore, plants are difficult at best to determine. Care should be taken in all cases to collect only flowering specimens.

Halophila Thouars

Gen. Nov. Madagasc. 2 (1806). Type: Halophila madagascarensis Doty et Stone.

Plants monoecious or dioecious, annual or perennial, glabrous or pubescent, entirely submersed, in marine waters. Stems of two types, the lower rhizomatous, the lateral erect and foliaceous; rhizome monopodial, creeping, rooting at the nodes, with 1-few unbranched roots covered with fine root-hairs, the nodes with 2 scales, one of which surrounds the rhizome and the other subtends a lateral, often undeveloped, foliaceous shoot; lateral shoot 1-40 mm long, often with a pair of scales midway or higher on the stem, a second lateral shoot often developing from the axillary bud between the leaves, the second shoot producing a pair of leaves and the inflorescence. Leaves

A generic treatment ...
mostly in terminal pairs or pseudowhorls, rarely distichous, sessile or petiolate, linear to ovate, entire or serrulate, mostly glabrous, rarely pubescent. Inflorescence of 1 or rarely two flowers, dioecious or rarely monoecious; spathe of 2 sessile bracts, the bracts membranous, elliptic to ovate, overlapping, separate, acute to emarginate, entire or rarely ciliate to serrulate, keeled, the keel often serrulate. Flowers imperfect; staminate flowers pedicellate, the perianth of 3 imbricate segments, the androecium of 3 stamens, the stamens alternating with the tepals, the anthers 2- or 4-loculed, dehiscing lengthwise and extrorsely, the pollen united into moniliform chains; carpellate flowers sessile or subsessile, the perianth of 3 reduced segments, the gynoecium of 3-5 united carpels, the ovary ellipsoid to ovoid, unilocular, the ovules few to numerous, the placentation parietal, protruding slightly into the locule, the styles linear, equal to the carpels. Fruit ovoid to globose, rostrate, membranous, opening by decay of pericarp. Seeds few to numerous, globose or sub-globose.

A genus of 8 species widely distributed in the tropical and subtropical waters. Three species, *H. decipiens*, *H. engelmannii*, and *H. baillonis*, occur in the neotropics including Brazil. The species can be separated by *H. decipiens* being monoecious, without scales partially up the lateral shoot, and with pubescent leaves, whereas the other two species are dioecious, have 2 scales about halfway up the lateral shoot, and are glabrous. *Halophila baillonis* can be separated from *H. engelmannii* by the former species having distinctly petiolate leaves whereas the latter species has subsessile leaves.

**Hydrilla Rich.**

Mém. Cl. Sci. Math. Phys. Inst. France 12(2): 9, 61, 73 (1814). Type: *Hydrilla ovalifolia* Rich, nom. illeg. (= *H. verticillate* (L.f.) Royle).

Plants dioecious or monoecious, perennial, glabrous, submersed, in fresh or brackish waters, propagated by seeds, turions, or stem fragments. Roots smooth, unbranched, from lower nodes. Stems erect, branched or unbranched. Leaves whorled, sessile, linear or rarely slightly elliptic, 1-veined, serrate, the midrib with dorsal prickles. Inflorescence solitary, axillary; spathe of 2 connate bracts, the staminate subsessile, globose, dorsiventrally flattened, with subulate appendages and a minute central knob, the carpellate sessile, tubular, bifid. Flowers imperfect; staminate flowers floating, long pedicellate, the perianth biseriate, the sepals 3, ovate to oblong-elliptic, reflexed, strongly convexed, the petals 3, linear to spatulate, narrower than the sepals, spreading to reflexed, the androecium of 3 stamens, the anthers erect, linear, 4-loculed, laterally dehiscent, the filament slender, short, the pollen globular, smooth, rather large; carpellate flowers sessile, with a long hypanthium, the perianth biseriate, the sepals 3, oblong to obovate, convex, the petals 3, spatulate, narrower than the sepals, the gynoecium of 3 united carpels, the ovary linear, unilocular, the ovules several, ortho- to anatropous, the placentation parietal, the styles 3, filiform to subulate,
Fruits linear, cylindrical to narrowly conical. Seeds cylindrical, glabrous, 2-6 in one row.

A monotypic genus, native to the Eastern Hemisphere, that has been introduced into the Americas in the last two decades. *Hydrilla verticillata* has become quite a problem species in many tropical and subtropical regions. In fact, the species in Florida is known to completely choke waterways and is forbidden to be transported by individuals. The species to date is restricted to Mexico, Central America, and Venezuela in the neotropics.

**Limnobium Rich.**

Mém. Cl. Sci. Math. Phys. Inst. France 12(2): 66 (1814). Type: *Limnobium bosci* Rich. (=*L. spongia* (Bosc) Steudel).

*Hydrocharella* Spruce ex Benth. in Bentham and Hooker, Gen. Pl. 3(2): 452 (1883). Type: *Hydrocharella echinospora* Spruce.

*Hydromystria* G. Mey., Prim. Fl. Essequ. 152 (1818). Type: *Hydromystria stolonifera* G. Meyer.

*Jalambicea* Cervantes in La Llave and Lexarza, Nov. Veg. Descr. 2:12 (1825). Type: *Jalambicea repens* Cervantes.

*Rhizakenia* Raf., Autik. Bot. 188 (1840). Type: *Rhizakenia ovata* Raf.

*Trianea* H. Karst., Linnaea 28: 424 (1857). Type: *Trianea bogotensis* H. Karst.

Plants monoecious, perennial, glabrous, emersed or with stems floating, in fresh waters, propagated by seeds or stolons. Roots one per node, branched, fibrous, with large root hairs. Stems dimorphic; shortened stems erect, unbranched, bearing leaves in a rosette; elongate stems stoloniferous, branching. Leaves dimorphic, the lower scale-like, the upper differentiated; scale-like leaves 2 at base of each rosette, membranous, ovate; differentiated leaves emergent or floating, petiolate, stipulate, laminate, the stipules membranous, ovate, sheathing the developing apex, the petiole stout, sometimes inflated, the blade elliptic to circular, the apex obtuse to acuminate, the base reniform or cordate, the abaxial surface smooth on emergent leaves or with aerenchymous tissue on floating leaves. Inflorescence imperfect, cymose; staminate inflorescence sessile or pedunculate, with up to 25 flowers, with 2 bracts, the bracts ovate, the lower shorter than upper; carpellate inflorescences mostly sessile, rarely short pedunculate, with 1-6 flowers, with 1 or 2 separate bracts the bracts ovate. Flowers imperfect, pedicellate, projected above the surface of water; staminate flowers withering after anthesis, the sepals 3, narrowly to widely elliptic, the apex reflexed at anthesis, greenish-white to yellowish, the stamens in 1-6 whorls of 3, inserted on a column of fused filament bases, the anthers 4-loculed, dehiscing lengthwise, the pollen spherical, yellow, separate; carpellate flowers with pedicels reflexed after anthesis, the sepals 3, narrowly to widely elliptic, spreading at anthesis, greenish-white, absent or to 3, separate, linear to lanceolate or oblanceolate, spreading at...
anthesis, greenish-white, the staminodia 2-6, in one whorl, the ovary of 3-9 united carpels, unilocular, ellipsoid to oblong, the ovules 5 to numerous, the placentation parietal, the styles equal the carpels, each split into 2 filiform stigmata, the stigma much shorter than the style, with unicellular papillae. Fruit ellipsoid to spherical, beaked, developing in mud or under water, the pericarp splitting irregularly. Seeds few to numerous, ellipsoidal, with a short micropylar beak, the funiculus persistent, the testa covered with cylindrical blunt trichomes.

A genus of two species; one species, Limnobium laevigatum, occurs in Amazonia. The other species, L. spongia, is restricted to the eastern United States of America. Limnobium laevigatum occurs in the neotropics from central Mexico to Argentina. Several authors, e.g. Días-Miranda et al. (1981) and Hunziker (1981, 1982), have placed this species in the monotypic genus Hydromystria. Cook and Urmí-König (1983), however, demonstrate the species should be considered within the genus Limnobium.

Ottelia Pers.

Syn. Pl. 1: 400 (1805). Type: Ottelia alismoides (L.) Pers.

Beneditaea Toledo, Arq. Bot. Estado São Paulo 1(4): 81 (1942). Type: Beneditaea brasiliensis (Planch.) Walpers.

Damasonium Schreber, Gen. Pl. 1: 242 (1789). Type: Damasonium indicum Willd., nom. illeg., (=Ottelia alismoides (L.) Pers.).

Plants monoclinous or dioecious, annual or perennial, glabrous, submersed or with floating leaves, in fresh waters, propagated by seeds. Roots fibrous. Stems short, erect, bulb-like axis with greatly condensed internodes. Leaves petiolate, petioles terete to 3-5-angled, sheathing at base, often gradually merging into the blade; blade linear to reniform, entire to crisped on the margin, the apex rounded to acute, the base cuneate to cordate, the venation parallel, the veins 3-11, connected by parallel cross-veins. Inflorescences 1-30, scapose, pedunculate, with terminal 1-many-flowered spathe; peduncles elongate, projecting the flowers to surface of water, terete, to 3-5-angled; spathes elliptic or ovate, with 6 ribs or 2-10 wings, 1-flowered if with perfect or carpellate flowers, many-flowered if with staminate flowers. Flowers perfect or imperfect, the perfect and carpellate sessile, the staminate pedicelled, sepals 3, linear to ovate, green with scarious margins; petals 3, oblong to orbicular, 2-3 times as long as sepals, white, yellow, orange, pink, or blue; stamens, when present, 3-15, the filaments flattened, the anthers linear or oblong, dehiscing lengthwise; carpels, when present, 6, the ovules numerous, the placentation parietal, the stigma bifid. Fruits oblong, the apex attenuate, the pericarp splitting irregularly. Seeds numerous, minute, oblong or fusiform.

A genus of perhaps 40 species; one species, Ottelia brasiliensis, occurs in the neotropics, being restricted to Minas Gerais, the remaining species are native to the paleotropics. Ottelia alismoides, however, has become naturalized in the southeastern

172 Haynes & Holm-Nielsen
United States of America.

Thalassia Banks et Solander ex Koenig

Ann. Bot. 2: 96 (1805). Type: Thalassia testudinum K.D. Koenig.

Schizotheca Ehrenb., Abh. Königl. Akad. Wiss. Berlin 1: 429 (1834). Type: Schizotheca hemprichii Ehrenb.

Plants dioecious, perennial, glabrous, entirely submerged, in marine waters, propagated by seeds or rhizomes. Roots one per node, unbranched, from nodes. Stems rhizomatous, monopodial, scaly, the nodes with short erect shoots bearing 2-6 eligulate leaves, the internodes short, with fine longitudinal grooves. Leaves sessile, linear often somewhat, falcate, distichous, differentiated into green blade and pale basal sheath; blade entire, the venation parallel, the veins 9-17, the apex obtuse. Inflorescence pedunculate, with 1-2 flowers in staminate plants and 1 flower in carpellate plants; spathes of staminate plant connate on one side only, those of carpellate plant connate on both sides. Flowers imperfect, short pedicellate to subsessile; perianth segments 3, elliptic; staminate flower of 3-12 subsessile stamens, the anthers elongate, erect, 4-locular, dehiscent lengthwise, the pollen spherical, yellow, embedded in gelatinous matrix, forming a moniliform chain later, germinating before reaching the stigma; carpellate flowers of 6-8 carpels, the ovary muricate, the locules 1, the ovules few, the placentation parietal, the styles equal the carpels, each split into 2 filiform stigmata, the stigmata 2 or more times as long as the style. Fruit globose, beaked, the pericarp splitting irregularly. Seeds few, conical, thickened basally; endosperm of the helobial pattern, absent in the mature seed.

A genus of 2 species; one species, T. testudinum occurs in the neotropics Thalassia hemprichii is restricted to the Indian Ocean and western Pacific Ocean.

Thalassia testudinum is widely distributed in the Caribbean Sea and Gulf of Mexico. The species forms dense colonies in the sublittoral region from the low water mark to depths of ca. 10 meters. The species can colonize soft substrata, coral, sand dead reef-platform, and rocky substrata. Den Hartog (1970) states: "Thalassia testudinum without doubt is the most important sea-grass along the coasts of the Caribbean and Gulf of Mexico". One of the species most important functions is stabilization and protection of the substrate. This is especially true during hurricanes when wave action moves huge amounts of substrate in areas not covered by Thalassia.

Vallisneria Linnaeus

Sp. Pl. 1015. 1753. Type: Vallisneria spiralis L.

Physkium Lour., Fl. Cochinch. 662 (1790). Type: Physkium natans Lour.

Plants dioecious, perennial, glabrous, submerged, in fresh or brackish waters, propagated by seeds or rhizomes. Roots fibrous, many per node. Stems rhizomatous,

A generic treatment ...
monopodial, the nodes with short erect shoots bearing 2-6 eligulate leaves. Leaves linear, strap-shaped, finely serrulate, 3-zoned, the venation parallel, the veins 3-9, the apex obtuse. Inflorescences pedunculate; staminate inflorescences with numerous minute flowers enclosed by 2-valved spathe, the peduncles short, the spathe valves reflexing at anthesis; carpellate inflorescences mostly 1-flowered, rarely few- to many-flowered, subtended by a bivalved spathe, the peduncles long, projecting the inflorescences to surface of water, becoming spirally coiled after anthesis. Flowers imperfect, sessile; staminate flowers released by the spathe and floating to surface of water, the sepals 3, 2 larger, 1 smaller, elliptic, green, the petals 1, rudimentary, the stamens 3, 2 fertile, 1 sterile, the fertile often with united filaments, the anthers oblong to globose, the pollen spherical, separate; carpellate flowers pedicellate, the pedicel enclosed in or projecting from spathe, the sepals mostly 3, the petals rudimentary, mostly 3, the staminodia mostly 3, the carpels mostly 3, the ovary cylindrical, the locules 1, the ovules numerous, the placentation parietal the style 1, the stigma equal the carpels, bifid, the stigmata as long as the style. Fruit cylindrical to ellipsoid, beaked, the pericarp splitting irregularly. Seeds numerous, ellipsoid. A genus of two species; one species, Vallisneria americana, occurs in the neotropics but not in Brazil. Vallisneria spiralis is restricted to the Eastern Hemisphere.

Vallisneria americana is most common in North America. However, the species is occasional in the Caribbean Islands, Mesoamerica, and Venezuela. Lowden (1982) separates the species into two varieties, var. americana, which is restricted in the neotropics to Mexico, Guatemala, Cuba, and Honduras, and var. biwaensis, which is restricted in the neotropics to the Caribbean Islands and Venezuela.

JUNCAGINACEAE Rich.

References: Buchenau, F. Scheuzeriaceae. In Engl., Pflanzenr. IV 14:1-20 (1906). -- Hieronymus, G. Monografia de Lilaea subulata. Acta Acad. Nac. Sci. Cordova 4:1-52 (1882). -- Larsen, K. Cytotaxonomical note of Lilaea. Bot. Not. 119:496-497 (1966).

Plants herbaceous, without milky juice, monoclinous, monoecious or dioecious, perennials or annuals, glabrous, emergent or floating-leaved, of fresh or brackish waters. Roots fibrous or tuberous, numerous, at the nodes. Stems slender to stout, rhizomatous, the internodes without teeth, the tips without turions or tubers. Leaves basal, linear 1-several-veined, flattened to terete, sessile, with sheathing base; sheath adnate to the blade, bi-auriculate, fibrous, often remaining as fibrous cluster after leaves decay, the auricles obtuse; infravaginal scales present, membranous. Inflorescence either all scapose or both scapose and basal, without a subtending spathe; scapose inflorescences terminated by spike or spike-like raceme, with all perfect or perfect and imperfect flowers, then carpellate below, perfect median, and staminate above, or possibly carpellate absent; basal inflorescence of carpellate flowers only, hidden
amongst the leaf sheaths. Perfect and carpellate flowers hypogynous; perianth mostly present, rarely absent, the segments 1 or 6, in 1 or 2 series, when in 1 series, then with 1 segment adnate to the anther, when in 2 series, then each series with 3 free segments; stamens epi-tepalous, 0, 1, 4 or 6, sessile or subsessile, when 4 or 6 in 2 series of 2 or 3, the anthers 2-loculed, dehiscing by longitudinal slits, the pollen globose, separate; carpels 0, 1, 3, or 6, when 3 or 6 then coherent or weakly connate but separating when mature, the locules equal to the carpels, the ovules 1- few per locule, erect, anatropous, the placentation basal, the styles long and filamentous with capitate stigmas when carpels 1, absent with plumose or papillose stigmas when carpels 3-6. Fruits follicles or angled nutlets, rarely with hooks or horns at apex. Seeds 1- few, the embryo straight; endosperm nuclear in development, absent in mature seed. Type genus: Juncago Séguier, nom. illeg. (=Triglochin L.).

A family of four genera and about 15 species. Two genera, Triglochin and Lilaea, occur in the neotropics.

Key to the Genera

1. Inflorescences all scapose spike-like racemes with perfect flowers; carpels 3 or 6
   Triglochin

1. Inflorescences both scapose spike-like racemes with perfect and staminate flowers
   and basal inflorescences of carpellate flowers; carpel 1
   Lilaea

Lilaea Humboldt & Bonpland

Pl. Aequinoct. 1:221 (1808). Type: Lilaea subulata Humboldt & Bonpland (=L. scilloides (Poir.) Hauman).

Plants monoecious, annual, emersed or floating-leaved, in ephemeral fresh water pools. Roots fibrous, without terminal tubers. Stems, short, slender. Leaves erect, with aerenchyma tissue, the infravaginal scales membranous. Inflorescence both scapose and basal; scapose inflorescences with both perfect and staminate flowers; basal inflorescences with carpellate flowers only. Perfect flowers with one perianth segment, one sessile anther adnate to perianth segment, and one carpel; staminate flowers with one perianth segment and one sessile anther adnate to perianth segment; carpellate flowers with the perianth absent, one carpel, with one anatropous ovule, the style filiform, to 30 cm long. Fruit a flattened to angular nutlet.

A monotypic genus restricted to temperate areas and montane tropical marshes from British Columbia, Canada south to Chile and Argentina.

Triglochin Linnaeus

Sp. pl. 1:338 (1753); Gen. Pl. 157 (1754). Type: Triglochin palustre L.

Plants monoclinous, perennial, emersed, in fresh or brackish waters. Roots

A generic treatment...
Fig. 6. *Triglochin striata*. A, habit of flowering plant; B, habit of fruiting plant; C, enlargement of partially mature inflorescence with lower portion after loss of anthers following anthesis but before fruit maturation, middle portion in flower at anthesis, and upper portion in bud; D, flower at anthesis illustrating the 6 stamens in 2 series, 6 perianth segments in 2 series, and 3 carpels embedded between the 3-winged receptacle; E, enlargement of fruiting inflorescence illustrating three nutlets between the 3-winged receptacle; E, nutlet. (A, C-D from Böcher, et al. 497, C; B, E-F from Hjerting & Rahn 556, C).
fibrous, occasionally tuberous. Stems stout, short. Leaves basal, erect, few, terete, the infravaginal scales membranous. Inflorescences scapose, the scapes terminated by long-peduncled spike-like racemes. Flowers perfect; perianth of 6 separate segments in 2 series, similar in texture and color, the segments conchiform; stamens mostly 4 or 6, subsessile, in 2 series of 2 or 3; carpels 3 or 6, coherent or weakly connate but separating when mature, often embedded in angled receptacle, the ovules 1 per locule, the styles absent, the stigmas plumose or papillose. Fruits angled nutlets.

A cosmopolitan genus of about 12 species represented by two species, *Triglochin striata* Ruiz & Pavon and *T. palustris* L., in the neotropics. The two species can be separated by *T. striata* having nutlets that are semicircular in shape, giving the entire fruit cluster a spherical appearance. The nutlets of *T. palustris*, by contrast, are linear, yielding fruit cluster then is much longer than wide.

**POTAMOGETONACEAE** Dumortier

References: Ascherson, P. and P. Graebner. Potamogetonaceae. In Engl., Pflanzenr. IV. 11:1-184 (1907). -- Fernald, M.L. The linear-leaved North American species of *Potamogeton* section *Axillares*. Mem. Gray Herb. 3:1-183 (1932). -- Hagström, J.O. Critical researches on the Potamogetons. Kongl. Svenska Vetenskapskad. Handl. VI. 55:1-281 (1916). -- Haynes, R.R. A revision of North American *Potamogeton* subsection *Pusilli* (Potamogetonaceae). Rhodora 76:564-649 (1974). -- The Potamogetonaceae in the southeastern United States. J. Arnold Arbor. 59:170-191 (1978). -- Ogden, E.C. The broad-leaved species of *Potamogeton* of North America north of Mexico. Rhodora 45:57-105, 119-163, 171-214 (1943). -- St. John, H. A revision of the North American species of *Potamogeton* of the section *Coleophylli*. Rhodora 18:121-138 (1916). -- Taylor, N. Zannichelliaceae. N. Amer. Fl. 17:13-27 (1909). -- Tur, N.M. Potamogetonaceae, pp. 279-288. In A.L. Cabrera, Flora de la Provincia de Buenos Aires, Pt. 1. Coleccion Científica del I.N.T.A. Buenos Aires (1968).

Plants herbaceous, without milky juice, monoclinous, perennial or rarely annual, glabrous, entirely submersed or with both floating and submersed leaves, in fresh or brackish waters. Roots fibrous, few, aseptate, at nodes of lower stems. Stems slender, branched or unbranched, often dimorphic, the lower stems rhizomatous, the upper erect, leafy, elongate, the internodes without spinulose teeth, the tips often modified into turions, without tubers. Leaves alternate or subopposite, entire to serrulate, sessile or petiolate, 1-many-veined, stipulate, the stipules forming a tubular sheath around the stem, free from or adnate to the base of the blade, the venation parallel, connected by perpendicular cross-veins, the infravaginal scales present, membranous; submersed leaves thin, linear to orbicular; floating leaves often leathery, lanceolate, to elliptic or ovate. Inflorescence an axillary or terminal spike or panicle of spikes, without a subtending spathe. Flowers perfect, hypogynous, actinomorphic; perianth absent.

A generic treatment ...
or of 4 separate, rounded, short-clawed, greenish or brownish segments in one series; androecium of 2 or 4 stamens, the anthers 1- or 2-loculed, dehiscing by vertical slits, the filaments adnate to the perianth claw or absent, the pollen inaperturate, spherical to arcuate, separate; gynoecium of 2-16 distinct carpels, the carpels unilocular, with or without a gynophore, the ovules one, bitegmic, orthotropus, the placentation parietal, the styles short, the stigma capitate. Fruit drupaceous, with membranous exocarp, fleshy mesocarp, and stony endocarp, opening by decay of the pericarp. Seeds solitary, the embryo straight or coiled; endosperm helobial in development, absent in mature seed.

A family of nearly cosmopolitan distribution with three genera and about 110 species. Two genera, Potamogeton and Ruppia, occur in the neotropics. Groenlandia J. Gay (G. densa (L.) Fourr. Potamogeton densa L.) is native to western Europe, North Africa, and southwestern Asia. Members of the Potamogetonaceae have been placed in the Najadaeae by Fassett (1957) and Gleason (in Gleason and Cronquist 1963) and have been combined with members of Zannichelliaceae and Zosteraceae by den Hartog (1970), Fernald (1950), and Taylor (1909) to comprise a taxon that has been called, respectively, Potamogetonaceae, Zosteraceae, and Zannichelliaceae. The Potamogetonaceae, as here interpreted, are separated from the Zannichelliaceae and Zosteraceae by their perfect flowers, lack of a spathe-like bract, and in some species, the presence of turions.

**Key to Neotropical Genera of Potamogetonaceae**

1. Stamens four; perianth present; stipule free from leaf blade or, if adnate, with the tip free; fruits sessile or very short-stalked.................................Potamogeton

1. Stamens two; perianth absent; stipule adnate to leaf blade for entire length (without free tip); fruits long-stalked.................................Ruppia

**Potamogeton Linnaeus**

Sp. Pl. 1:126 (1753); Gen. Pl. ed. 5: 61 (1754). Type: P. natans L.

Hydrogeton Lour., Fl. Cochinch. 244 (1790). Type: Hydrogeton heterophyllum Lour. = Potamogeton octandrus Poir.

Peltopsis Raf., J. Phys. Chim, Hist. Nat. Arts 89:102 (1819). Type: Potamogeton perfoliatus L.

Spirillus J. Gay. Compt. Rend. Hebd. Séances Acad. Sci. 38:703 (1854). Type: Potamogeton diversifolius Raf.

Plants annual or perennial, submersed, in fresh or rarely brackish waters, propagated by seeds, turions, or rhizomes. Stem varying in length with water depth, branched or unbranched, terete or compressed, rooting at lower nodes, the nodes occasionally with oil glands. Leaves submersed or both submersed and floating, alternate to subopposite; submersed leaves pellucid, sessile or petiolate, linear to orbicular, subulate to obtuse at apex, acute to perfoliate at base, the margins entire to serrate, rarely crimped, the veins 1-35; floating leaves coriaceous, mostly petiolate or rarely
Fig. 7. A-D. *Potamogeton polygonus*. A, habit; B, details of stem illustrating leaves and large acuminate stipules; C, enlargement of leaf illustrating venation and the broad band of lacunae; D, keeled fruit; E-H. *Potamogeton gayii*. E, habit; F, shoot apex showing leaves and broad acute stipules; G, enlargement of leaf illustrating venation and four rows of lacunae along the midvein; H, seed with dorsal and lateral winged keels. (A from Warming 452, LE; B-C from Warming 452, P; D from Imers 4230, P; E-H from Tur, s.n., P).
subsessile, elliptic to ovate, acute to obtuse at apex, cuneate to rounded or cordate at base, the margins entire, the veins 1-5; stipules connate or convolute, either free or adnate to the base of the submersed leaves, free from base of floating leaves. Turions present or absent, with extremely shortened internodes, divided into inner and outer leaves; the inner few to numerous, rolled into a fusiform structure, shortened and oriented perpendicular to outer leaves, or unmodified; the outer 1-5 per side, mostly similar to vegetative leaves, rarely corrugated near base. Inflorescence axillary or terminal, a capitate or cylindrical spike or panicle of spikes with 1-20 whorls of flowers, compact or moniliform, with 2-4 flowers in each whorl, submersed or held above surface of water. Perianth of 4, free, rounded, short-clawed segments. Androecium of 4 stamens, the filaments adnate to the perianth claw, the anthers 2-loculed, extrorse, the tapetum amoeboid, the pollen spherical to fusiform, sculptured, 3-celled. Gynoecium of 4 carpels, the ovule orthotropous or campylotropous, the micropyle formed by the inner integument. Fruit dorsally rounded or keeled, beaked. Embryo coiled.

A genus of perhaps 100 species, in two subgenera, Potamogeton and Coleogeton, both almost cosmopolitan. Fourteen species, representing both subgenera, occur in the neotropics, five in Brazil, and tree, Potamogeton illinoensis, P. polygonus, and P. pusillus, in Amazonia. The subgenera can be separated by subgenus Potamogeton having peduncles which are mostly rigid and rarely with an endodermis, stigmatic papillae small, and pollination mostly by wind, whereas subgenus Coleogeton having peduncles which are mostly flexible and usually with an evident endodermis, stigmatic papillae large, and pollination mostly by water.

Ruppia Linnaeus

Sp. Pl. 1:127 (1753); Gen. Pl. ed. 5, 61 (1754). Type: Ruppia maritima L.

Plants annual or perennial, submersed in brackish or saline waters or fresh waters with very high calcium or sulphur ion concentrations, propagated by seeds, rhizomes, or rarely turions. Stems varying in length with water depth, branched or unbranched, terete, rooting at the lower nodes. Leaves submersed, alternate to subopposite, sessile, divided into blade and stipular sheath; blade linear or setaceous, the margins entire below, minutely serrulate above, the veins 1, the apex truncate to acute; stipular sheath formed by adnation of stipule to blade for entire length of stipule. Turions rare, with one internode, the leaves undifferentiated. Inflorescence a 1-few-flowered capitate spike, at first enclosed by sheathing leaf bases; peduncle elongating at anthesis, elevating the inflorescence to or near the water surface, or remaining short, occasionally becoming spirally twisted in fruit, then pulling the developing fruit below the water surface. Perianth absent. Androecium of 2 sessile anthers, the anthers 2-loculed, the locules separated by a broad connective, the dehiscence extrorse, the tapetum amoeboid, the pollen elongate, 4 times as long as broad, mostly arcuate, swollen at the ends and at the center on the convex side, 3-celled, the exine reticulate, ex-
Fig. 8. A-E. *Kupiia filifolia*. A, habit; B, node with spiralled peduncle; C, leaf apex illustrating obtuse serrulate apex and entire margin below apex; D, enlargement of node with young flower before peduncle elongation; E, mature inflorescence with fruit. F-I. *Potamogeton striatus*. F, habit illustrating stem leaves larger than branch leaves; G, inflorescence in flower; H, fruit; I, enlargement of leaf illustrating venation pattern. (A-E from Asplund 11711, UPS; F-I from Wurdack 891, P).

A generic treatment ...
ceedingly thin, discontinuous at the swellings, the intine rather, thick, further thickened in the swollen regions. Gynoecium of 4-16 distinct, stipitate or sessile carpels, the gynophore elongating after anthesis, the ovule campylotropous, the micropyle formed by both integuments, the placentation parietal. Fruit asymmetrical, dorsally rounded or with a prominent transversely ridged crest, beaked or beakless, long stipitate or sessile, the exocarp and mesocarp often decaying, leaving the operculate endocarp intact. Embryo straight.

An almost cosmopolitan genus of perhaps 10 species, represented in the neotropics by two species, *Ruppia maritima* and *R. filifolia*. The former species is known from Brazil, including Amazonia.

**ZANNICHELLIIACEAE** Dumortier

References: Ascherson, P. and P. Graebner. Potamogetonaceae. In Engl., Pflanzenr. IV. 11:1-184 (1907). -- Taylor, N. Zannichelliiaceae. N. Amer. Fl. 17:13-27 (1909).

Plants herbaceous, without milky juice, monoecious, annuals or perennials, glabrous, entirely submersed, of fresh or brackish waters. Roots fibrous, 1-7, aseptate at the lower nodes. Stems slender, dimorphic, the lower often stoloniferous, the upper erect and leafy, without teeth, turions, or tubers. Leaves alternate, opposite or pseudowhorled, scale-like, without vascular tissue, or foliaceous, linear, 1- or rarely 3-veined, subterete, sessile, with basal sheath, the sheath adnate to or free from the blade, the infravaginal scales membranous. Inflorescence axillary, with 2-several flowers. Flowers imperfect; staminate flowers short pedicellate, the perianth mostly absent, rarely minute and 3-lobed, the stamen 1, the connective extending into a blunt tip, the anther 2-12-loculed, dehiscing by longitudinal slits, the pollen inaperturate, globose, often contained in a gelatinous matrix; carpellate flowers short pedicellate, often enclosed by a membranous spathe-like envelope, the perianth absent, a small cup-like sheath, or of 3 separate segments, the carpels 1-8, separate, short-stipitate, 1-loculed, the ovule solitary, bitegmic, pendulous, anatropous, the placentation basal, the style short to long, the stigma enlarged, funnel-shaped, feathery, or peltate. Fruit drupaceous, with a membranous exocarp, fleshy mesocarp, and stony endocarp. Seed solitary; embryo straight; endosperm helobial in development, absent in mature seed. Type genus: *Zannichellia* Linnaeus.

A family of near cosmopolitan distribution with four genera and 10-12 species. One genus, *Zannichellia*, occurs in the neotropics.

**Zannichellia** Linnaeus

Sp. Pl. 2:969 (1753); Gen. Pl. ed. 5, 416 (1754). Type: *Zannichellia palustris* L.

Plants monoecious, annual or rarely perennial, of fresh or brackish waters.
Fig. 9. *Zannichellia andina*. A, habit; B, enlargement of flowering node, illustrating the staminate flower consisting of one stamen and the carpellate flower with four carpels and the subtending spathe-like envelope; C, enlargement of carpel, illustrating the asymmetrically funnel-shaped stigma; D, enlargement of fruiting node with two fruits, the one on the left with the exocarp intact and the one on the right with the exocarp partially decayed, exposing the spiny endocarp; E, endocarp illustrating the spines. (A, D-E from Illtis, et al. 845, US; B-C from Illtis, et al. 352, US).

Roots singular or in pairs. Leaves in pseudowhorls of 3 but usually on same plant also alternate and opposite, entire, stipulate, mostly less than 1 mm wide, 1- or rarely 3-veined. Inflorescence a cluster of usually 2 flowers, one staminate and one carpellate. Flowers without perianth; staminate flower with the stamen mostly 4-loculed, but rarely 2-8-loculed, the connective prolonged into a blunt tip; carpellate flowers with (1-)4-5(-8) carpels basally surrounded by a membranous envelope, the style less than 1 mm long, the stigma asymmetrically funnel-shaped. Fruit endocarp often spiny.

One species, *Zannichella andina*, is common in the lakes of the high Andes in Peru and Chile and should be expected throughout the Andes. Another species, *Z. palustris*, occurs in the lowlands, including the Rio Amazon delta. The two species can be separated by *Z. andina* having fruits 3 mm long or more and a rostrum ca. 1.7 mm long. *Zannichella palustris* has fruits ca. 2.5 mm long and a rostrum ca. 1.5 mm long.
NAJADACEAE A.L. Jussieu

References: Braun, A. Revision of the genus *Najas* of Linnaeus. J.Bot. 2:274-279 (1864). -- Clausen, R.T. *Najas arguta* in Central America and its relationship to *N. wrightiana*. Bull. Torrey Bot. Club 73:363-365 (1947). -- Haynes, R.R. The Najadaceae of the southeastern United States. J. Arnold Arbor. 58:161-170 (1977). -- Revision of North and Central American *Najas* (Najadaceae). Sida 8:34-56 (1979). -- Magnus, P. Beiträge zur Kenntniss der Gattung *Najas* L. Berlin viii + 64 pp. (1870). -- Najadaceae, In A. Engler and K. Prantl, Nat. Pflanzenfam. 2(1):217 (1889). -- Morong, T. The Najadaceae of North America. Mem. Torrey Bot. Club 3(2):1-65 (1893). -- Rendle, A.B. A systematic revision of the genus *Najas*. Trans. Linn. Soc. London, Bot. 11.5:379-444 (1899-1900). -- *Najadaceae*. In Engl., Pflanzenr. IV. 12:1-21 (1901).

A cosmopolitan family of herbaceous submersed monocotyledons with the characters of the single genus.

*Najas* Linnaeus

Sp. Pl. 2:1015 (1753); Gen. Pl. ed. 5. 445 (1754). Type: *Najas marina* L.
Carolinae Raf., J. Phys. Chim. Hist. Nat. Arts 89:259 (1819). (Type not designated).

*Caulinia* Willd., Mém. Acad. Roy. Sci. Hist. (Berlin) 87 (1798). Type: *C. fragilis* Willd. nom. illeg. (*Najas minor* All., *Caulinia minor* (All.) Cosson et Germain de St. Pierre).

*Fluvialis* Séquier, Pl. Veron. 3:99 (1754). (Based on same type as *Najas* L.).
*Fluvialis* Persoon, Syn. Pl. 2:530 (1807). (Based on same type as *Caulinia* Willd.)

*Hyas* Dumort., Anal. Fam. Pl. 61 (1829). (Type not designated)

*Ittnera* C.C. Gmel., Fl. Bad. 3:590 (1808). (Type not designated)

Plants herbaceous, monoecious or dioecious, annual or rarely perennial, glabrous, submersed in fresh or brackish waters. Stems slender, much branched, rooting at the lower nodes, sometimes armed with prickles on the internodes. Leaves subopposite or appearing whorled due to reduced internode length, sessile, each divided into lamina and sheath; laminae linear and flattened, 1-veined, sometimes dorsally armed with prickles on the 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 that decrease in cell number outward terminated by a large, sharp-tipped cell, or unicellular; sheaths variously shaped, each enclosing a pair of tiny hyaline scales, the margins usually toothed with 1-15 teeth per side. Flowers imperfect, axillary, sessile or short pedunculate, solitary or clustered, often subtended by an involucre; involucre clear, bronze, brown, light green, purple, or red-purple. Staminate flowers subtended by a membranous involucre or the involucre rarely absent, each consisting of a single stamen; peduncle at first short, elongating at anthesis, pushing the anther...
through the involucre; anther sessile, 1- or 4-loculed, dehiscing irregularly; pollen 3-celled, globular or ellipsoid, densely filled with starch, monocolpate, the wall with shallow reticulations, thin, not divided into exine and intine. Carpellate flowers sessile, 1-loculed, 1-ovuled; involucre absent or rarely present, ending in a short style with 2-4 branches. Fruit 1-seeded, dehiscing by decay of gynoecial wall; gynoecial wall extremely delicate, closely enveloping the seed. Seeds without endosperm, areolate, with a basal raphe, fusiform to obovate, occasionally asymmetrical at apex or recurved;

Fig. 10. A-H. *Najas guadalupensis*. A, habit; B, enlargement of leaf; C, leaf apex; D, axil with staminate flower after anthesis; E, transverse section of anther indicating 4-loculed anther; F, axil with ovulate flower; G, mature seed; H, enlargement of testa with 6-sided aerolae. I-O. *Najas podostemon*. I, habit; J, enlargement of leaf; K, leaf apex; L, enlarged leaf axils with immature staminate flower in axil on left, mature staminate flower after release of pollen in lower right axil, mature ovulate flower in middle right axil, and immature ovulate flower in upper right axil; M, transverse section of anther indicating 4-loculed anther; N, mature seed; O, enlargement of testa with 4-6-sided aerolae. (A-H from Haynes 8283, AAU; I-O from Dodson and Thien 699,S)

A generic treatment...
testa hard, brittle, 3 or several cell-layered, pitted or smooth; areolate formed by outer two layers of testa, variously rectangularly shaped, irregularly arranged or in 15-60 rows, the end walls often raised, giving the testa a papillose appearance; embryo elongate, without lateral enlargement of cotyledons.

A nearly cosmopolitan genus of perhaps 40 species, divided into 2 subgenera, *Najas*, with only one species, and *Caulinia*. The genus is represented in the neotropics by four species, at least two of which are widely distributed. Three species, *N. guadalupensis*, *N. arguta*, and *N. wrightiana* occur in Amazonia. All four species occur in Brazil.

Seed characters within *Najas* are most important for distinguishing the various taxa. Among the most distinctive characters are the arrangement of the areolae, either irregular (*N. marina*) or in rows (all other neotropical species of *Najas*); the shape of the areolae, longer than broad (*N. arguta*) or broader than long (*N. guadalupensis*) or 6-angled (*N. wrightiana*); the length of the seeds; and the shape of the seeds, fusiform (*N. guadalupensis*, *N. wrightiana*) 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 by layers of cells that decrease in cell number outward and terminated by a large, sharp-tipped cell. Because of the importance of seeds for the identification of *Najas*, care should be taken to collect seed-bearing specimens.

**CYMODOCEACEAE** N. Taylor

References: Hartog, C. den. An approach to the taxonomy of the sea-grass genus *Halodule* Endl. (Potamogetonaceae). Blumea 12: 289-312 (1964). -- The Sea-grasses of the World. North-Holland Publ. Co., Amsterdam. 275 pp + 31 pl. (1970).

Plants herbaceous, without milky juice, dioecious, perennial, glabrous, entirely submersed, in marine waters. Roots fibrous, few, aseptate, at lower noder or internodes. Stems slender, dimorphic, the lower rhizomatous, with a short erect stem at the nodes, the erect subtended by scarious scales, the scales ovate to elliptic, marked with more or less dark longitudinal strips or dots, without teeth, tubers, or turions. Leaves alternate or subopposite, divided into a blade and a sheath; sheath persisting longer than blade, leaving a circular scar when shed, stipulate, bi-auriculate, with membranous infravaginal scales in the axils, the auricles obtuse; blades entire, linear or subulate, often narrowed at the base, 3-several-veined, the venation parallel, the lateral veins inconspicuous, often ending in a tooth. Inflorescence solitary to cymose, without a subtending spathe. Flowers imperfect, the perianth absent; staminate flowers sub sessile or stalked, consisting of 2 anthers, the anthers 4-loculed, dehiscing vertically, dorsally connate at least a portion of length, attached to the filament at the same or different levels, the pollen filamentous; carpellate flowers sessile or sub sessile,
consisting of 2 distinct 1-ovuled carpels, each carpel with a style, the style occasionally divided into 2-3 stigmata, the ovule suborthotropus, pendulous. Fruit achene-like with a stony pericarp or drupaceous with a stony endocarp and a fleshy mesocarp. Seed solitary, straight; endosperm helobial in development, absent in mature seed. Type genus: Cymodocea König., nom. cons.

Members of the Cymodoceaceae have been combined with members of Potamogetonaceae and Zosteraeaceae by den Hartog (1970) and Radford, Ahles & Bell (1968) to comprise a taxon that has been called, respectively, Potamogetonaceae and Zosteraeaceae. The Cymodoceaceae, as here interpreted, are separated from the Zannichelliaceae and Zosteraeaceae by the Cymodoceaceae lacking of a spathe-like bract and from the Potamogetonaceae by the Cymodoceaceae having imperfect flowers.

Key to Genera

1. Leaves terete or semiterete; flowers in cymes; styles divided into 2 stigmata; anthers attached at same point on filament................................. Syringodium 1. Leaves flat; flowers solitary; styles with one stigma; anthers attached at different levels on filament............................................................ Halodule

Halodule Endl.

Gen. Pl. 1368 (1841). Type: Halodule tridentata (Steinheil) Endl. ex Unger.

Diplanthera Thouars, Gen. Nov. Madagasc. 3 (1806). Type: Diplanthera tridentata Steinheil.

Lower stems creeping, monopodial, rooting at the nodes; upper stems, erect, with 1-4 leaves and subtended by scarious elliptic or ovate scales. Leaves alternate or sub-opposite, sessile; sheath 1-6 cm long; blade linear, compressed, entire except apically, often narrowed at the base, 3-veined, the midrib conspicuous, widened at the apex, the lateral veins inconspicuous, each ending in a tooth, the apex 2-3 toothed. Flowers terminal, solitary, each enclosed in a leafy bract; staminate flowers stalked, consisting of two anthers attached to the filament at different levels and joined dorsally at their base; carpellate flowers subsessile, the carpels each with an elongate distinct style. Fruit achene-like, with a stony pericarp, slightly compressed, subglobose to ovoid, with a short beak.

A genus of perhaps six species, Halodule is widely distributed along the shores of tropical and subtropical oceans in both hemispheres. Three species, H. beaudettii, H. ciliata, and H. wrightii, are reported from the neotropics by den Hartog (1964, 1970). It is difficult to say whether three species actually occur in the neotropics as two of the species reported, H. beaudettii and H. ciliata, are not known in flower or fruit. Den Hartog separates all species of the genus on the shape of the leaf apex. Halodule wrightii is said to have a bicuspidate leaf apex, whereas H. beaudettii and H. ciliata are said to have tridentate leaf apices. The latter two species are sup-
posedly separated by *H. beaudettei* having median teeth that are acute and *H. ciliata* with obtuse median teeth. Phillips (1967), however, demonstrated that leaf tip variation within a single population of *Halodule* in southern Florida fully encompassed the morphological ranges of all three taxa. This raises questions as to the taxonomic validity of *H. beaudettei* and *H. ciliata*. Phillips, in fact, concluded that, at least in southern Florida, *H. beaudettei* was synonymous with *H. wrightii*. If only one taxon is accepted, *H. wrightii* is the correct name since it has priority.

**Syringodium** Kütz. in Hohen.

Alg. Marine Exsicc. 9. n. 426 (1860); Dandy & Taylor, J. Bot. 77: 116 (1939).
Type: *Syringodium filiforme* Kütz.

**Phycoschoenus** (Aschers.) Nakai, Ord. Fam. 211 (1943). Type: *Phycoschoenus isoetifolia* (Aschers.) Nakai.

Lower stems monopodial, with one or more roots; erect stems with 2-3 leaves and subtended by scarious, ovate, acute scales. Leaves alternate or subopposite, sessile; sheath 1.5-7 cm long; blades linear, terete, often narrowed at base, with one central

![Fig. 11](https://example.com/fig11.png)

Fig. 11. A-F. *Syringodium filiforme*. A and C, habit illustrating monopodial rhizomes and the cymose inflorescence; B, denticulate leaf apex, illustrating the near terete leaf just below apex; D, stalked staminate flower with 2 anthers, subtended by a reduced auriculate leaf; E, sessile carpellate flowers with 2 free carpels, subtended by a reduced auriculate leaf; F, fruit. (A-B from Ekman 17393, S; C-D from Stearn 327, S; E-F from Buchenau 3719, US).
vein and 2-10 peripheral veins. Inflorescence cymose, the lower branches dichasial, the upper monochasial. Flowers, axillary to a reduced leaf, the sheath of which is inflated; staminate flowers stalked, the anthers dorsally connate at base and attached at same height on the stalk, the stalk elongating at anthesis; carpellate flowers sessile, the carpels each with a short style which divides into 2 long stigmata. Fruits achene-like with a stony pericarp, ellipsoid to obovoid, quadrangular in cross section and with an inconspicuous dorsal median ridge.

A genus of two species, *Syringodium* is restricted to the Gulf of Mexico, Caribbean Sea, the Indian and western Pacific Oceans. One species, *S. filiforme* is known to occur in the neotropics.

ZOSTERACEAE Dumortier

References: Hartog, C. den. *The Sea-grasses of the World*. North-Holland Publ. Co., Amsterdam. 275 pp + 31 pl. (1970).

Plants herbaceous, without milky juice, monoecious or dioecious, perennial, glabrous, entirely submersed, in marine waters. Roots fibrous, few, aseptate, at lower nodes. Stems slender, branched, monopodial or sympodial, at each node a leaf or a bladeless prophyllum with a short foliaceous lateral branch, with teeth, tubers, or turions. Leaves alternate, divided into sheath and blade; sheath compressed, amplexicaul, either membranous and tubular or open and auriculate with scarious lobes, persisting longer than the blade, with 2 membranous, axillary, intravaginal scales, blades linear, entire, irregularly toothed, or slightly denticulate near apex, 3-11-veined, the veins parallel, the apex round-obtuse or retuse. Inflorescence a spadix surrounded by a peduncled spathe, the peduncle often partially adnate to the axis; spathe divided into blade and sheath, the sheath open with 2 partially overlapping margins, the blade flattened, photosynthetic; spadix linear to lanceolate, dorsally flattened, either enclosed within spathe sheath permanently or projecting out when mature, monoecious, with staminate and carpellate flowers alternating, or dioecious. Flowers imperfect, embedded in the spadix; perianth absent; staminate flowers often subtended by a bract (retinacula), the stamens 1, the anthers of 2 separate 2-loculed, deciduous thecae, the thecae dehiscent lengthwise, connected by a ridge-like connective, the pollen linear; carpellate flowers often subtended by a bract (retinacula), the carpels 1, elliptic or crescent-shaped, the ovule 1, orthotropus, pendulous, the style 1, the stigmata 2. Fruit achene-like, ovoid to ellipsoid or drupe-like and crescent-shaped, with soft exocarp and stony endocarp. Seed 1, ovoid or ellipsoid; embryo with a groove ventrally on hypocotyle in which cotyledon lies; endosperm helobial in development, absent in mature seed. Type genus: *Zostera* Linnaeus.

A family of three genera distributed in the temperate oceans of both northern and southern hemispheres. Two genera, *Zostera* and *Phyllospadix*, occur in the neotro-
pics, just reaching the Tropic of Cancer along the west shore of Baja California, Mexico. Heterozostera is endemic to temperate Australia.

Members of the Zosteraceae, as here interpreted, have been included in the Najadaceae by Gleason and Cronquist (1963) and have been combined with members of the Potamogetonaceae and Zannichelliae by den Hartag (1970), Fernald (1950), and Taylor (1909) to comprise a taxon that has been called, respectively, Potamogetonaceae, Zosteraceae, and Zannichelliae. As here interpreted, the Zosteraceae can be separated from the Potamogetonaceae by imperfect flowers and from the Zannichelliae by the presence of a spadix.

Key to Genera

1. Plants monoecious; spadix always enclosed within the spathe sheath.............. Zostera

1. Plants dioecious; spadix, when mature, projecting from the spathe sheath..........

Phyllospadix

Phyllospadix Hook.

Fl. Bor.-amer. 2: 171 (1838). Type: Phyllospadix scouleri Hook.

Plants dioecious. Stems monopodial, at each node a leaf and 2 or more unbranched roots with a short foliaceous lateral branch. Leaves distichous; sheath to 40 cm long, open with membranous margins, auriculate, ligulate, the basal portion decaying in age into bundles of woolly fibers; blade coriaceous, fibrous, irregularly toothed, 3-7 veined, the apex round-obtuse to retuse. Peduncle free; spadix linear, enclosed by spathe sheath when young, projecting out of sheath when mature, dioecious, but carpel-late spadix with rudimentary staminate flowers. Flowers embedded in the spadix in a zig-zag pattern, subtended by a bract (retinacula), the retinacula 1-veined, coriaceous, larger than the flowers; staminate flowers with thecae connected by an extremely reduced ridge-like connective, the retinacula recurved, inserted alongside the flowers; carpel-late flowers of 1 crescent-shaped carpel, the style short, the stigmas irregularly lobed or laciniate, the retinacula alternating with the flowers. Fruit drupaceous, crescent-shaped, with soft exocarp and hard fibrous endocarp. Seed ellipsoid.

A genus of five species widely distributed in the northern Pacific Ocean. Two species, P. scouleri and P. torreyi, occur in the neotropics, just reaching the Tropic of Cancer along the west coast of Baja California, Mexico.

Phyllospadix, according to Hartog (1970), grows attached to the rocky substrate in well-aerated, surf-beaten places. The species protects the rocky substratum from erosion and, by accumulating sand in and between the tussocks, transforms these areas into sandy beaches.

The neotropical species can be separated by the number of spathes per upper nodes, 2-5 in P. torreyi and rarely more than one in P. scouleri; by width of the leaves, 1.5
mm or less in *P. torreyi* and mostly 2–4 mm in *P. scouleri*; and by retinacula of the carpellate spadix being distinctly narrowed in *P. torreyi* whereas they are not narrowed in *P. scouleri*.

Fig. 12. A–E. *Phyllospadix scouleri*. A, habit illustrating the partly enclosed spadix; B, spathe with blade and sheath, the mature inflorescence coming out of the sheath; C, carpellate flowers, each carpel subtended by a bract; D, staminate flowers, each bract subtending one stamen with two bilocular thecae; E, fruits. (A–E from Dawson 13256, US; D from Moran 4188, US).

**Zostera L.**

Sp. Pl. 968 (1753). Type: *Zostera marina* L.

Plants monoecious. Lower stems rhizomatous with one or more unbranched roots and a bladeless prophyllum or complete leaf at each node; upper stems foliaceous. Leaf sheaths membranous, auriculate, ligulate, tubular or open with scarious margins; leaf-blade entire or slightly denticulate near the apex, 3–11-veined, the apex round-obtuse to retuse. Inflorescence with peduncle partially adnate to the axis; spadix lanceolate, enclosed permanently within spathe sheath, monoecious, with staminate and carpellate

A generic treatment ...
flowers alternating. Staminate flowers often subtended by a bract (retinacula), carpelate flowers without subtending bract (retinacula), consisting of 1 unilocular elliptic carpel. Fruit achene-like, ovoid to elliptic. Seed ovoid to ellipsoid, smooth, ribbed or ridged.

A genus of 12 species widely distributed in the temperate waters of both hemispheres. One species, Zostera marina, occurs in the neotropics along the Pacific coast of Baja California.

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