

**POTAMOGETONACEAE, ZOSTERACEAE,  
AND CYMODOCEACEAE**

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INTRODUCTION TO THE SEA-GRASSES

(C. den Hartog)

In earlier papers the sea-grasses were classified within two families, the *Potamogetonaceae* and the *Hydrocharitaceae*. As a result of thorough research of all genera of the order *Helobiae* (*Alismatidae*) by Tomlinson (1982), it has become evident that the very heterogeneous family *Potamogetonaceae* had to be split into a number of independent families. The sea-grasses which already had subfamily status, became families in their own right, the *Cymodoceaceae*, the *Zosteraceae*, and the *Posidoniaceae* (not in Malesia). The independence of these families is not contradicted by molecular genetical evidence (Les et al. 1997). According to the new vision the *Potamogetonaceae* are restricted to the genera *Potamogeton*, *Groenlandia* (not in Malesia), and *Ruppia*; however, there are molecular genetic indications that the latter genus may present a family of its own (Les et al. 1997). Therefore, and because of the comparable role in the vegetation of the different genera, an introduction to sea-grasses in general is given here, with a Key to the different families and genera of sea-grasses. The phytochemistry of all these groups is given by R. Hegnauer.

The few angiosperms that have penetrated into the marine environment, and are able to fulfil their vegetative and generative cycle when completely submerged, are generally known as sea-grasses. The name refers to the superficial resemblance to grasses, because of the linear leaves of most of the species. In spite of the fact that the number of sea-grass species is very small (only 60 to 65), they are of paramount importance in the coastal environment, where, when they occur, they generally form extensive beds. The sea-grass beds play an important part in the coastal ecological processes as they stabilise the muddy and sandy substrates on which they grow and they function as a nursery for many fishes, crustaceans, and other invertebrates. Apart from shelter they provide food to these organisms, but also to migrating birds, sirenias, turtles, and a lot of organisms from adjacent environments. In their turn the accompanying organisms leave their droppings, their shells or other protecting structures and in this way contribute to a slight alteration of the substrate. Furthermore there is export of sea-grass material to adjacent environments, for example the beaches on one side, and the deeper waters (including the abyssal sea) on the other side. Although nowadays the ecological importance of sea-grass beds seems obvious, this has not always been the case. In contrast to coral reefs and mangrove swamps, sea-grass beds are not confined to the tropics; they are also widely distributed along most of the temperate coasts, intruding even into the Arctic. However, the sea-grass beds of the tropical seas are formed by other species than those of the temperate seas. In the temperate seas representatives of the genera *Zostera*,

1) With contributions on palynology by R.W.J.M. van der Ham (Leiden) and phytochemistry by R. Hegnauer (Leiden).

*Phyllospadix* (North Pacific only), *Heterozostera* (Australia, Chile), *Posidonia* (Mediterranean, Australia) and *Amphibolis* (Australia only) build up the beds; of these only some *Zostera* species extend slightly into the tropics. The tropical sea-grasses belong to seven genera, viz. *Halodule*, *Cymodocea* (Indo-Pacific only, with one Mediterranean species), *Syringodium*, *Thalassodendron* (Indo-Pacific, with a widely distributed tropical species and an endemic species on the southwestern coast of Australia), *Enhalus* (Indo-Pacific), *Thalassia*, and *Halophila* (one temperate species in Australia, and a few species extending into the temperate zone). In the seas of Malesia eight of the twelve genera are represented by one or more species. So far 14 species of sea-grasses have been recorded, but this number may increase as the deeper coastal waters become better explored. In Indonesia hitherto 12 species have been found. The Philippines and Papua New Guinea have 13 species. Special surveys have been published about the sea-grasses of the Philippines (Meñez et al. 1983) and New Guinea (Brouns 1986). For the Indonesian sea-grasses a very fine study has been published by Tomascik et al. (1997) as chapter 18 in their standard work 'The ecology of the Indonesian seas'.

*References:* Brouns, J.J.W.M., Science in New Guinea 12 (1986) 66–92. — Les, D.H., M.A. Cleland & M. Waycott, Syst. Bot. 22 (1997) 443–463. — Meñez, E.G., R.C. Phillips & H.P. Calumpong, Smithson. Contr. Mar. Sci. 21 (1983) 1–40. — Tomascik, T., A.J. Mah, A. Nontji & M.K. Moosa, The ecology of the Indonesian seas 2 (1997) 829–906. — Tomlinson, P.B., Anatomy of the Monocotyledons 7, Helobiae (Alismatidae) (1982).

#### KEY TO THE SEA-GRASS GENERA OF MALESIA

- 1a. Leaves ligulate. Roots branched or unbranched ..... 2
- b. Leaves without a ligula. Roots unbranched (HYDROCHARITACEAE, Flora Malesiana I, 5: 381; 6: 952; 7: 828; 9: 566; 10: 717) ..... 6
- 2a. Leaves without tannin cells. Roots unbranched. Monoecious. Flowers arranged on one side of a flattened spadix enclosed by a spathe (ZOSTERACEAE, p. 197) ..... *Zostera* (p. 198)
- b. Leaves with numerous tannin cells. Roots branched or unbranched. Dioecious. Flowers solitary or in pairs, terminating a short branch arising from a leaf axil, or arranged in a cymose inflorescence (CYMODOCEACEAE, p. 201) ..... 3
- 3a. Rhizome monopodial, herbaceous, with a short erect shoot at each node. Leaf sheaths persisting longer than the blades. Anthers pedunculate ..... 4
- b. Rhizome sympodial, ligneous, with 1 or 2 unbranched or little branched erect stems at every fourth node; 1–5 branched roots on the internode preceding the stem-bearing node. Leaf blades 6–13 mm wide, with 17–27 nerves; leaf blades shed with their sheaths. Anthers sessile, each with an apical appendage. Ovary with a short style, divided into 2 stigmata ..... *Thalassodendron* (p. 213)
- 4a. Leaves flat. Flowers solitary ..... 5
- b. Leaves subulate. Roots branched. Flowers arranged in a conspicuous cymose inflorescence. Anthers attached at the same height on the peduncle, without an apical process. Ovary with a short style and 2 short stigmata .... *Syringodium* (p. 211)
- 5a. Leaves up to 3.5 mm wide, with 3 nerves. Roots unbranched. Anthers not attached at the same height on the peduncle. Ovary with 1 undivided style ..... *Halodule* (p. 207)

- b. Leaves up to 9 mm wide, with 7–17 nerves. Roots branched. Anthers attached at the same height on the peduncle, each crowned by a subulate process. Style long, divided into 2 stigmata ..... *Cymodocea* (p. 203)
- 6a. Leaves linear, not differentiated into a blade and a petiole, with numerous tannin cells ..... 7
- b. Leaves differentiated into a petiole and a blade; leaf blades ovate, elliptic, or lanceolate; tannin cells absent. Flowers unisexual, solitary. Male flowers pedicellate, with 3 tepals and 3 stamens. Female flowers consisting of a sessile ovary with reduced perianth and a style with 3–5(–6) stigmata ..... *Halophila* Thouars
- 7a. Rhizome at least 1 cm thick, covered with persistent black, fibrous strands. Roots cord-like. Leaves 1.25–1.75 cm wide. Dioecious. Flowers with 3 petals and 3 sepals. Male spathe with numerous flower buds which become detached just before flowering, the flowers then freely floating on the surface. Female spathe with only one flower on a very long peduncle which contracts spirally after anthesis. Fruit densely set with erect bifid appendages ..... *Enhalus* Rich.
- b. Rhizome at most 0.5 cm thick, with thin roots. Internodes longitudinally grooved and with a scale at each node. Leaf bearing shoots arising from the rhizome at distances of several internodes. Leaves 4–11 mm wide, with 10–17 nerves. Leaf tip obtuse. Dioecious. Male and female spathe containing 1 flower. Flowers with 3 tepals only. Stamens 3–12, subsessile. Ovary with 6 bifid styles. Fruit shortly stalked, globose, echinate, stellately dehiscent ..... *Thalassia* Banks ex König

## PHYTOCHEMISTRY

(R. Hegnauer)

Formerly a number of families of aquatic plants were united in an order, *Helobiae* or *Fluviatiles*. In modern systems (Dahlgren et al. 1985; Takhtajan 1980) the same taxa form the superorder *Alismatiflorae* or *Alismatanae* with two orders, *Alismatales* and *Najadales*. In these two classifications some of the larger families are split into several smaller ones. The marine taxa, the sea-grasses, form now *Cymodoceaceae*, *Posidoniaceae*, *Zosteraceae* (all formerly tribes of *Potamogetonaceae*) and two subfamilies of *Hydrocharitaceae*: *Halophiloideae* and *Thalassioideae*. Still another genus, *Enhalus*, belonging to *Hydrocharitaceae*–*Vallisnerioideae*, is a true sea-grass taxon. The rest of *Alismatanae* comprises marsh-plants and plants living in fresh or brackish water. During evolution representatives of *Helobiae* acquired many adaptations to aquatic life, and sea-grasses additionally had to adapt to saline conditions. Physiological processes are largely involved in adaptations to such habitats, but much has still to be learnt about metabolism and chemistry of these plants. For Flora Malesiana a combined treatment of the chemical characters of all members of the former *Helobiae* (i.e. *Butomaceae*, *Limnocharitaceae*, *Alismataceae*, *Hydrocharitaceae* with four subfamilies, *Aponogetonaceae*, *Scheuchzeriaceae* s.s., *Juncaginaceae* incl. *Lilaeaceae*, *Posidoniaceae*, *Potamogetonaceae* s.s., *Ruppiaceae*, *Zannichelliaceae*, *Cymodoceaceae*, *Zosteraceae* and *Najadaceae*, all sensu Takhtajan 1980) seems to be adequate. There are two main reasons for such an approach. First the chemistry of many of these taxa is still unknown or only superficially known at present. Secondly, many chemical features of *Helobiae* resulted from adaptations to aquatic habitats. This makes taxonomic interpretation of several of their chemi-

cal characters difficult, because ecologically conditioned parallelisms and convergencies occur frequently.

More or less comprehensive reviews of primary and secondary metabolites known to be stored by *Helobiae* are available in Dahlgren et al. (1985), Harborne and Williams (1994), Hegnauer (1963, 1986) and Tomlinson (1982). The last-mentioned author pays specifically attention to excretory structures (*Alismataceae*, *Limnocharitaceae*, *Aponogetonaceae*, *Lilaeaceae*), crystals (oxalates of calcium), starch and 'tannins' which often are deposited in idioblastic tannin cells corresponding to idioblasts formerly known as myriophyllin cells. Such cells were discussed from a chemical point of view on pp. 11–18 of Hegnauer (1963). The following summary is mainly based on Hegnauer (1963, 1986) and some more recent publications and accepts two main subdivisions of *Helobiae*: Sea-grasses, which additionally needed halophytic adaptations, and *Helobiae* as a whole.

Sea-grasses tend to accumulate phenolic acids such as caffeic, ferulic, protocatechuic, gallic (quite unusual in monocots) and still other acids and acidic sulphates of caffeic acid derivatives and/or flavonoids. Sulphates occur also in many non-halophytic *Helobiae*. Moreover, sea-grasses contain extremely large amounts of sugars and sugar-like compounds. Sucrose, fructose, glucose and, *Posidoniaceae* excepted, cyclitols are the main 'compatible solutes' of sea-grasses. Myoinositol is present in *Cymodoceaceae*, *Hydrocharitaceae* and *Zosteraceae*. Chiro- and mucoinositol are present in *Amphibolis*, *Cymodocea*, *Syringodium* and *Thalassodendron*, but not in *Halodule* (all *Cymodoceaceae*), and a methylether of mucoinositol seems to be characteristic of the genus *Amphibolis*. The production of apiose-containing pectin-like cellwall components is a striking feature of probably all sea-grasses and of some *Helobiae* living in brackish water (detected in *Ruppia spiralis* and *Potamogeton pectinatus*, but not in *P. crispus*, *natans* and *pusillus*). The apiose-containing cell wall-heteropolysaccharide of *Zostera marina* and *Z. pacifica* and *Phyllospadix scouleri* was called zosterin; it has an (1 $\alpha$ -4)-linked polygalacturonane core bearing side-chains composed of apiose, xylose, O-methylxylose, arabinose, galactose and possibly still other monoses. Investigations with *Phyllospadix torreyi* showed that 'zosterin' is rather a mixture of acidic, apiose-containing heteropolysaccharides of variable composition than an individual compound. Paradoxically, apiose-containing 'pectins' also occur in the cell walls of all *Lemnaceae*, a family of freshwater plants, with an extremely reduced morphological and anatomical organization. The simultaneous occurrence of such unusual cell wall constituents in sea-grasses and *Lemnaceae* may represent one of the many convergencies which can be expected with ecological superspecialists. Apiosylpectins of *Lemnaceae* are chemically better known than those of sea-grasses (see pp. 683–684 in Hegnauer 1986). Lipid fractions of Australian sea-grasses were studied thoroughly; they contain alkanes, alkanols, phytosterols, several types of fatty acids, phytol, chlorophylls, triglycerides and still other constituents. According to Gillan et al. (1984) and Nichols et al. (1982) some particular points of lipid spectra of individual taxa may be taxonomically useful. Examples are a phytosterol fraction with a high amount of 28-isofucosterol in the genus *Halophila* (3 species investigated) and a total lack of C<sub>24</sub>-C<sub>28</sub>- $\alpha,\omega$ -dicarboxylic acids and a very low concentration of C<sub>20</sub>-C<sub>28</sub>- $\omega$ -hydroxyacids in *Heterozostera tasmanica*. Gillan et al. (1984) recommended to reconsider the classification of *Halophila*.

*Helobiae* as a whole — Starch seems to be the main storage product of perennial parts of all *Helobiae*. In non-seagrasses it is usually accompanied by lesser amounts of su-

crose, raffinose and stachyose. The latter was for the first time demonstrated to occur in monocots by its isolation from rhizomes of *Butomus umbellatus* and by its identification in rhizomes of *Aponogeton distachyum*.

Secondary metabolites are represented mainly by flavonoids and related phenolic compounds and by isoprenoids, predominantly sesqui-, di- and triterpenes, in helobial families.

**Flavonoids:** Flavones, flavone-O-glycosides and flavone-C-glycosides dominate leaf flavonoid patterns. They occur as such or as acidic sulphates; 7-sulphates of apigenin, luteolin, chrysoeriol and diosmetin and 7,3'-disulphate of diosmetin. Flavone sulphates are often accompanied or replaced by sulphates of chlorogenic acids or similar esters of caffeic acid. No sulphates were detected in *Butomaceae* (only *Butomus umbellatus* investigated), 16 species of *Potamogeton* and a few members of *Alismataceae* (*Sagittaria sagittifolia*), *Juncaginaceae* (*Triglochin maritima*), *Ruppiaceae* (*Ruppia rostellata* and *spiralis*) and *Najadaceae* (*Najas graminea* and *guadalupensis*). *Phyllospadix iwatensis* yielded phyllospadin, a new alkaloidal flavonoid which was shown to be a C-C-conjugate between 6-methoxyapigenin and N-methylpyrrolidine. Derivatives of 6-hydroxyapigenin and 6-hydroxyluteolin were also isolated from *Phyllospadix japonica*. Proanthocyanidins are of sporadic occurrence; they were only detected in *Butomus umbellatus*, *Elodea canadensis*, *Hydrocharis morsus-ranae*, *Posidonia oceanica*, *Stratiotes aloides* and *Syringodium filiforme*. Flavonols seem to be rare; they were tentatively identified in a few taxa and isolated only once. Leaves of *Cymodocea nodosa* yielded monoglucosides of quercetin and isorhamnetin. Red colours of leaves may be caused by anthocyanins; a new compound, the 3-glucoside of the 5-methylether of cyanidin, was isolated from fresh spring shoots of *Egeria densa* and *Elodea nuttallii*. Anthocyanins, however, were never detected in *Potamogeton*; in this genus reddish colorations of stems and leaves always seem to be caused by the carotenoid rhodoxanthin. In *Helobiae* with only submersed leaves flavonoid accumulation may be reduced or totally suppressed. Les and Sheridan (1990) published remarkable results of investigations with 17 species of *Potamogeton*. A total of 12 flavonoids was detected and identified in their leaves, i. e. the aglyca apigenin, luteolin, chrysoeriol (= 3'-methylether of luteolin) and luteolin-7-methylether, the 6-C-glucoflavones isovitexin, iso-orientin and isoscoparin and five 7-glucosides and 7-glucuronides of apigenin, luteolin and chrysoeriol. 6-C-Glucoflavones were shown to predominate in floating leaves of heterophyllous species. These compounds are assumed to be highly effective as UV-filters. Six of the eight investigated heterophyllous species had strongly reduced flavonoid patterns in their submersed leaves. Homophyllous, wholly submersed species can be divided into two groups: broad-leaved species with a flavonoid chemistry similar to floating leaves of heterophyllous taxa, and linear-leaved ones with mostly flavonoid-poor leaf spectra. An exception in the latter group was *P. zosteriformis* with luteolin, the 7-glucosides of luteolin and chrysoeriol and the 7-glucuronides of apigenin and luteolin. The authors discuss thoroughly possible ecological and evolutionary backgrounds of the observed flavonoid patterns and offer a hypothetical scheme for the evolution of chemical heterophylly in *Potamogeton*.

**Terpenoids** (C<sub>15</sub>-C<sub>30</sub>) became somewhat better known from a few species of *Alismataceae*, *Hydrocharitaceae* and *Potamogetonaceae*.

*Alismataceae* (Fl. Males. I, 5: 317; 6: 915): Rhizomes of *Alisma orientale* (Sam.) Juz. (= *A. plantago-aquatica* L. var. *orientale* Sam.) are of considerable importance in orien-

tal medicine (China, Japan). The crude drug 'Alismatis Rhizoma' was investigated by Japanese and Chinese scientists and shown to contain an array of sesquiterpenes and tetracyclic triterpenes belonging structurally and stereochemically to the so-called protostane-type; the *Alisma* protostanes are called alisols A to G and also occur as acetates, epoxides and still other derivatives. One diterpene, *ent*-kaurane-2,12-dione, and a mixture of phytosterols were also isolated. The sesquiterpenoids are the bicyclic guaiane-type compounds alismol, alismoxide, its methylether, the orientalols a–d and their acidic sulphates, the likewise bicyclic eudesma-4(14)-en-1 $\beta$ ,6 $\alpha$ -diol and the two monocyclic sesquiterpene hydrocarbones germacrene C and D. In some recent papers Yoshikawa et al. (1993a, b) and Nakajima et al. (1994) have shown that several of the constituents isolated from Chinese, Taiwanese and Japanese crude drugs are not present in appreciable amounts in fresh rhizomes, but rather originate during crude drug production and extraction processes from genuine constituents. Moreover, differences between plants collected in different regions may exist. A large part of 'Alismatis Rhizoma' presently used in Japan is no longer of Japanese origin. At present this crude drug seems to be mainly imported from two different regions of China: A crude drug known as 'Sentaku' comes from the province Szechwan (= Sichuan) and another known as 'Kentaku' is imported from Fukien (= Fujian). Protostane-type compounds are assumed to yield by additional methyl migrations lanosterol- and cycloartane-type tetracyclic triterpenes. The alisols of *Alisma* were the first natural products shown to have the protostane-type skeleton. As far as sesquiterpenes of 'Alismatis Rhizoma' are concerned, Yoshikawa et al. and Nakajima et al. assume that eudesmane- and guaiane-type compounds mainly arise during processings from the germacrenes. 'Alismatis Rhizoma' ('Zexie') is treated on pp. 75–77 in Tang and Eisenbrand (1992). Alisols were also isolated from inflorescences of European *Alisma plantago-aquatica* (Eich et al. 1987).

*Echinodorus grandiflorus* is believed to have antirheumatic properties in Brazil; its leaves yielded the novel cembrene-type diterpene echinodol, C<sub>20</sub>H<sub>32</sub>O, and stigmasterol (Manns & Hartmann 1993). *Sagittaria sagittifolia*, an Eurasian plant, is said to be used in China to treat skin diseases; whole plants collected in India yielded sitosterin, hentriacontanone and a clerodanoid diterpene sagittariol, C<sub>20</sub>H<sub>34</sub>O<sub>2</sub>, and a congener, an oxodeoxyderivative of sagittariol. *Sagittaria trifolia*, 'Kuwai', is of culinary importance in Japan. This plant was shown to contain four anti-allergically active *ent*-isopimaradiene-type diterpenes; it yielded additionally some other diterpenes, two diterpene glucosides, the sagittariosides a and b, and an arabinoside of the *Thalictrum*-glucoside thalictoside, which is 1-nitro-2-*p*-glucosyloxyphenylethane (Yamaguchi et al. 1993).

*Cymodoceaceae*: Leaf lipids of *Amphibolis antarctica* of the south- and westcoast of Australia change drastically with leaf age. Young leaves contain appreciable amounts of alkanes, but no diterpenes, and mature leaves lack alkanes, but contain the diterpenedienes cleistanthene in leaves sampled in Stark Bay and cleistanthene, sandaracopimaradiene and isopimaradiene in leaves sampled in the neighbourhood of Perth (Dunlop 1985; Kaufman et al. 1987).

*Hydrocharitaceae* (Fl. Males. I, 5: 381; 6: 952; 7: 828; 9: 566; 10: 717): Lipidic constituents of *Elodea canadensis* were studied comprehensively; they yielded a strange tetraterpene, the ubiquitous aliphatic diterpene phytol, two stereoisomers of an endoperoxide of abieta-8(14)-en-18-oic acid, two unusual hydroxyhexadecatrienic acids and two C<sub>17</sub> alka-triene derivatives, one of which was proved to be identical with

avocadynofuran (C<sub>17</sub>-chain containing a terminal furan-ring and a terminal acetylenic unsaturation) of *Persea americana* (Mangoni et al. 1984; Previtera et al. 1985; Monaco et al. 1987).

*Potamogetonaceae*: Flavonoids were already treated above. An additional chemotaxonomic paper devoted to three species of *Potamogeton* subg. *Potamogeton* sect. *Axillares* has to be mentioned. Roberts and Haynes (1986) studied 11 populations (4 Europe, 6 USA, 1 Guatemala) of *P. perfoliatus*, 3 populations (1 Denmark, 2 Michigan) of *P. praelongus* and 6 American populations of *P. richardsonii*, which is believed by some authors to have evolved from hybrid populations of the two first mentioned species. A total of 9 flavonoids, i. e. the aglyca apigenin, luteolin and chrysoeriol, the 7-glucosides of these three flavones, apigenin-7-diglucoside, luteolin-7-glucuronide and the 6-C-glucoside of luteolin (iso-orientin), were isolated. Presence of apigenin derivatives and isovitexin in *P. perfoliatus* and *P. praelongus* and absence of these 'marker' metabolites in *P. richardsonii* favour authors who deny the hybrid theory for *P. richardsonii*. A labdanoid diterpene called potamogetonin was isolated from seeds (probably fruits) of *Potamogeton ferrugineus* in Uruguay.

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## POTAMOGETONACEAE

(G. Wiegleb)<sup>1</sup>

*Potamogetonaceae* Dumort., Anal. Fam. Pl. (1829) 59, 61, nom. cons. — Type genus: *Potamogeton* L.

*Ruppiaceae* Horan ex. Hutch., Fam. Flow. Pl. 2 (1934) 48, nom. cons. — Type genus: *Ruppia* L.

Perennial or annual aquatic herbs, rarely semi-terrestrial. *Stems* elongate, flexible, vertical shoots ascending in the water, horizontal shoots mostly creeping, stoloniferous; vessels absent or restricted to the roots, if present with scalariform perforation plates. *Leaves* alternate (distichous) or subopposite or rarely in whorls of 3 (not in Malesian species), simple, entire or dentate, often heteromorphic (in *Potamogeton*); lamina with dense or sparse, parallel or arching veins; often with distinct transverse veinlets; stomata rudimentary; floating leaves broad and petiolate; submerged leaves capillary to lanceolate or elliptic; stipule-like appendages ('stipules') present or absent; squamulae intravaginales present. *Inflorescence* a pedunculate spike, simple (in *Potamogeton*) or umbel-like (in *Ruppia*) in fruit. *Flowers* small, bisexual, dimerous, trimerous, or (generally) tetramerous. *Perianth* (sepaloid tepals) of 2–4, bract-like, clawed scales inserted opposite each stamen. *Androecium* of 2–4 stamens, adnate to the perianth at the base; anthers sessile; pollen grains globose, elliptic or elongate, isobilateral and three-celled when dispersed; endothelial cells with Girdle type of wall-thickening. *Gynoecium* superior, of 1–4 (rarely 8 or 14) free or partly united carpels; style 1, usually short, with a stigmatic surface of the Dry type; ovule ventral, anatropous or varying ontogenetically from anatropous to campylotropous, crassinucellate and with a parietal cell; embryo sack formation of *Polygonum* type; endosperm formation helobial. *Fruit* drupaceous or achene-like, or rarely (not in Malesia) baccate; 1-seeded; embryo slightly to distinctly curved, macropodous.

### DISTRIBUTION

Three genera, with c. 80 species all over the world. The non-Malesian genus is the monotypic *Groenlandia* Gay.

### HABITAT AND ECOLOGY

The family comprises aquatic herbs, colonising both fresh and brackish water. The altitude ranges from sea level to 4500 m (in Malesia 2400 m).

### LIFE HISTORY AND REPRODUCTIVE BIOLOGY

Flowers are usually strongly protogynous. Pollination is anemophilous, epihydrophilous or hypo-hydrophilous (submerged autogamy). Diaspores are achenes with fleshy exocarp and stony endocarp, dispersed by waterfowl and also by water. Additionally, various modes of vegetative reproduction are developed (see respective genera).

1) *Ruppia* by C. den Hartog. Pollen morphology by R.W.J.M. van der Ham.



## TAXONOMY

Affiliation and subdivision of *Potamogetonaceae* have largely differed. Engler classified the family with his *Helobiae*. It is now generally agreed to be classified with the *Potamogetonales* (*Najadales, Zosterales*), from which *Alismatales* (incl. *Hydrocharitales*) are excluded. Cladistic analyses (Dahlgren et al. 1985) showed that *Potamogetonaceae* (incl. *Ruppiceae*) are closely associated with *Zosteraceae* and *Posidoniaceae*, while *Zannichelliaceae* and *Cymodoceaceae* are more closely allied with *Najadaceae*. *Juncaginaceae* and *Scheuchzeriaceae* form a distinct third clade. Recent molecular evidence indicates however a close relationship between *Potamogeton* subg. *Coleogeton* and *Zannichellia* (Les et al. 1996; Kubitzki 1998).

*Potamogetonaceae* s.s. are subdivided into 2 subfamilies (Tomlinson 1982), which have also been regarded as separate families:

Subfamily *Potamogetonoideae*: Differentiation of shoot system into horizontal and vertical shoots mostly well developed; branching mainly sympodial; leaves diverse, often heterophyllous; stipules mostly axillary, independent of the blade; leaf trace system from the stele consisting of at least 3 separate vascular bundles; flowers usually more than 2 per spike; stamens and carpels usually 4; sepaloïd tepal adnate to the stamen connective; peduncle not elongating in fruit; carpel stalk not elongating after pollination.

Subfamily *Ruppioideae*. Differentiation of the shoot system poor; branching monopodial; leaves uniformly linear, with an attached sheathing base; leaf trace system from the stele consisting of a single bundle; flowers 2 per spike; each with 2 stamens and few to several carpels; tepals absent; peduncle elongated; carpel stalk often elongating after pollination.

*References*: Dahlgren, R.M.T., H.T. Clifford & P.F. Yeo, *Fam. Monocot.* (1985) 312–315. — Kubitzki, K, *Families and genera of vascular plants*, vol. 4 (1998). — Les, D.H., M.A. Cleland & C.T. Philbrick, *Am. J. Bot.* 82/6, Suppl. (1985) 144. — Tomlinson, P.B., *Anatomy of the Monocotyledons 7, Helobiae (Alismatidae)* (1982) 270–335.

## MORPHOLOGY

Both vegetative and generative morphology have been reviewed by Tomlinson (1982). *Potamogeton* has a complex modular organisation being difficult to describe both in terms of classical and functional morphology. Some terms concerning shoot types, branching patterns, and longevity used in the descriptions need some explanation (see also Kadono & Wiegleb 1989; Wiegleb & Brux 1991). Two different shoot types are distinguished, namely the 'vertical shoot' (incl. also the lateral 'renewal shoots') and the 'horizontal shoot'. Both are differentiated by leaf insertion, vegetative anatomy, and their potential to bear spikes (Tomlinson 1982). This differentiation is visible in all species, despite the fact that some species can change their growth pattern in an opportunistic way (like e.g. *P. oxyphyllus*). The term 'stem' is used for the main axis of the vertical shoot. In contrast to Tomlinson the term 'rhizome' is avoided as it is morphologically incorrect. Instead the term 'horizontal shoot' is used throughout. In Malesian species it is mainly found as 'lower horizontal shoot' being mostly stoloniferous, rarely rhizomatous, or developed as complex of differently shaped parts.

A complete account of the branching pattern is avoided as it would require an extensive explanation. An expression like 'stem of vertical shoot unbranched' indicates that the respective species does not produce renewal shoots below the pseudo-opposite involucreal leaves. But it may produce e.g. turion-bearing 'upper horizontal shoots' serving for vegetative reproduction and short-range dispersal. In accordance with Tomlinson (1982) the term 'inflorescence' refers to the 'spike-peduncle unit' in total. This contrasts with Hagström's (1916) use of this term who considered the whole architecture of a plant individual.

Undifferentiated expressions like 'annual' or 'perennial' for species are avoided. The terms used always relate to the above-ground and below-ground parts separately. Additional information on seasonality is given, if available. For the description of winter buds, a simplified system following Hutchinson (1975) is used, distinguishing among turions (mostly on vertical shoots), tubers, and multiple complexes (both mostly on horizontal shoots).

Recently, Sorsa (1988) reviewed the pollen morphology of *Potamogeton* and *Groenlandia*.

*References:* Hagström, J.O., Kungl. Svenska Vetenskapsakad. Handl. 55, 5 (1916) 1–281. — Hutchinson, G.E., Treatise of Limnology 3 (1975) 236–238. — Kadono, Y. & G. Wiegleb, Nordic J. Bot. 9 (1989) 167–178. — Sorsa, P., Ann. Bot. Fenn. 25 (1988) 179–199. — Tomlinson, P.B., Anatomy of the Monocotyledons 7, Helobiae (Alismatidae) (1982) 270–335. — Wiegleb, G. & H. Brux, Aquat. Bot. 39 (1991) 131–146.

## POLLEN MORPHOLOGY

(R.W.J.M. van der Ham)

The *Potamogetonaceae* show two main pollen types, one occurring in *Potamogeton* and *Groenlandia*, the other in *Ruppia*. The pollen grains of *Potamogeton* and *Groenlandia* (Cranwell 1953; Valdes et al. 1987; Sorsa 1988; Wang 1990; Grayum 1992) are inaperturate, spheroidal to ellipsoidal monads, and are anemo- or hydrophilous. Grain size is 16–49 µm (ratio long and short axis 1.08–1.49). Monocolpate pollen was reported by Sharma (1968) and Huang (1972), but the colpus-like structures observed are probably due to tearing. Although the exine is inaperturate, Wodehouse (1959) found a prominent elongate thickening of the intine in the pollen of *P. natans*, which suggests a crypto-aperturate condition. Schwanitz (1967) found an evenly thick (0.3 µm) intine in *P. pectinatus* and *P. perfoliatus*. The exine is 0.7–1.4 µm thick (exines up to 2.4 µm have been reported by Mitroiu 1970). The sexine is semitectate-columellate, and always thicker than the nexine (endexine absent). Ornamentation is reticulate, more or less homobrochate, with angular lumina up to 4 µm across. The muri are simplicolumellate, and usually covered with scabrae. Based on grain shape and size, and on features relating to ornamentation, Sorsa (1988) distinguished 5 pollen types in *Potamogeton* and *Groenlandia*, but the mutual differences are rather small. The two subgenera *Potamogeton* and *Coleogeton* are more or less distinct: grain size and size of the lumina are relatively large in the latter. *Groenlandia* pollen is intermediate between that of *Coleogeton* and that of linear-leaved members of subgenus *Potamogeton*.

The pollen grains of *Ruppia* (Cranwell 1953; Schwanitz 1967; Valdes et al. 1987; Grayum 1992) are 3-porate heteropolar, arcuate, bilateral monads. The distal pole is

convex, the proximal one concave. Grain size (largest equatorial diameter) is 35–105  $\mu\text{m}$ ; the polar axis is approximately half as long. The three apertures are situated at the distal pole and at both ends of the long equatorial axis. They represent thin areas with a reduced, indistinctly reticulate pattern, which are bulging in fresh, unacetolysed grains. They were sometimes observed to be fused in *R. cirrhosa* (Díez et al. 1988). The exine is 1.5–2  $\mu\text{m}$  thick. The nexine is  $\leq 0.1 \mu\text{m}$  (endexine absent), and the columellate infratectum is 0.5–1  $\mu\text{m}$  thick. The tectum is about twice as thick as the nexine, and bears scabrate processes where the columellae meet. The ornamentation is reticulate, more or less heterobrochate, with angular lumina up to 5  $\mu\text{m}$  in diameter, and narrow simplicolumellate muri. The intine is c. 0.4  $\mu\text{m}$  thick, evenly thick, or maybe slightly thicker under the apertures (Wodehouse 1959). Pollination in *Ruppia* is hydrophilous (see literature cited in Cox & Humphries 1993). The pollen grains, when shed on the water, float on the water surface (convex pole downwards) by means of air bubbles adhering to the reticulate sexine; when shed below the surface the grains will sink (Schwanitz 1967).

The oldest fossil *Potamogeton* pollen dates from the Upper Miocene of Spain (Muller 1981). A record of Palaeocene *Ruppia* pollen needs confirmation (Muller 1981).

*References:* Cox, P.A. & C.J. Humphries, Bot. J. Linn. Soc. 113 (1993) 217–226. — Cranwell, L.M., Bull. Auckl. Inst. Mus. 3 (1953) 3–91. — Díez, M.J., S. Talavera & P. García-Murillo, Candollea 43 (1988) 147–158. — Grayum, M.H., Monogr. Syst. Bot. Missouri Bot. Gard. 43 (1992) 1–167. — Huang, T.C., Pollen flora of Taiwan (1972). — Mitroiu, N., Acta Bot. Hort. Bucurest. 1969 (1970) 3–243. — Muller, J., Bot. Review 47 (1981) 1–142. — Schwanitz, G., Pollen et Spores 9 (1967) 9–48, 183–209. — Sharma, M., J. Palynol. Spec. Vol. (1968) 1–98. — Sorsa, P., Ann. Bot. Fennici 25 (1988) 179–199. — Valdes, B., M.J. Díez & I. Fernández, Atlas polínico de Andalucía Occidental (1987). — Wang, J.G., Acta Phytotax. Sin. 28 (1990) 372–378. — Wodehouse, R.P., Pollen grains (1959).

## USES

Some species are cultivated for decorative purposes in artificial ponds, some are used as aquarium plants. In tropical areas *Potamogeton*, like other aquatic plants, is used as green manure.

## KEY TO THE GENERA

- 1a. Fruits in simple spikes, sessile; stamens 4 or rarely 3; perianth of 3 or 4, clawed, scale-like segments ..... **Potamogeton** (p. 177)  
 b. Fruits in umbels, borne on flexible peduncles; stamens 2; perianth absent .....  
 ..... **Ruppia** (p. 193)

## POTAMOGETON

*Potamogeton* L., Sp. Pl. (1753) 126; Gen. Pl. ed. 5 (1754) 61. — Type species: *Potamogeton natans* L.

*Hydrogeton* Lour., Fl. Cochinch. 1 (1790) 244. — Type species: *Hydrogeton heterophyllus* Lour.

Aquatic herbs, rarely with terrestrial forms, perennial, forming more or less persistent shoot complexes, under seasonal conditions partly annual, reproducing by seeds. *Stems* usually branched, terete or subterete, sometimes compressed to subquadrangular,

forming a shoot complex of vertical and horizontal shoots; vertical shoots ascending in the water, branched or unbranched; horizontal shoots stoloniferous or rhizomatous, creeping in or above the sediment, often repeatedly branched. Adventitious roots born from the lower nodes of vertical shoots and at each node of horizontal shoots, either single or in bunches up to 10. *Leaves* alternate, but subopposite in the flowering region, margin entire or dentate, only submerged or both submerged and floating leaves present, all leaves with stipules; floating leaves long petiolate, usually oblong or oblong-lanceolate, leathery, coriaceous; submerged leaves membranous, translucent, sessile or petiolate, laminar or phyllodial, capillary, lanceolate or oblong-lanceolate; stipules either adnate to the leaf base for a  $\pm$  long portion, or axillary, free from the leaf base, in either case either connate or convolute, persistent or caducous, often decaying to fibres starting from the apex. *Inflorescence* a bractless cylindrical spike, long-peduncled, mostly emergent, with 1–20 contiguous or distant whorls of flowers, whorls 1–4-flowered; peduncle about the same diameter as the stem or thickened at the tip or thickened throughout, straight or slightly curved, in the axils of subopposite leaves, rarely in the axils of alternate leaves or opposite to alternate leaves. *Flowers* small, yellow, green or brown, actinomorphic. *Perianth* segments 4, free, rounded, short-clawed, valvate, opposite to stamens and alternating with carpels. *Androeceium* of 4 stamens, inserted on the base of the sepaloïd claws; anthers 2-celled, longitudinally dehiscent, apparently sessile, extrorse. *Gynoeceium* superior, of (1–)4(–7) carpels, free or connate at base, sessile, unilocular; stigma mostly sessile, slightly compressed, usually keeled; ovule solitary, attached to the adaxial angle of the carpel, campylotropous; embryo unciform or spiral. *Fruit* a drupaceous achene, sessile, 1-seeded, indehiscent, ovoid to subglobose, with a short terminal beak, surface smooth or ridged or tuberculate; endocarp stony, splitting by separation of vertically oriented operculum on outer face; seed connate to the endocarp, without endosperm. — **Fig. 1–3.**

**Distribution** — Cosmopolitan, highest species densities in North America, West Europe, Siberia and Japan, almost lacking in Amazonia, c. 70 species; in *Malesia* 13 species, 2 of which may be recently introduced; 1 species is endemic to the region.

**Habitat & Ecology** — Nearly all species (exception: *P. suboblungus* Hagstr.) are strict aquatics. Short phases of drought can be survived by terrestrial forms or turions ('winter buds'). All kinds of water bodies are colonised, stagnant waters to a depth of 7 m, running waters to a current velocity of 1.5 m/s.

Reproduction and short-range dispersal is mainly performed by vegetative means (ripped-off shoots, turions, tubers). Seeds serve for surviving of longer drought periods and for long-range dispersal. Endozoic dispersal is recorded for several species, the hard and thick endocarp withstands the passage of the guts.

**Taxonomy** — All *Potamogeton* species, living in a variable habitat, show a high degree of phenotypic plasticity, thus the vegetative habit is often extremely variable. This led to the description of a large number of forms, varieties, 'hybrids' and 'species' without taxonomic value. In general it is difficult to identify sterile specimens of broad-leaved species without checking the stem anatomical characters. In narrow-leaved species specimens without fruits or turions often cannot be identified to the species level.

Despite the high diversity of growth forms subdivision of the genus is complicated by the irregular distribution of supposed key characters. Wallman (1812) was the first to recognise the special position of *P. crispus*. A subdivision of the genus based on the shape and size of leaves and stipules was proposed by Koch (1837). Gay (1854) excluded the section *Enantiophylla* as a separate genus *Groenlandia*. Raunkiaer (1896) divided remaining *Potamogeton* into two subgenera, namely *Coleogeton* and *Potamogeton* ('*Eupotamogeton*'). The difference is as follows:

Subgenus *Coleogeton* – Submerged leaf phyllodial. Stipules always adnate to the leaf for largest part. Winter buds tuber-like on horizontal shoots, the renewal shoot and the parent shoot partly adnate. Vascular bundles of the peduncle each with an individual endodermis; cortical bundles absent (in Malesian species); hypodermis often absent. Peduncle not erect; pollination at water surface. Pollen grain size and size of the lumina larger.

Subgenus *Potamogeton* – Submerged leaf phyllodial or laminar. Stipules mostly axillary, forming an open or fused ochrea, rarely adnate in the lowermost part. Winter buds as turions in the axils of vertical shoots, or as turions, tubers or complex structures on horizontal shoots. Vascular bundles of the peduncle without endodermis, each with a fibrous sheath; hypodermis present, even if absent in vegetative stem. Peduncle erect; pollination above water surface.

*Coleogeton* has also been treated as a separate genus *Stuckenia* by Börner (1912) respectively *Coleogeton* by Les & Haynes (1996).

Hagström (1916) presented a sophisticated classification into sections and subsections, which was a further development of Graebner's treatment (1907). It was based both on morphological and stem anatomical characters. Data on endocarp structure (Aalto 1970), chromosome number (Les 1983), pollen type (Sorsa 1988), flavonoid chemistry (Haynes 1985; Les & Sheridan 1990a) as well as a re-evaluation of stem anatomy (Wiegleb 1990), morphology and life history partly corroborate, partly question the grouping of Hagström. Therefore, Wiegleb (1988) proposed to use an informal grouping into species groups. Further attempts to elucidate the infra-generic relations were made by Les & Sheridan (1990b) and Hettiarachchi & Triest (1991). All results mentioned are likewise speculative and based on insufficient evidence. At present no acceptable classification into sections and subsections is available.

In the following a conservative approach to species delimitation is adopted. There are several specimens that do not fit exactly into the species as circumscribed here. These specimens are mentioned in the notes of the most similar species. Supposed hybrids are not included into the species list and key but are described in the notes. The present treatment should be regarded as a working hypothesis and a basis for further study. In Malesia the following species occur:

Subgenus *Coleogeton* (Rchb.) Raunk.: *P. pectinatus*

Subgenus *Potamogeton*: *P. maackianus*, *P. crispus*, *P. furcatus*, *P. oxyphyllus*, *P. pusillus*, *P. octandrus*, *P. solomonensis*, *P. nodosus*, *P. distinctus*, *P. papuanicus*, *P. lucens*, *P. wrightii*, *P. perfoliatus*

*References*: Aalto, M., Acta Bot. Fenn. 88 (1970) 1–85. — Börner, C., Abh. Naturwiss. Ver. Bremen 21 (1912) 258. — Gay, J., C. R. Hebd. Acad. Sc. Paris (1854) 703. — Graebner, P., in Engler, Pflanzenreich 31 (1907) 1–142. — Hagström, J.O., Kungl. Svenska Vetenskapskad. Handl. 55,

5 (1916) 1–281. — Haynes, R.R., Sida 11 (1985) 173–188. — Hettiarachchi, P. & L. Triest, Opera Bot. Belg. 4 (1991) 87–114. — Koch, W.D.J., Syn. Fl. Germ. Helv. ed. 1 (1837) 672–677. — Les, D.H., Rhodora 85 (1983) 301–323. — Les, D.H. & R.H. Haynes, Novon 6 (1996) 389. — Les, D.H. & D.J. Sheridan, Amer. J. Bot. 77 (1990a) 453–465; Taxon 39 (1990b) 41–58. — Raunkiaer, C.C., Danske Blomsterpl. Naturhist. 1, 1 (1896) 108. — Sorsa, P., Ann. Bot. Fenn. 25 (1988) 179–199. — Wallman, J.H. in S. Liljeblad, Utkast Sv. Flora (1816) 706. — Wiegleb, G., Fedde Repert. 99 (1988) 249–266; Flora 144 (1990) 197–208.

**Vegetative anatomy** — Besides morphological characters, stem anatomical characters are most useful for identification of *Potamogeton* specimens, particularly such ones in fragmentary state on old herbarium sheets. Five groups of characters can be used for species identification (see Raunkiaer 1903; Hagström 1916; Wiegleb 1990): shape and size of the stele, shape of the endodermis cells, numbers and size of interlacunar and subepidermal bundles, shape of the pseudohypodermis.

*References:* Hagström, J.O., Kungl. Svenska Vetenskapsakad. Handl. 55, 5 (1916) 1–281. — Raunkiaer, C.C., Bot. Tidsskr. 25 (1903) 253–280. — Wiegleb, G., Flora 144 (1990) 197–208.

**Chromosomes** — The chromosome numbers mentioned under several species are all based on counts of non-Malesian material. Only the most reliable counts are reported (Hatusima 1961; Preston 1995). Chromosome counts are often obscured by methodological difficulties like disregarding the B-chromosomes (Preston 1995) and false determination (Wiegleb 1988). A lot of deviating numbers have been reported for most species (see Les 1983; Preston 1995).

*References:* Hatusima, H., Shimane Bull. Agric. Coll. 9, sér. A 1 (1961) 237–267. — Les, D.H., Rhodora 85 (1983) 301–323. — Preston, C.D., Potamogeton of Great Britain and Ireland (1995) 55–58. — Wiegleb, G., Fedde Repert. 99 (1988) 249–266.

#### KEY TO THE SPECIES

- 1a. Stipules for a  $\pm$  long part adnate to the leaf base, all leaves linear to lanceolate, submerged ..... 2
- b. Stipules completely free or almost so, floating leaves present or absent ..... 3
- 2a. Stipules adnate to the leaf for at least 3/4 of its length, adnate part 8–65 mm long, leaves entire, 0.5–1 mm wide, apex acute ..... **10. P. pectinatus**
- b. Stipules adnate to the leaf for less than half of its length, adnate part 2–6 mm long, leaves strongly serrulate, 1.5–4 mm wide, apex rounded or truncately acute ..... **5. P. maackianus**
- 3a. Submerged leaves linear, less than 5 mm wide, sessile, entire ..... 4
- b. Submerged leaves linear-lanceolate to roundish, usually more than 5 mm wide, rarely reduced to narrow phyllodia, sessile or petiolate, entire or dentate ..... 7
- 4a. Floating leaves often present, submerged leaves linear, less than 1 mm wide, with more than 6 rows of lacunae along the midrib, fruit with a prominent beak ..... **7. P. octandrus**
- b. Floating leaves always absent, submerged leaves to 4 mm wide, lacunae not more than 3 rows, fruit with short or indistinct beak ..... 5

- 5a. Submerged leaves less than 2 mm wide, 3(–5)-veined, without additional sclerenchymatous strands, stipules often connate in the lower part, particularly when young ..... **12. P. pusillus**
- b. Submerged leaves 2–4(–6) mm wide, (3–)5–7(–9)-veined, with few to many additional sclerenchymatous strands, stipules convolute ..... 6
- 6a. Leaves 3–7(–9)-veined, with 2–16 indistinct sclerenchymatous strands, stipules persistent, stem terete ..... **8. P. oxyphyllus**
- b. Leaves (3–)5-veined, with 20–32 sclerenchymatous strands, stipules decaying to fibres, stem compressed ..... **3. P. furcatus**
- 7a. Stem compressed, subquadrangular, fruits adnate at base, with long curved beak, leaves serrate with teeth visible to the naked eye, margin often undulate ..... **1. P. crispus**
- b. Stem terete, achenes free, beak short, margin entire or minutely denticulate .. 8
- 8a. Submerged leaves sessile, clasping the stem, floating leaves always absent ..... **11. P. perfoliatus**
- b. Submerged leaves usually petiolate, floating leaves present or absent ..... 9
- 9a. Peduncles in fruit significantly thicker than uppermost part of the stem, floating leaves present or absent ..... 10
- b. Peduncles not or only slightly thickened, floating leaves usually present .... 11
- 10a. Floating leaves always absent, submerged leaves shortly petiolate (–15 mm), apex with acute tip ..... **4. P. lucens**
- b. Floating leaves often present, most leaves long petiolate, petioles of involucreal leaves approximately as long as the peduncle, submerged leaves partly cordate or sagittate at base, apex obtuse ..... **9. P. papuanicus**
- 11a. Submerged leaves linear-lanceolate or ribbon-like, less than 15 mm wide, floating leaves oblong-lanceolate, acute, peduncles often opposite to leaves ..... **P. solomonensis (p. 193)**
- b. Submerged leaves lanceolate to oblong-lanceolate, usually wider, peduncles regularly in the axils of subopposite leaves ..... 12
- 12a. Carpels 1–2(–3), floating leaves partly very long petiolate (–400 mm). ..... **2. P. distinctus**
- b. Carpels (3–)4, floating leaves, if present, shorter petiolate (–200 mm) ..... 13
- 13a. Submerged leaves 9–13-veined, apex acute to acuminate, floating leaves usually absent ..... **13. P. wrightii**
- b. Submerged leaves 11–21-veined, apex rounded or obtuse, floating leaves abundantly present ..... **6. P. nodosus**

### 1. *Potamogeton crispus* L.

*Potamogeton crispus* L., Sp. Pl. (1753) 126; A. Benn., Philipp. J. Sc., Bot. 9 (1914) 341; Hagstr., Kungl. Svenska Vetenskapsakad. Handl. 55, 5 (1916) 58. — Lectotype (Haynes): *LINN* 175.6, Europe.

Vertical shoots short-lived, seasonal; stems filiform to slender, compressed, subquadrangular, to 1 m long, mostly sparsely branched, producing specialised non-dormant axillary turions; horizontal shoots short but strongly branched. *Floating leaves* absent; submerged leaves linear to broadly linear-ovate, sessile, sometimes slightly clasping,

lamina 40–70(–90) by 4–8(–15) mm, 3-veined, margin serrate and often undulate, base obtuse, apex rounded to obtuse; stipules axillary, convolute, 9–15 mm, thinly membranous. *Spikes* suborbicular to cylindrical, contiguous or shortly remote, 10–15 mm; peduncle 20–50 mm, not thickened. *Flowers* 5–8, with 4 carpels. *Fruits* broadly ovate, 4–6 mm, adnate at base, obscurely toothed on the median ridge of the back, beak elongate, c. 2 mm. *Stem anatomy*: Stele of oblong type. Endodermis of O-type. Interlacunar bundles and subepidermal bundles absent. Pseudo-hypodermis present, 1-layered. Chromosome number  $2n = 52$ .

Distribution — Subcosmopolitan (N America, southern S America, Europe, Asia, Africa, Australia, New Zealand, probably only recently introduced in some areas); in *Malesia*: Sumatra, one record only, fide Bennett, *Philipp. J. Sc., Bot.* 9 (1914) 339–344.

Habitat & Ecology — The species has a broad ecological amplitude, colonising both running and stagnant waters. It is characterised by the aseasonal production of turions.

## 2. *Potamogeton distinctus* A. Benn.

*Potamogeton distinctus* A. Benn., *J. Bot.* 42 (1904) 72; Graebn. in Engl., *Pflanzenr.* 31 (1907) 84; A. Camus in *Fl. Gén. Indo-Chine* 6 (1942) 1221; Yang in *Fl. Taiwan* 5 (1978) 28. — Lectotype (Cuong & Vidal): *Litwinow 2424*, Manchuria.

*Potamogeton digynus* Wall., *Numer. List* (1832) 181, no. 5177, nom. nud. — Singapore.

*Potamogeton natans* L. forma *indicus* Miq., *Fl. Ind. Bat., Suppl.* (1861) 597. ('*indica*') — Type: *Teijsmann s. n.*, Sumatra.

*Potamogeton malaiianus* Miq. var. *tenuior* Miq., *Illus. Fl. Arch. Ind.* (1870) 47. — Type: *Junghuhn 172*, Java.

*Potamogeton franchetii* A. Benn. & Baagoe, *J. Bot.* 45 (1907) 234; Graebn. in Engl., *Pflanzenr.* 31 (1907) 67; Hagstr., *Kungl. Svenska Vetenskapsakad. Handl.* 55, 5 (1916) 156. — Types: from Japan.

*Potamogeton perversus* A. Benn., *Philipp. J. Sc., Bot.* 9 (1914) 343; Mendoza & Del Rosario, *Philipp. Aquat. Flow. Pl. Ferns* (1967) 41. — Types: from Asia.

*Potamogeton polygonifolius* auct. non Pourr.: A. Benn., *Bull. Herb. Boiss.* 4 (1896) 546; Graebn. in Engl., *Pflanzenr.* 31 (1907) 66, p.p.; A. Benn., *Philipp. J. Sc., Bot.* 9 (1914) 344.

*Potamogeton indicus* auct. non Roxb.: A. Benn., *Bull. Herb. Boiss.* 4 (1896) 548; Graebn. in Engl., *Pflanzenr.* 31 (1907) 64, p.p.; A. Benn., *Philipp. J. Sc., Bot.* 9 (1914) 340.

*Potamogeton oblongus* auct. non Viv.: Hook. f., *Fl. Brit. India* (1894) 566; Backer & Bakh. f., *Fl. Java* 3 (1968) 9.

Vertical shoot short-lived or annual, seasonal; stem slender, terete, to 2 m long, mostly unbranched; horizontal shoots slender to robust, long creeping, annual or biennial, much branched, producing dormant multiple apical turions. *Floating leaves* always present, long lanceolate to obovoid, petiolate, lamina (30–)60–125 by 10–35 mm, 11–19-veined, base cuneate, apex acute or obtuse, petioles 48–255(–390) mm, the longest petioles being found below the flowering region; submerged leaves present or absent, mostly lanceolate, petiolate, lamina 45–140 by (5–)10–23 mm, 9–17-veined, margin minutely denticulate, base cuneate, apex acute, petioles 30–190(–230) mm; stipules axillary, convolute, 42–85 mm, acute, persistent. *Spikes* cylindrical, contiguous, 25–80 mm; peduncles 45–105 mm, slightly thicker than stem. *Flowers* numerous; with 1(–3) carpels. *Fruits* 3–3.5 mm, with 1–3 more or less distinct keels. *Stem anatomy*: Stele invariably of trio type. Endodermis of O-type. Interlacunar bundles always absent, subepidermal bundles rarely present. Pseudo-hypodermis mostly absent. Chromosome number:  $2n = 52$ .



Distribution — E and SE Asia and Pacific region: Russia (East Siberia), Korea, China, Tibet, Nepal, Taiwan, Japan, most probably also Vietnam, Thailand, Bhutan, Kashmir, New Hebrides; in *Malesia*: Sumatra (Alahan Pandjang), Singapore, Java, Philippines (Luzon), Lesser Sunda Islands (?Flores).

Habitat & Ecology — Found in different kinds of habitat, most frequent in artificial ponds, reservoirs, rice fields, irrigation ditches and even swamps. It is also found in rivers and lakes at a depth of more than one metre. The current velocities in rivers and rivulets may range up to 0.6 m/sec. Both sandy and muddy substrates are colonised. It is most frequent in lowland areas, but is also found in mountains up to an altitude of 3600 m (in the Himalaya area).

Note — The optical impression of several southern and eastern Asian specimens caused some students of *Potamogeton* to assume the occurrence of *P. polygonifolius* Pourret, Mem. Acad. Sci. Toulouse 3 (1788) 325 (= *P. oblongus* Viviani, Fragm. Fl. Ital. 1 (1802) 1, t. 2). The vegetative similarities are in fact often surprising. Also in stem anatomical characters some overlap can be found. However, *P. polygonifolius* has smaller fruits than both *P. nodosus* and *P. distinctus*, lacks specialised winter buds, and possesses only  $2n = 26$  chromosomes. The observation of living material should soon resolve the question under concern.

### 3. *Potamogeton furcatus* Hagstr.

*Potamogeton furcatus* Hagstr., Kungl. Svenska Vetenskapskad. Handl. 55, 5 (1916) 80. — Types: from Australia.

*Potamogeton spec. A*: Leach & Osborne, Freshw. Pl. Papua New Guinea (1985) 226. — Types: from Papua New Guinea.

*Potamogeton acutifolius* auct. non Link: Aston, Aquat. Pl. Austral. (1973) 281.

Vertical shoots short-lived or perennial with continuous growth, stem filiform to slender, terete, richly branched upwards, nodal glands present, specialised turions not produced; horizontal shoots slender, short. *Floating leaves* absent; submerged leaves linear, falcate, sessile, lamina 85–140 by 2–4 mm, (3–)5-veined, with 20–32 longitudinal sclerenchymatous strands (bast fibres), margin entire, apex acute to apiculate; stipules axillary, convolute, 8–15 mm, soon decaying and persisting as stringy fibres. *Spikes* cylindrical, contiguous, 7–10 mm; peduncle 10–24 mm, not thickened. *Flowers* c. 8, in 3 whorls, with 4 carpels. *Ripe fruit* not seen. *Stem anatomy*: Stele of oblong type. Endodermis of O-type. Interlacunar bundles absent, subepidermal bundles absent. Pseudohypodermis present, 2–3-layered.

Distribution — Australian-Pacific (Australia, New Caledonia). In *Malesia*: Papua New Guinea (Enga, W Highlands Provinces).

Habitat — In fast flowing rivulets, at an altitude of 1000–2600 m.

Note — The species is closely related to *P. ochreatus* Raoul, Ann. Sci. Nat. sér. 3, 2 (1844) 117. Affinity is indicated by the organisation of the shoot system, the fibrous stipules, and the leaf venation. The leaves of *P. ochreatus*, however, are usually shorter (max. 10 cm), have obtuse tips, and are not falcate.

#### 4. *Potamogeton lucens* L.

*Potamogeton lucens* L., Sp. Pl. (1753) 127. — Lectotype (Haynes): *LINN 175.5*, Europe.

*Potamogeton gaudichaudii* Cham. & Schldl., *Linnaea* 2 (1827) 199. — Type: *Gaudichaud s.n.*, Marianne Islands.

*Potamogeton dentatus* Hagstr., *Bot. Notis.* (1908) 61; *Kungl. Svenska Vetenskapsakad. Handl.* 55, 5 (1916) 249. — Type: *Maximowicz s.n.*, Japan.

*Potamogeton angustifolius* auct. non Berchtold & Presl: *A.Benn., Philipp. J. Sc., Bot.* 9 (1914) 340.

Vertical shoots short-lived or biennial, seasonal; stem robust, terete, to 3 m long, much branched from the base; horizontal shoots much branched, robust to very robust, forming dormant apical and lateral multiple winter buds. *Floating leaves* absent; submerged leaves lanceolate to oblong, petiolate, sometimes the lower ones reduced to phyllodes, lamina 50–150 by 15–30 mm, 9–13-veined, margin serrulate toward the tip, base cuneate, apex mucronate; petioles 3–12(–20) mm; stipules axillary, convolute, 25–50 mm, obtuse or rounded at apex. *Spikes* cylindrical, contiguous, 30–50 mm; peduncles 50–200 mm, twice as thick as stem. *Flowers* numerous, with 4 carpels. *Fruits* 3.2–4 mm long, dorsal keel indistinct. *Stem anatomy*: Stele of oblong type (rarely trio or proto type). Endodermis of U-type. Interlacunar bundles present, multicellular, in 3 circles, subepidermal bundles present. Pseudo-hypodermis present, 1-layered. Chromosome number:  $2n = 52$ .

Distribution — Northern part of the Old World, exact southern limit unknown because of the frequent confusion with *P. schweinfurthii* A.Benn. (Africa) and *P. wrightii* Morong (Asia); in *Malesia*: Philippines (Luzon).

Habitat — A characteristic species of lakes and slow flowing rivers. The only occurrence in Malesia is in a highland lake.

#### 5. *Potamogeton maackianus* A. Benn.

*Potamogeton maackianus* A. Benn., *J. Bot.* 42 (1904) 74 ('*Maackianus*') [nom. cons. propos.]; Hagstr., *Kungl. Svenska Vetenskapsakad. Handl.* 55, 5 (1916) 56; Mendoza & Del Rosario, *Philipp. Aquat. Flow. Pl. Ferns* (1967) 41. — Type: *Maack s.n.*, Russia (Far East).

Vertical shoot continuously growing, aseasonal, specialised turions not produced; stem slender, terete, much branched; horizontal shoots short, not much differentiated. *Floating leaves* absent; submerged leaves linear to lanceolate, sessile, lamina 20–80 by 2–4 mm, 3(–5)-veined, with 4–8 inconspicuous sclerenchymatous strands, margin finely serrulate, base rounded, apex obtuse to truncately acute; stipules adnate, convolute, 4–12 mm, fused to the leaf for 2–6 mm. *Spikes* suborbicular or cylindrical, contiguous or shortly distant, 5–10 mm; peduncle 10–30 mm, often in an umbel-like arrangement at the top of the vertical shoot. *Flowers* 2–4, with 4 carpels. *Fruits* broadly ovate-elliptic, c. 3 mm, acutely keeled, beak short. *Stem anatomy*: Stele of oblong type. Endodermis of O-type. Interlacunar bundles absent, subepidermal bundles present. Pseudo-hypodermis present, 1-layered. Chromosome number:  $2n = 52$ . — **Fig. 1.**

Distribution — Eastern and southern Asia (Russia: Siberia, Far East; Korea; China; Japan; Indochina; India); in *Malesia*: Sumatra [Lake Toba; fide Van Steenis & Ruttner, *Arch. Hydrobiol. Suppl.* 11 (1933) 231–387], Philippines (Mindanao).

Habitat — In Malesia the species is found in shallow parts of lakes. Elsewhere it also colonises streams, ditches, and ponds.

Note — In Malesia also a hybrid of *Potamogeton maackianus* occurs:

***Potamogeton* × *philippinensis* A. Benn.**

*Potamogeton* × *philippinensis* A. Benn., Philipp. J. Sc., Bot. 9 (1914) 342; Hagstr., Kungl. Svenska Vetenskapsakad. Handl. 55, 5 (1916) 57; Mendoza & Del Rosario, Philipp. Aquat. Flow. Pl. Ferns (1967) 41 (= *P. maackianus* × *wrightii*). — Type: *Clemens 2548*, Mindanao.

General habit intermediate between the parents. Internodes mostly short, the leaves dense, with the lamina 80 by 8 mm, the apex acute to apiculate, stipules shortly adnate.

Distribution — Only known from the type locality in the Philippines (Mindanao).



→  
Fig. 1. *Potamogeton maackianus* A. Benn. — Reproduced from Ascherson & Graebner in Engl., Pflanzenreich IV.11, 31 (1907) 108, f. 26.

**6. *Potamogeton nodosus* Poir.**

*Potamogeton nodosus* Poir. in Lam., Encycl. Méth. Bot. Suppl. 4 (1816) 55 ('*nodosum*'); Hagstr., Kungl. Svenska Vetenskapsakad. Handl. 55, 5 (1916) 183. — Type: *Broussonet s.n.*, Canary Islands.

*Potamogeton indicus* Roxb., Fl. Ind. 1 (1820) 471, nom. illeg. ('*indicum*'), non Roth ex Roem. & Schult.; Hook. f., Fl. Brit. India (1894) 656; Graebn. in Engl., Pflanzenr. 31 (1907) 64. — Type: *Roxburgh s.n.*, India.

*Potamogeton malaianus* Miq., Illus. Fl. Arch. Ind. (1870) 46. ('*malaina*'). — Type: *Teijsmann s.n.*, Celebes.

*Potamogeton tepperi* auct. non A. Benn. (1887): A. Benn., Philipp. J. Sc., Bot. 9 (1914) 340; Mendoza & Del Rosario, Philipp. Aquat. Flow. Pl. Ferns (1967) 42.

*Potamogeton polygonifolius* auct. non Pourret: Chai-anan, Thai For. Bull. 15 (1985) 25.

Vertical shoots short-lived or annual, seasonal; stem slender to robust, terete, to 2 m long, mostly unbranched; horizontal shoots robust, long-creeping, biennial or perennial, much branched, producing dormant apical multiple winter buds. *Submersed leaves* lanceolate to oblong-lanceolate, petiolate, often absent after fructification, lamina 50–280 by 10–40(–50) mm, 11–21-veined, margin denticulate, at least when young, base cuneate, apex rounded to acute; petioles 30–150 mm; floating leaves lanceolate-elliptical to obovoid, petiolate, lamina 50–150 by 20–50 mm, 11–23-veined, base cuneate, apex acute, petioles 100–250 mm, longer than lamina; stipules axillary, convolute, 20–60 mm, inconspicuously 2-keeled. *Spike* cylindrical, contiguous, 20–50 mm; peduncle 40–130 mm, slightly thickened. Flowers numerous, with (3–)4 carpels. *Fruits* variable in shape and colour, 2.7–4.1 mm long, dorsally and ventrally keeled, sometimes carinate. *Stem anatomy*: Stele of trio or proto type. Endodermis of O-type. Interlacunar bundles absent, rarely a few in the outer ring; subepidermal bundles absent. Pseudo-hypodermis absent. Chromosome number:  $2n = 52$ .

**Distribution** — Widely distributed in the northern hemisphere and the tropics, occurring in N and C America, Europe, N and W Africa, Madagascar, the Mascarene Islands, W Siberia, C and S Asia: Pakistan, Afghanistan, Kashmir, Nepal, India, Sri Lanka, Burma, Thailand, Andaman Islands, China (Yunnan), Taiwan, Vietnam, Pacific area (Marianne Islands, New Caledonia, New Hebrides); Australia (Western Australia., Northern Territory); in *Malesia*: Sumatra, Philippines (Luzon), Celebes, Lesser Sunda Islands (Alor, Flores, Timor?), New Guinea.

**Habitat** — *Potamogeton nodosus* grows in all kinds of water bodies. It is particularly abundant in slow flowing rivers, ponds and shallow parts of lakes.

**Note** — The distinction between *P. nodosus* and *P. distinctus* is difficult, as it depends on various characters that show a wide overlap. Several *P. nodosus*-like plants cannot exactly be assigned to either of these species. The following specimens are examples for such forms. Alor: *Jaag 1014* (ZT); Flores: *Jaag 1619* (ZT); Timor: *van Steenis 18113*, plants with cordate leaf bases in floating leaves; New Guinea: *Jermy 3940* (BM, K), plants with short petioled submersed leaves and abruptly long petioled floating leaves; *Raynal 16697* (L) is the same form, but is lacking floating leaves.

## 7. *Potamogeton octandrus* Poir.

*Potamogeton octandrus* Poir. in Lam., Encycl. Méth. Bot. Suppl. 4 (1816) 534 ('*octandrum*'); Backer & Bakh. f., Fl. Java 3 (1968) 9; Yang in Fl. Taiwan 5 (1978) 30. — *Hydrogeton heterophyllus* Lour., Fl. Cochinch. 1 (1790) 244. — *Potamogeton heterophyllus* Hamilton in Wallich, Cat. (1832) no. 5181, nom. illeg. (non Schreber). — Type: *Loureiro s.n.*, Cochinchina (Vietnam).

*Potamogeton javanicus* Hassk., Verh. Natuurk. Ver. Ned. Ind. 1 (1856) 26; Hook. f., Fl. Brit. India (1894) 566; Koord., Exk. Fl. Java (1911) 89; A. Benn., Philipp. J. Sc., Bot. 9 (1914) 339; Hagstr., Kungl. Svenska Vetenskapsakad. Handl. 55, 5 (1916) 131; Leach & Osborne, Freshw. Pl. Papua New Guinea (1985) 225. — Type: from W Java.

*Potamogeton tenuicaulis* F. Muell., Fragm. Phyt. Austral. 1 (1858) 90, 244. — Type: from Australia.

*Potamogeton pusillus* auct. non L.: Miq., Illus. Fl. Arch. Ind. (1870) 47.

Vertical shoots short-lived or annual, seasonal; stem filiform, terete, much branched, producing numerous axillary turions; horizontal shoot system poorly developed. *Floating leaves* present or absent, narrow-elliptic to oblong-elliptic, petiolate, lamina 10–20(–40) by 3–4(–6) mm, 5–7-veined, margin entire, base cuneate, apex acute, petioles 3–12(–20) mm; intermediate leaves often present, petiolate, lanceolate; submerged leaves narrowly linear, sessile, lamina 25–35(–60) by 0.5–0.8(–1) mm, 3-veined, with up to six rows of prominent lacunae, margin entire, apex acute to acuminate; stipules axillary, convolute, 5–10 mm, thinly membranous, acute. *Spike* cylindrical, contiguous, 5–16 mm; peduncle 9–21 mm. *Flowers* 7–9, with 4(–5) carpels. *Fruits* 1.5–2.4 mm, smooth or keeled, with a prominent beak. *Stem anatomy*: Stele of oblong or circular type. Endodermis of O-type. Interlacunar bundles absent, subepidermal bundles present. Pseudohypodermis often absent, rarely 1-layered. Chromosome number:  $2n = 28$ .

**Distribution** — Tropical and subtropical parts of the Old World: Asia (Japan, China, Taiwan, India, Sikkim, Thailand, Vietnam), Africa (S of the Sahara), Madagascar, Australia; in *Malesia*: Java (highland), New Guinea (Gulf, E Highlands Provinces).

**Habitat** — Most frequent in ponds, ditches and rivulets from sea level to 2060 m.

**Notes** — 1. *Potamogeton octandrus* is a morphologically variable species. Special attention must be paid to forms without floating leaves which have been confused with *P. pusillus*. Furthermore, both hybrids with *P. pusillus* (*P. × apertus* Miki) and *P. oxyphyllus* (*P. × kamogawaensis* Miki) may occur.

2. Closely related is *P. cristatus* Regel & Maack in Regel, Tent. Fl. Ussur. (1861) 153, which has been reported from Taiwan (Yang in Fl. Taiwan 5, 1978, 28). *Potamogeton cristatus* cannot be distinguished by vegetative characters. It differs from *P. octandrus* in the rather short and densely flowered spike, the cristate dorsal margin of the ripe fruit, and the long and slender style.

## 8. *Potamogeton oxyphyllus* Miq.

*Potamogeton oxyphyllus* Miq., Ann. Mus. Bot. Lugd.-Bat. 3 (1867) 161 (Prol. Fl. Jap., p. 325); A. Benn., Philipp. J. Sc., Bot. 9 (1914) 341; Hagstr., Kungl. Svenska Vetenskapsakad. Handl. 55, 5 (1916) 83. — Type: from Japan.

Vertical shoot aseasonal, continuously growing, without specialised winter buds; stem filiform, terete, much branched, horizontal shoots not much differentiated, much branched. *Floating leaves* absent; submerged leaves linear, slightly falcate, sessile, lamina 50–120 by 2–3.5 mm, 5–7(–9)-veined, with 2–16 inconspicuous sclerenchymatous strands, apex acuminate, margin entire; stipules axillary, convolute, 15–25 mm, obtuse. *Spikes* cylindrical, contiguous, 10–15 mm; peduncles 20–40 cm. *Flowers* 5–9, with 4 carpels. *Fruits* broadly elliptic-ovate, 3.2–3.8 mm, rarely developed, beak short. *Stem anatomy*: Stele of oblong type. Endodermis of O-type. Interlacunar bundles absent, subepidermal bundles present. Pseudohypodermis absent. Chromosome number:  $2n = 26$ .

**Distribution** — E Asia (Far East Russia, China, Korea, Japan); in *Malesia*: N Sumatra.

**Habitat** — Fast flowing rivers on gravel, at an altitude of c. 1250 m.

**Note** — *Potamogeton oxyphyllus* easily hybridises with *P. pusillus* (*P. × orientalis* Hagstr.), *P. maackianus* (*P. × kyushuensis* Kadono & Wiegleb) and *P. octandrus* (*P. × kamogawaensis* Miki). In case of a common occurrence those hybrids may be expected also in *Malesia*.

### 9. *Potamogeton papuanicus* Wiegleb

*Potamogeton papuanicus* Wiegleb, *Blumea* 37 (1993) 379. — Type: *Walker ANU 650*, Papua New Guinea.

*Potamogeton malaianus* auct. non Miq.: Osborne & Leach, *Freshw. Pl. Papua New Guinea* (1985) 226, f. 51, p. p.

Vertical shoot annual or continuously growing, aseasonal; stem slender, terete, unbranched or with short axillary leafy shoots; horizontal shoot slender to robust, much branched. *Floating leaves* elliptic to oblong-lanceolate with rounded tip, petiolate, lamina 65–115 by 18–27 mm, 13–17-veined, base cuneate, apex rounded, petioles 115–185 mm; submerged leaves oblong-lanceolate to lanceolate, petiolate, lamina 105–160 by 12–28 mm, 9–13-veined, margin entire, base cuneate to slightly cordate or sagittate, apex rounded to acute, petioles (2–)8–45 mm; stipules axillary, convolute, 60 mm, acute. *Spikes* cylindrical, contiguous, 21–28 mm; peduncles 130–180 cm, approximately as long as the petioles of the adjacent floating leaves, considerably thicker than the stem. *Flowers* numerous, with 4 carpels. *Ripe fruits* not seen. *Stem anatomy*: Stele of trio or proto type. Endodermis of O-type. Interlacunar bundles and subepidermal bundles absent. Pseudo-hypodermis absent.

Distribution — *Malesia*: restricted to the highland region of Papua New Guinea. Similar plants have been collected in Timor.

Habitat — The species has been found in a high lake in water ranging from shallow to deep.

### 10. *Potamogeton pectinatus* L.

*Potamogeton pectinatus* L., *Sp. Pl.* (1753) 127 ('*pectinatum*'); Miq., *Illus. Fl. Arch. Ind.* (1870) 47; Hook. f., *Fl. Brit. India* 6 (1894) 567; Koord., *Exk. Fl. Java* 1 (1911) 88; Hagstr., *Kungl. Svenska Vetenskapsakad. Handl.* 55, 5 (1916) 39; Mendoza & Del Rosario, *Philipp. Aquat. Flow. Pl. Ferns* (1967) 41. — Type (Haynes): *Burser X: 124* (UPS), Europe.

Vertical shoots short-lived, seasonal; stem filiform to slender, terete, to 4 m long, much branched from base; horizontal shoot slender to robust, perennial, much branched, producing tubers both in axillary and apical position. *Floating leaves* absent; submerged leaves filiform, sessile, 30–100(–200) by 0.5–1 mm, 3–5-veined, margin entire, apex acute; stipules adnate, convolute, 12–70 mm, adnate to the leaves for at least 3/4 of their length, forming an open sheath, margins of the open portion whitish. *Spikes* cylindrical, with 2–4 remote flower whorls, 20–40(–50) mm; peduncle 20–100 mm, not thickened. *Flowers* 8–14, with 4 carpels. *Fruits* broadly obovate to roundish, 3.3–4.7 mm, yellowish brown, beak short. *Stem anatomy*: Stele of four bundles type. Endodermis of U-type. Interlacunar bundles present (1 ring), subepidermal bundles few or absent. Pseudo-hypodermis present, 1-layered. Chromosome number:  $2n = (52), 78$ . — **Fig. 2.**

Distribution — Almost cosmopolitan; in *Malesia*: Sumatra (Toba Lake, Palembang), Philippines (Luzon), Celebes (Minahassa), Lesser Sunda Islands (Bali), Solomons.

Habitat — Both fresh and brackish water.

Ecology — In the northern hemisphere regarded as an indicator of polluted water.

Note — On a worldwide scale, *P. pectinatus* is a very variable species with respect to leaf shape and size, branching pattern, as well as fruit shape and size. In Malesia, infraspecific variation is negligible. Only narrow-leaved forms have been found.

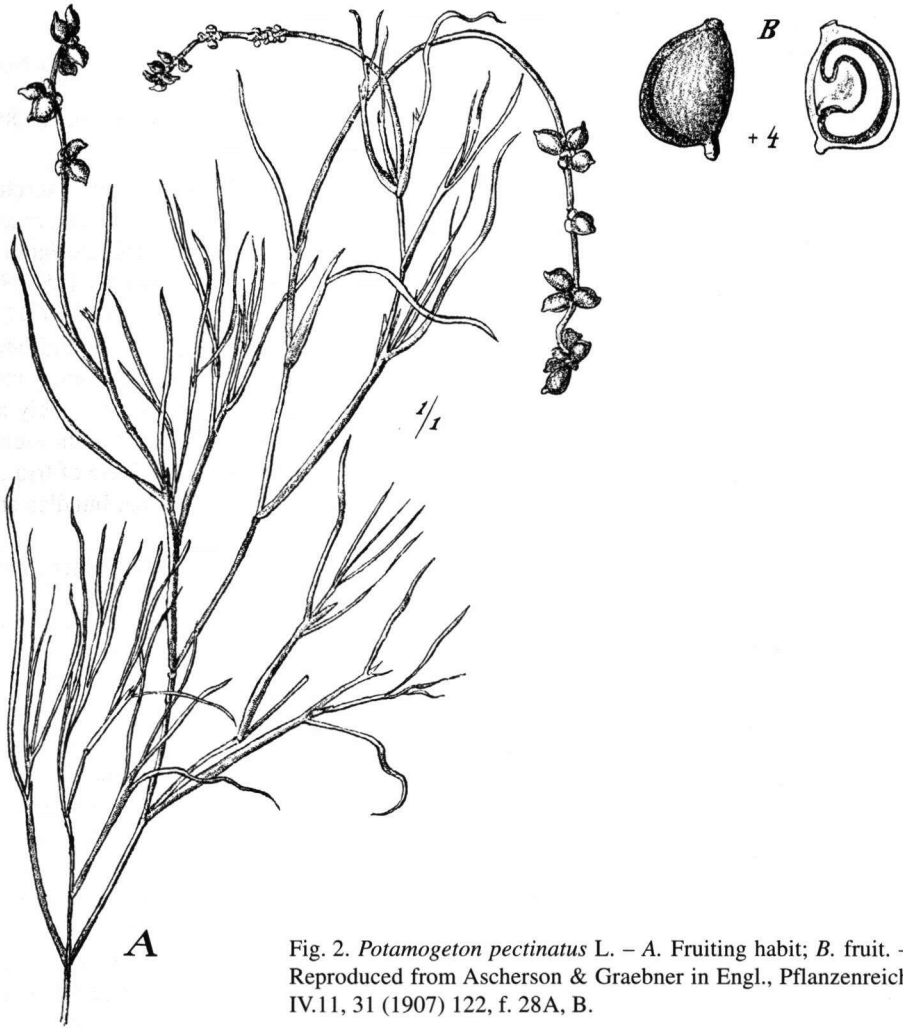


Fig. 2. *Potamogeton pectinatus* L. — A. Fruiting habit; B. fruit. — Reproduced from Ascherson & Graebner in Engl., Pflanzenreich IV.11, 31 (1907) 122, f. 28A, B.

### 11. *Potamogeton perfoliatus* L.

*Potamogeton perfoliatus* L., Sp. Pl. 1 (1753) 127; Hagstr., Kungl. Svenska Vetenskapsakad. Handl. 55, 5 (1916) 254; Haynes, SIDA 11 (1985) 178. — Type (Haynes): LINN, Sweden/Finland.

Vertical shoots short-lived, seasonal; stem filiform to slender, terete, to 6 m long, much branched, particularly in the upper part; horizontal shoots slender to robust, perennial, branched, producing dormant lateral multiple winter buds. *Floating leaves* always absent; submersed leaves broadly ovate to broadly lanceolate, sessile, clasping the stem, lamina 20–60(–120) by 10–35(–60) mm, 11–25-veined with 2–4 more conspicuous side-veins, margin minutely dentate, sometimes undulate, base cordate, apex obtuse; stipules axillary, convolute, 10–20 mm, early decaying. *Spikes* cylindrical, contiguous,

10–30 mm; peduncle 20–50 mm, not thickened. *Flowers* numerous, with 4 carpels. *Fruits* obliquely oblong, 2–3 mm, unkeeled, with a backwards curved beak. *Stem anatomy*: Stele of trio type with one bundle in central position. Endodermis without thickening or of faint O-type. Interlacunar bundles absent, subepidermal bundles absent or few. Pseudo-hypodermis absent. Chromosome number:  $2n = (26), 52$ .

*Distribution* — Subcosmopolitan, recently introduced in several areas; in *Malesia*: Sumatra (Lake Toba).

*Habitat* — In Sumatra it is found in an upland lake.

*Ecology* — *Potamogeton perfoliatus* has a wide ecological amplitude. It is particularly frequent in lakes up to 6 m depth and in slow flowing rivers.

*Notes* — 1. This species has not been recorded in earlier collections of the Lake Toba site. It might be a recent introduction.

2. Two forms that are commonly regarded as hybrids of *P. perfoliatus* also occur in Malesia:

### *Potamogeton* × *nitens* Weber

*Potamogeton* × *nitens* Weber, Fl. Holsat. (1787) 5. (= *P. perfoliatus* × *gramineus*). — Type: from Germany.

*Potamogeton* × *nipponicus* Makino, Illus. Fl. Japan (1891) 2; Ostenf., Philipp. J. Sc., Bot. 9 (1914) 260. — Type: from Japan.

General habit intermediate between the parents. Stem of the vertical shoots filiform to slender, branched. Submerged leaves sessile, subperfoliate, oblong-lanceolate, lamina c. 50 by 11 mm, apex obtuse or rounded. Stipules c. 15 mm, deciduous. Stem anatomy: Stele of reduced trio type. Endodermis of O-type or without thickening. Interlacunar and subepidermal bundles absent. Pseudo-hypodermis absent. Chromosome number:  $2n = 52$ .

*Distribution* — East Asia (Japan); in *Malesia*: Philippines (Mindanao).

### *Potamogeton* × *anguillanus* Koidz.

*Potamogeton* × *anguillanus* Koidz., Bot. Mag. Tokyo 43 (1919) 398 (= *P. perfoliatus* × *wrightii*). — Types: from Japan.

*Potamogeton spec. B*: Leach & Osborne, Freshw. Pl. Papua New Guinea (1985) 228. — Types: from Papua New Guinea.

General habit intermediate among the parents. Stem of vertical shoot slender, unbranched. Submerged leaves sessile, subperfoliate, lanceolate, lamina 40–110 by 10–17 mm, apex acute. Stipules 8–20 mm, deciduous. Spike 9–20 mm; peduncles 30–45 mm, not thickened. Stem anatomy: Stele of trio type with one of the median bundles tending to a central position. Endodermis of O-type. Interlacunar bundles and subepidermal bundles absent. Pseudo-hypodermis absent.

*Distribution* — East Asia (Japan); in *Malesia*: Papua New Guinea (Milne Bay Prov.).

## 12. *Potamogeton pusillus* L.

*Potamogeton pusillus* L., Sp. Pl. (1753) 127; A. Benn., Philipp. J. Sc., Bot. 9 (1914) 342; Mendoza & Del Rosario, Philipp. Aquat. Flow. Pl. Ferns (1967) 42; Leach & Osborne, Freshw. Pl. Papua New Guinea (1985) 226. — Type (Haynes): *LINN 175.15*, Europe.



*Potamogeton panormitanus* Biv., Nuov. Pl. (1838) 6; Hagstr., Kungl. Svenska Vetenskapsakad. Handl. 55, 5 (1916) 98. — Type: from Sicily.

*Potamogeton berchtoldii* Fieber in Bercht. & Opiz, Ökon.-Techn. Fl. Böhm. 2, 1 (1838) 277. — Type: from Czech Republic.

Vertical shoots short-lived or annual, seasonal; stem filiform, terete, to 1 m long, much branched, producing numerous axillary and apical turions, nodal glands present; horizontal shoots usually not developed. *Floating leaves* absent, involucral leaves rarely spatulate; submersed leaves narrowly linear, sessile, lamina 50(–80) by (0.5–)1–1.5 (–2) mm, 3-veined, midrib bordered by 1–3 rows of lacunae, margin entire, apex acute; stipules axillary, convolute or connate at base, 6–11(–20) mm, truncate, membranous. *Spikes* cylindrical, contiguous or sometimes the lowest flower remote, 5–13 mm; peduncle 10–15 mm, not thickened. *Flowers* 4–7, usually with 4 carpels. *Fruit* 2–2.5 mm, olive-green. *Stem anatomy*: Stele of the circular type. Endodermis of O-type. Interlacunar bundles absent, subepidermal bundles present. Pseudo-hypodermis absent. Chromosome number:  $2n = 26$ .

Distribution — Widely distributed (America except Amazonia, Europe, N Africa, West Asia, Russia, China, Japan); in *Malesia*: Philippines (Luzon), Papua New Guinea (Enga Province).

Habitat — In water bodies of different trophic status. Even slightly saline conditions are tolerated. It is found most abundantly under unstable ecological conditions and in disturbed places (ditches, ponds, reservoirs).

Note — *Potamogeton pusillus* is rare in Malesia. Most records refer to confusions with *P. octandrus*.

### 13. *Potamogeton wrightii* Morong

*Potamogeton wrightii* Morong, Bull. Torrey Bot. Club 13 (1886) 158; A. Benn., J. Bot. 28 (1890) 298; Wiegleb, Pl. Syst. Evol. 170 (1990) 59. — Type: *Wright s.n.*, Loo Choo (Ryu Kyu) Islands.

*Potamogeton mucronatus* C. B. Presl, Epimel. Bot. (1851, '1849') 245, nom. illeg. (non Schrader ex Sonder); A. Benn., Ann. Naturhist. Hofmus. Wien 7 (1892) 289; Hook. f., Fl. Brit. India 6 (1894) 567; Chai-anan, Thai For. Bull. 15 (1985) 25. — Type: *Cuming 1381*, Luzon.

*Potamogeton lucens* auct. non L.: Vidal ex Rolfe, J. Bot. 24 (1886) 60; Cuming & Vidal ex A. Benn., Ann. Naturhist. Hofmus. Wien 7 (1892) 289; Naves, Noviss. App. (1892) 297.

*Potamogeton malaianus* auct. non Miq.: A. Benn., J. Bot. 42 (1904) 73 ('*malianus*'); Graebn. in Engl., Pflanzenz. 31 (1907) 83 ('*malainus*'); A. Benn., Philipp. J. Sc., Bot. 9 (1914) 341 ('*mala-ina*'); Hagstr., Kungl. Svenska Vetenskapsakad. Handl. 55, 5 (1916) 248; Mendoza & Del Rosario, Philipp. Aquat. Flow. Pl. Ferns (1967) 41 ('*malainus*'); Merr., Fl. Manila (1968) 67 ('*malainus*'); Yang in Fl. Taiwan 5 (1978) 28; Cuong & Vidal in Fl. Camb., Laos & Vietnam 20 (1983) 58; Leach & Osborne, Freshw. Pl. Papua New Guinea (1985) 226, p. p.

*Potamogeton gaudichaudii* auct. non Cham. & Schldtl.: A. Benn., Bull. Herb. Boiss. 4 (1896) 548.

Vertical shoot annual or biennial, seasonal; stem slender, terete, to 3 m long, mostly unbranched except at the end of the growing season; horizontal shoots slender to robust, long, creeping, much branched, forming dormant apical multiple rhizomatous tubers. *Floating leaves*, if present, lanceolate to ovate-lanceolate, petiolate, lamina 52–125 by 12–25 mm, 11–21-veined, base cuneate, apex acute, petioles 25–135 mm; intermediate leaves often present; petiolate; submerged leaves lanceolate, with parallel margins, peti-

olate, lamina 80–200(–310) by 7–20(–30) mm, 9–13-veined, margin dentate, at least around the tip, base cuneate, apex acute to acuminate, petioles 16–70(–140) mm; stipules axillary, convolute, 25–85 mm, whitish, persistent. *Spikes* cylindrical, contiguous, 25–56 mm; peduncles 46–70(–103) mm, slightly thicker than stem. *Flowers* numerous, with 4 carpels. *Fruit* 2–3.2 mm, with a ventral protrusion, sometimes with 1–3 dorsal keels. *Stem anatomy*: Stele of trio or proto type. Endodermis mostly of U-type, sometimes O-U-type or no thickening. Interlacunar bundles present, multicellular, in 1 or 2 rings, subepidermal bundles absent. Pseudo-hypodermis present, 1-layered. Chromosome number:  $2n = 52$ .

**Distribution** — Asia (C, E & S) to the Pacific region; Kazakhstan, Far East Russia, Korea, China, Japan, Ryukyu Islands, Taiwan, Marianne Islands, Pakistan, India (Kashmir, Bengal), Bangladesh, Thailand, Vietnam; in *Malesia*: Sumatra (widespread), Peninsular Malaya, ?Java (fide Backer & Bakh. f.), Borneo, Philippines (Luzon, Mindoro, Palawan, Mindanao, Samar), Celebes (Minahassa), Lesser Sunda Islands (Lombok, ?Flores), Moluccas (Halmahera), New Guinea (widespread), ?New Hannover.

**Habitat & Ecology** — Both rivers (incl. rivulets) and lakes are colonised. Current velocities up to 1 m/s are tolerated. The species is frequently found in irrigation ditches and canals, while it is less frequent in ponds, paddy fields, springs and coastal lagoons. The range of altitude is from sea level to more than 2000 m. The water depth mostly ranges between 50 and 200 cm, the maximum reported is 310 cm. All kinds of substrate are colonised with a slight preference for sandy substrates. As to water chemistry, Kadono, Bot. Mag. Tokyo 95 (1981) 63–76, recognised a preference for high alkalinity in combination with high pH and calcium concentrations. Slightly saline conditions are tolerated. The species is found in muddy and polluted water courses.

**Notes** — 1. *Potamogeton wrightii* is the most frequent species of the genus in Malesia. It is highly polymorphic forming several local variants. The most aberrant ones are the following:

- a) from Papua New Guinea: *Leach 7805* (UPNG). It unites characters of *P. wrightii*, *P. lucens*, and *P. papuanicus* and may also be regarded as a hybrid or as a species in its own right;
- b) from Mindoro: *Britton 277* (L). A broad-leaved form with undulate margins and asymmetric leaf ground.

2. The identity of *P. sumatranus* Miq. [Fl. Ind. Bat., Suppl. 1 (1861) 259; A. Benn., Ann. Naturhist. Hofmus. Wien 7 (1892) 289; Phillipp. J. Sc., Bot. 9 (1914) 341 (Type: *Teijsmann s.n.*, Sumatra)] is still uncertain. Various specimens of *P. sumatranus* were studied by Wiegand [Pl. Syst. Evol. 170 (1990) 53–70], without reaching a final conclusion on the identity of the species. *Potamogeton sumatranus* is very similar to *P. wrightii*, but not completely identical, differing from *P. wrightii* by the less well developed interlacunar bundles, the wider leaves, and the more regular floating leaf formation. All these differentiating characters are only gradual. *Potamogeton sumatranus* may either prove to be a special form of *P. wrightii* or a product of hybridization between *P. wrightii* and *P. nodosus*. If the identity of *P. wrightii* and *P. sumatranus* can be proved, the name *P. sumatranus* must have priority. The form is endemic to Sumatra and occurs in lakes and ditches besides typical *P. wrightii*.

## SPECIES TO BE EXPECTED

*Potamogeton solomonensis* Wiegleb

*Potamogeton solomonensis* Wiegleb, *Blumea* 37 (1993) 381. — Type: *Gray 10*, Guadalcanal.

So far this species has been found only in the Solomon Islands (Guadalcanal, New Georgia). It grows in rivers and ditches and other shallow waters of a coastal floodplain. In habit and stem anatomy the plant resembles *Potamogeton cheesemanii* A. Benn. from New Zealand.

## RUPPIA

(C. den Hartog)

*Ruppia* L., *Sp. Pl.* (1753) 127; *Gen. Pl. ed. 5* (1754) 61; Benth. & Hook. f., *Gen. Pl.* 3 (1883) 1014; Graebn. in Asch. & Graebn., in *Engl., Pflanzenz.* IV.11, 31 (1907) 142; Setchell, *Proc. Cal. Ac. Sc. ser. 4*, 25 (1946) 469. — *Bucafer* Adans., *Fam.* 2 (1763) 469. — *Bucaferrea* Petagna, *Inst. Bot.* 5 (1787) 1826. — Type species: *Ruppia maritima* L.  
*Dzieduszyckia* Rehmman, *Oesterr. Bot. Z.* 18 (1868) 374.

Monoecious. Annual or perennial submerged aquatic herbs. *Rhizomes* creeping, monopodial, but often also laterally branched; in annual species often considerably reduced. Central cylinder with a vascular strand, with in the centre a xylem canal; cortex consisting of parenchyma with a circle of air channels. From each node 1 or 2 unbranched roots with numerous very fine root hairs arise, as well as an erect shoot. Shoots very short to up to more than 2.5 m high, in the latter case profusely branched. Internodes elongate, variable in length. *Leaves* linear, distichous, with very many tannin cells; leaf sheath amplexicaulous, with on either side a slightly auriculate membranous flap; flaps overlapping; no ligula; leaf blade with only a midrib; margins smooth, but near the leaf tip irregularly serrulate; on either side of the midrib a wide air lacune. Uppermost leaves of generative branches opposite. *Inflorescence* terminal, consisting of a peduncle which has at its top a two-flowered spike. Peduncle arising from between the inflated sheathing bases of the 2 apical leaves; short, erect and sometimes thickened after flowering, or thin and varying in length from a few cm to more than a metre (often still lengthening itself by cell stretching during the flowering process), and in most of the species after flowering coiled or spirally contracted, pulling the ripening fruits down to the bottom. Flowering takes place at the water surface, or submerged. *Flowers* placed at opposite sides of the axis, but very closely together, bisexual, without a perianth, consisting of 2 opposite stamens and 4~carpels. Stamens consisting of one (sub)sessile, bilocular anther; connective broad with at each side a theca; thecae circular to broad-elliptic, extrorsely dehiscent, shed after emission of pollen. Pollen boomerang-shaped with reticulate exine. Pollination aerial, on the water surface, or under water in an air bubble. Carpels free, sessile or subsessile; ovary ovoid; no style, but a small peltate disc-like stigma. In most species a podogynium develops at the base of each carpel after fertilisation, giving the infructescence an umbellate appearance. Ovule solitary, pendulous, campylotropous. *Fruit* an achene, sessile or stalked (podogyne and fruit form a morphological entity without abscission zone), symmetric to very asymmetric; exocarp spongy, soon decomposing; endocarp

hard, persistent with beak and usually a podogyne; at the apical part of the endocarp a small foramen occurs, the shape of which has diagnostic value at the species level. — **Fig. 3.**

**Distribution & Ecology** — Widely distributed in temperate and tropical regions all over the world, in the northern hemisphere even extending beyond the polar circle, and from sea level up to 4000 m altitude. The greatest species diversity seems to occur in Mediterranean-type climates, in poikilohaline environments. It occurs in brackish waters as well as in continental salt waters, but also in highly diluted fresh waters and in hyperhaline waters where it tolerates salinity up to three times the salinity of the sea. It has also been found under marine conditions, but only in very sheltered places. Its occurrence in the tropics is very local, probably because the environments where representatives of this genus would abound are ephemeral under tropical conditions. Lagoons which become detached from the sea will be brackish only very temporarily; in the wet tropics they will develop into freshwater marshes due to dilution with rain, and in the dry tropics they will become desiccated and transformed into a salty desert.

In *Malesia* the genus is represented only by one species.

**Taxonomy** — Circa 10 species are known. As a consequence of great morphological variation between populations, partly due to environmental differences and partly genetically determined, the taxonomy of the genus is still unsatisfactory. Another difficulty is that in the past it was not recognised that in the herbarium material the flowering and fruiting organs were not always in the same stage, so the number of described varieties is large; most of them cannot be maintained. However, many investigators have concluded from the chaotic taxonomic situation that the best solution of the problem was to consider the genus as consisting of one very variable species; later investigations, based on the study of live plants, herbarium material and chromosome analyses in Europe [Reese, *Z. Bot.* 50 (1962) 237], Australia [Jacobs & Brock, *Aquat. Bot.* 14 (1982) 325] and New Zealand [Mason, *New Zeal. J. Bot.* 5 (1967) 519] have shown that this is not correct. So far there are no special taxonomic studies of any tropical population. From East Asia no morphological studies have been published, and the only study that records chromosome numbers gives no indication of the morphological characteristics of the material studied [Harada, *Cytologia* 21 (1955) 306, f. 29a, b].

The genus *Ruppia* has been classified in the past in various manners; several authors considered it as a family on its own, the *Ruppiaceae*, but it has also been regarded as a subfamily of the *Potamogetonaceae*. According to Jacobs & Brock, l. c., the differences with *Potamogeton* are not sufficient to warrant a separate position within the *Potamogetonaceae* sensu stricto. However, a subfamily status is certainly justified, and the status of a family in its own right needs to be considered, particularly as Les, Cleland & Waycott (*Syst. Bot.* 22, 1997, 443) have found that molecular *rbcL* data indicate that *Ruppia* is phylogenetically much closer to *Posidonia* than to *Potamogeton*.

From the above follows very obviously that the genus is urgently in need of revision on a world scale. This revision should not only be based on herbarium material, but also on the study of live material cultured under various ecological circumstances; further chromosome and isoenzym studies should be included.

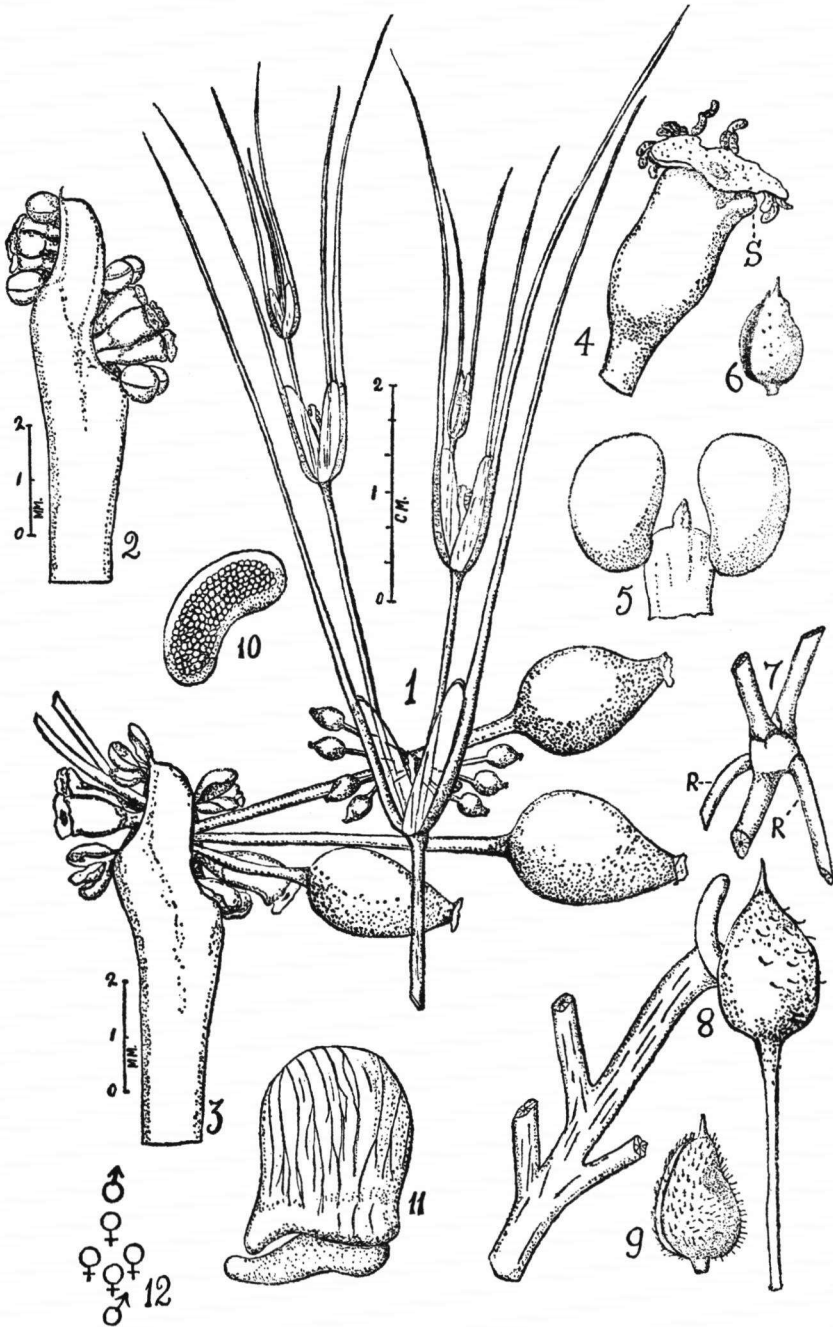


Fig. 3. *Ruppia maritima* L. — 1. Portion of plant; 2 & 3. peduncle and flowers; 4. pistil (S = stigma); 5. stamen. 6. dehiscent achene; 7. node with roots (R = root); 8. rhizome with shell of achene attached. 9. Achene after decomposition of pericarp; 11. embryo; 12. disposition of flowers. — Reproduced from J. Bomb. Nat. Hist. Soc. 45 (1949).

***Ruppia maritima* L.**

*Ruppia maritima* L., Sp. Pl. (1753) 127; Ridl., Fl. Malay Penins. 4 (1924) 367; Backer & Bakh. f., Fl. Java 3 (1968) 9; Merr., Enum. Philip. Flow. Pl. 1 (1922) 24. — Type: unknown.

*Ruppia rostellata* Koch ex Rchb., Icon. Bot. Pl. Crit. 2 (1824) 66. — Type: Traeviranus (Rostock).

Submerged annuals (rarely perennial) with a reduced rhizome; roots up to 7 cm long; stems upright, up to 75 cm long. *Leaves* up to 15 cm long, usually not longer than 10 cm, and 0.5–1 mm wide, light green; margin entire, except near the apex where it is irregularly toothed; apex acute. No turions. *Inflorescence* pedunculate. Peduncle c. 5 cm long, not straight, recurved with a conspicuous bend when fruiting. *Flowers* 2, with 2 stamens and usually 4 subsessile carpels each. When the carpels ripen they develop a podogyne of 1–2 cm length, giving the infructescence an umbellate appearance. *Fruits* ovoid, asymmetric, rather swollen; foramen more or less ovate to triangular; the endocarpous beak 0.5 mm long. In European material the chromosome number is  $2n = 20$ , but in the Mediterranean area morphologically identical populations show often  $2n = 40$ . Harada (1955) found  $2n = 40$  in a Japanese *Ruppia* population, but did not give any description of his plant material, so his identification as *R. maritima* needs confirmation. — **Fig. 3.**

**Distribution** — The species has a worldwide distribution, in the north as well as the south temperate zone and in the tropics, in brackish water and in continental salt lakes. The distribution of the species in Malesia is poorly known. It has been recorded from Peninsular Malay and the Philippines. Wood & Baas Becking (Blumea 2, 1937, 335) record the occurrence of extensive beds of *R. maritima* var. *spiralis* in healthy condition in waters with a salinity of 6‰ and a temperature of 30 °C on Madura. Recently it was collected on Lombok.

**Ecology** — In shallow, standing brackish water it may form dense beds, without other aquatic plants. According to McCann (J. Bombay Nat. Hist. Soc. 45, 1949, 396) aquatic birds are largely responsible for the dispersal of the seeds of *Ruppia*; indeed, young flamingoes seem very dependent on the seeds as a food source, but as these birds do not migrate their role as agents of dispersal is doubtful; moreover, it has not been checked whether some seeds are actually passing the intestinal tract unharmed.

**Note** — In Malesia some variation has been observed in the *Ruppia* material. Ridley, l.c., mentioned specimens from Wellesley, Peninsular Malaya, which had straight peduncles with a length of 1–6 inches; this is outside the normal range of peduncle length in this species, but would fit *R. maritima* var. *longipes* Hagstr. The latter variety has been described from Central Asia (Buchara), and has been found in southern Spain and the east coast of North America; it may turn out to be a proper species. The record of Wood & Baas Becking, l.c., of *R. maritima* var. *spiralis* Koch (material not seen) from Madura may also relate to another taxon.

## ZOSTERACEAE

(C. den Hartog)

*Zosteraceae* Dumort., Anal. Fam. Pl. (1829) 65, 66.

Monoecious or dioecious marine plants. *Rhizome* creeping, monopodial or sympodial; when monopodial with 2 vascular bundles in the cortical layer and at each node (*Zostera*) or internode (*Phyllospadix*) 2 or more unbranched roots and a leaf or a prophyllum, with in its axil a short lateral branch bearing a bunch of distichously arranged leaves; roots and rhizomatic leaves alternating; when sympodial (*Heterozostera*) with 4–12 vascular bundles in the cortical layer and at each node 2 unbranched roots and an erect stem with distichously arranged leaves and without roots at its nodes. *Leaf sheath* compressed, amplexicaulous, ligulate, either membranous and tubular or open and then auriculate with scarios flaps. *Leaf blade* linear, with 3–9(–11) nerves and with several accessory bundles between every two of these; nerves parallel, connected by perpendicular cross veins, margin entire, sometimes slightly denticulate or provided with a fringe of uncoloured, sclerenchymatic ‘fin cells’; tip variable in shape. *Generative shoot* terminal or lateral, sympodial, erect, consisting of a panicle of rhipidia, but often reduced to a single rhipidium; each rhipidium consisting of 2–5 spathes, but sometimes reduced to a single one; peduncle of each spathe partially coalescent with the axis from which it springs, or completely free. *Spathe* consisting of a sheath and a blade; spathal sheath ligulate, open with 2 more or less overlapping, auriculate flaps, enclosing a sessile or stalked *spadix* on the dorsal side of which the male flowers (stamens) and female flowers (gynoecea) are alternately arranged. *Stamens* consisting of 2 free, bilocular, extrorsely lengthwise dehiscent, deciduous thecae connected by a ridge-like connective; pollen confervoid. *Retinaculum* intramarginal, one beside each stamen, sometimes absent (*Zostera* subg. *Zostera*); on the female spadices of *Phyllospadix* alternating with the gynoecea. *Gynoeceum* consisting of an ellipsoid or crescent-shaped ovary with short style and 2 stigmata; ovule 1, orthotropous, pendulous. *Fruit* ovoid or ellipsoid with scarios pericarp or else crescent-shaped with the pericarp differentiated into a soft exocarp and a hard fibrous endocarp. *Seed* 1, ovoid or ellipsoid; embryo consisting for the larger part of the ventrally grooved hypocotyl; in this groove the short, straight, tubular cotyledon which serves as a sheath for the plumula; primary root usually not developing. Tannin cells absent.

### DISTRIBUTION

Three genera with together 17 species distributed in the temperate seas of the northern and southern hemispheres, the area of a few species extending into the tropical waters. In *Malesia* only one genus with one species.

### TAXONOMY

In the past this family has been considered a subfamily or tribe of the heterogeneous family *Potamogetonaceae* (Ascherson 1907; Markgraf 1936; Eckardt 1964; Den Hartog 1970). Tomlinson (1982), who made a thorough study of all helobian families came to the conclusion that the *Zosteraceae* form a clearly circumscribed group whose affinities with other helobian families are obscure, and maintained them at family level.

*References:* Ascherson, P., in Ascherson & Graebner, Pflanzenr. 31 (1907) 27–35. — Markgraf, F., Berichte Deutsche Bot. Ges. 54 (1936) 191–229. — Eckardt, Th., in Engl., Syllabus ed. 12 (1964) 499–512. — Den Hartog, C., Sea-grasses of the World (1970) 10–11, 40–42. — Tomlinson, P.B., Anatomy of the Monocotyledons 7, Helobiales (Alismatidae) (1982).

## PALYNOLOGY

(R. W. J. M. van de Ham)

The pollen grains of the *Zosteraceae* are filamentous monads, 1000–2900  $\mu\text{m}$  long and 3.5–10  $\mu\text{m}$  in diameter, and are hydrophilous (Cranwell 1953; Wodehouse 1959; Schwanitz 1967; Ducker et al. 1978; Stewart & Rüdénberger 1980; Cox & Humphries 1993). The pollen mother cells already have an elongate shape. During meiosis the nucleus spindles show a 90° rotation, so that the microspores lie side by side in the tetrad. Within an anther the pollen grains have a parallel orientation.

Pollen of the *Zosteraceae* is inaperturate. Grains with 1 to 20 pollen tubes, up to several tens of microns (very seldom > 100  $\mu\text{m}$ ) long, were observed on stigmas in flowers of *Zostera marina* (De Cock 1978). The tubes had the same diameter (8–10  $\mu\text{m}$ ) as the pollen threads, which may account for reports of branched pollen (Cranwell 1953; Heusser 1971).

It has often been acknowledged that *Zosteraceae* pollen has no exine. However, a very thin (c. 0.05  $\mu\text{m}$ ) homogeneous exine was demonstrated to be present by Schwanitz (1967). Scanning electron microscopy shows that the exine surface is smooth (Díez et al. 1988). The bulges observed by Wodehouse (1959), suggested to be ‘vestiges of a vanished exine’, may actually represent developing pollen tubes. The intine is c. 0.2  $\mu\text{m}$  thick, and is not differentiated.

Filamentous pollen is restricted to the *Zosteraceae*, *Cymodoceaceae* and *Posidoniaceae*. A phylogenetic analysis (Cox & Humphries 1993) shows the *Zosteraceae* to be the sister group of both other families, and filamentous pollen appears to be a synapomorphy of the whole group.

*References:* Ackerman, J.D., Evol. Ecol. 9 (1995) 139–153. — Cox, P.A. & C.J. Humphries, Bot. J. Linn. Soc. 113 (1993) 217–226. — Cranwell, L.M., Bull. Auckl. Inst. Mus. 3 (1953) 3–91. — De Cock, A.W.A.M., Bull. Soc. Bot. France 125, Actual. Bot. 1/2 (1978) 145–148. — Díez, M.J., S. Talavera & P. García-Murillo, Candollea 43 (1988) 147–158. — Ducker, S.C., J.M. Pettitt & R.B. Knox, Austral. J. Bot. 26 (1978) 265–285. — Heusser, C.J., Pollen and spores of Chile (1971). — Schwanitz, G., Pollen et Spores 9 (1967) 183–209. — Stewart, J.G. & L. Rüdénberger, Amer. J. Bot. 67 (1980) 949–954. — Wodehouse, R.P., Pollen grains (1959).

## ZOSTERA

*Zostera* L., Sp. Pl. (1753) 968; Gen. Pl., ed. 5 (1754) 415; Asch. in Engl., Pflanzenr. IV.11, 31 (1907) 27; Hartog, Sea-grasses of the World (1970) 42. — Type species: *Zostera marina* L.

Monoecious. *Rhizome* creeping or suberect, branched, herbaceous, monopodial, with 2 vascular bundles in the cortical layer; one or more unbranched roots and a bladeless prophyllum or a complete leaf at each node. Roots, when more than one, generally arranged in 2 groups. Internodes variable in length, more or less elongate. From the axils of the rhizomatic leaves short branches arise bearing a bunch of leaves. *Leaves* distichously



arranged. *Leaf sheath* compressed, amplexicaulous, membranous, open or closed, auriculate and ligulate, persisting longer than the blades. *Leaf blade* linear, with 3–9(–11) nerves and several accessory bundles between every two of these; margin entire, sometimes slightly denticulate in the apical part; tip variable. *Generative shoot* terminal or lateral, sympodial, usually consisting of a panicle of rhipidia, but often reduced to a single rhipidium; each rhipidium composed of 2–5 spathes; peduncle of each spathe partially coalescent with the axis from which it springs; spathal sheath containing a lanceolate, sessile spadix on which the male and female flowers are alternately arranged. *Stamens* consisting of 2 free thecae, connected by a ridge-like connective. *Retinacula* membranous, often absent. *Gynoeceium* consisting of a centrally attached ovary with 1 ovule, a broad short style and 2 stigmata. *Fruit* ellipsoid or ovoid; pericarp scarious. *Seed* ellipsoid or ovoid, smooth, ribbed or ridged.

Distribution — The genus is widely distributed along the temperate coasts of the northern Atlantic and Pacific Oceans; in the southern hemisphere it occurs along the temperate coasts of southern and eastern Africa and in the temperate seas of Australia and New Zealand. Some species penetrate to a considerable extent into tropical waters. Two subgenera can be distinguished, of which subg. *Zosterella* (Asch.) Ostenf. is represented by one species in Malesia. Another species of subg. *Zosterella*, *Z. japonica* Asch. & Graebn. [in Engl., Pflanzenz. IV.11, 31 (1907) 32], is widely distributed along the eastern coast of Asia. It has been found as far south as Vietnam and Taiwan and should be looked for in the northern Philippines. It differs from *Z. capricorni* by the following characters: rhizome with 2 roots at each node; leaf blades always with 3 nerves; retinacula smaller, 0.5–1 mm long; seeds smooth.

### ***Zostera capricorni* Asch.**

*Zostera capricorni* Asch., Sitz.-Ber. Ges. Naturf. Fr. Berlin (1876) 11; Abh. Bot. Ver. Prov. Brandenb. 18 (1876) 59; Sauv., J. Bot. 5 (1891) 59, f. 8; Ann. Sc. Nat. VII, 13 (1891) 141; Asch. in Engl., Pflanzenz. IV.11, 31 (1907) 31; Setch., Proc. Nat. Acad. Sc. Wash. 19 (1933) 814; Hartog, Seagrasses of the World (1970) 81, f. 21–23. — Type: *Naumann* (UC), Moreton Bay, Queensland.

*Zostera muelleri* auct. non Irmisch ex Asch.: Asch., Abh. Bot. Ver. Prov. Brandenb. 18 (1876) 56, f. 1 L.

*Zostera nana* auct. non Mertens ex Roth: F. Muell., Census Austral. Pl. (1882) 121, p. p.

*Zostera tasmanica* auct. non Martens ex Asch.: Cheeseman, Man. Fl. New Zeal. (1906) 754.

*Zostera* spec.: Johnstone, Aquat. Bot. 7 (1979) 198.

Rhizome creeping, with fibre bundles in the innermost layers of the outer cortex, 0.75–2 mm thick, with two groups of roots and a prophyllum at each node; internodes 4–40 mm long. Short branches with 2–6 leaves arising from the axils of the rhizomatic leaves. *Leaf sheath* 2–10 cm long, as wide as the base of the blade, open, with rather narrow membranous flaps which do not overlap, but just cover the space between the lateral and intermediate nerves; partially persistent as a scaly mass; auriculae obtuse, 1/3–1/2 mm long; ligula very short; nerves 3–5, intermediate and lateral nerves rather close; squamulae intravaginales not seen. *Leaf blade* 7–50 cm long and 2–5 mm wide, gradually narrowing towards the base, nerves (3–)5; midrib reaching the apex, dilated and sometimes furcate; intermediate nerves usually situated closer to the lateral nerves than

to the midrib, joining the midrib just below the apex; lateral nerves marginal or slightly intramarginal, in the apical region distinctly intramarginal, joining the intermediate nerves often far below the apex (at a distance of 3–5 times the width of the leaf) or just as often near the place where the intermediate nerves curve towards the midrib; between the midrib and each intermediate nerve 3–7 accessory bundles; between an intermediate and a lateral nerve 1–4 accessory bundles; between the lateral nerve and the leaf margin in the apical region 1 or 2 accessory bundles; lateral nerves sometimes absent; cross veins perpendicular, at intervals of 0.5–2 mm, also present in the apical region; tip rounded, truncate, sometimes slightly mucronate, slightly denticulate, seldom with a central cleft. *Generative shoot* lateral, with 1–30 cm long axis, usually with numerous spathes; peduncle of each spathe partly coalescent with the axis from which it springs; connate part in tidal habitats 5–8 mm long, but in still water up to 40 mm long; free part of the peduncle 9–20 cm long, 0.5 mm wide, flat. *Prophyllum* 15 by 2 mm, sheath-like, amplexicaulous, membranous, transparent, emarginate and bi-auriculate; nerves 3; midrib not reaching the apex; lateral nerves parallel, bending towards and crossing the midrib just below the apex; between each pair of nerves 6–7 accessory bundles; flaps very narrow; squamulae intravaginales not seen. *Spathe*: sheath 14–26 mm long and 1.5–2 mm wide, amplexicaulous with 2 obtuse auriculae and a very short ligula; dorsal side of sheath green; flaps overlapping, green except for a c. 0.5 mm wide, membranous, transparent marginal strip; nerves 3, between each pair of nerves 7 accessory bundles; exterior to the lateral nerves 3–4 accessory bundles; blade 30–80 by 1.5 mm, narrowed towards the base; nerves 3–5, near the base only 3; tip as in vegetative leaves. Squamulae intravaginales 2. *Spadix* linear to spatulate, with a short blunt mucro, with 7–10 female flowers and 7–10 male ones. *Stamens*: thecae 2–3 by 1–1.5 mm, oblong-ellipsoid, shed immediately after release of the pollen. *Retinacula* 7–10, obliquely triangular to obliquely ovate, acute but sometimes obtuse, c. 0.6–1.3 mm long, and at the base 1–1.3 mm wide. *Gynoeceium*: ovary cylindrical, 1.5–2 mm long; style 1–1.5 mm long; stigmata 2, 1.5–3 mm long. *Fruit* ellipsoid, 2 mm long and 1 mm wide, flattened, with a 1 mm long beak; pericarp scarious, brown. *Seed* ellipsoid, 2 by 1 mm; testa shiny, brown, with c. 16 longitudinal striae; a fine transverse striation also becoming visible at high magnification. Chromosome number:  $2n = 24$  (New South Wales, Australia; North Island, New Zealand).

**Distribution** — *Zostera capricorni* is widely distributed along the eastern coast of Australia, from northern Victoria to Torres Strait. Further it occurs on North Island, New Zealand and on Lord Howe Island. In *Malesia* it is only known from Daru on the S coast of Papua New Guinea (Johnstone 1979).

**Habitat** — In the lower part of the intertidal belt as well as in the upper sublittoral, forming extensive beds on sheltered sandy and muddy shores; in the tropics sometimes mixed with other sea-grasses. Also in pools in mangrove swamps.

**Note** — Johnstone, l.c., recorded the New Guinea material as *Zostera* spec., because it was almost identical to *Z. capricorni* “except for the leaf tips which are distinctly mucronate”. In this species, however, mucronate leaf tips are not a rare feature, particularly in young leaves. I have seen the Daru-material and cannot distinguish it from *Z. capricorni*.

## CYMODOCEACEAE

(C. den Hartog)

*Cymodoceaceae* N. Taylor in N. Amer. Fl. 17 (1909) 31.

Dioecious marine plants. *Rhizome* creeping, either herbaceous, monopodial and rooting at the nodes (*Cymodocea*, *Halodule*, *Syringodium*) or ligneous, sympodial and rooting from the internodes (*Amphibolis*, *Thalassodendron*). Scales scarious, ovate or elliptic, marked with more or less small, dark, longitudinal stripes and dots (tannin cells). *Leaves* distichous. *Leaf sheath* broad, completely or almost completely amplexicaulous, leaving open or closed circular scars when shed, bi-auriculate, ligulate; scarious flaps covered with numerous short dark, longitudinal stripes and dots (tannin cells). *Leaf blade* linear or subulate with 3 to several parallel or pseudoparallel (*Amphibolis*) nerves; parallel with the nerves more or less short, dark, longitudinal stripes and dots (tannin cells); leaf tip variable in outline. 'Flowers' without perigone, solitary, either terminal on a short branch or arranged in a cymose inflorescence (*Syringodium*). *Male 'flowers'* subsessile or stalked, consisting of 2 quadrilocular, extrorsely dehiscent anthers, which are dorsally connate over at least a part of their length and are attached either at the same height or at a slightly different level (*Halodule*). *Pollen* confervoid. *Female 'flowers'* sessile or shortly stalked, consisting of 2 free ovaries each with either a long style (*Halodule*) or a short style which is divided into 2 or 3 loriform stigmata. *Ovule* 1, sub-orthotropous, pendulous. *Fruit* either with a stony pericarp, more or less compressed (*Cymodocea*, *Halodule*, *Syringodium*) or with a stony endocarp and a fleshy exocarp from which 4 cuneate spreading lobes grow out (*Amphibolis*) or consisting of a fleshy bract which encloses the fertilised ovaries (*Thalassodendron*); not dehiscent. *Seed* 1. Embryo either consisting for the larger part of the plumula with a lateral primary root and a cylindrical hypocotyl, appressed to the upper part of the plumula (*Cymodocea*) or consisting of a long hypocotyl and a short plumula without a primary root (*Amphibolis*).

## DISTRIBUTION

Four genera with together 14 species, distributed in the tropical seas, some species extending into the subtropical and warm-temperate waters. The fifth genus, *Amphibolis* with 2 species, is limited to the Australian temperate waters. In *Malesia* 4 genera.

## TAXONOMY

In the past this family was considered a subfamily or tribe of the heterogeneous family *Potamogetonaceae* (Ascherson 1889, 1907; Markgraf 1936; Eckardt 1964; Den Hartog 1970). Following Tomlinson (1982) the *Cymodoceaceae* are now regarded as a family of its own. This view has been shared by Dahlgren et al. (1985) in their survey of the families of Monocotyledons. Hutchinson (1934) has classified the genera here presented as belonging to *Cymodoceaceae* within the family of the *Zannichelliaceae*. Although Tomlinson regards this as inappropriate, the combination of the two families is not unlogical, but as *Zannichelliaceae* s.s. do not occur in *Malesia* this subject will further not be discussed.

*References:* Ascherson, P., in Engl., Nat. Pflanzenfam. II, 1 (1889) 210; in Ascherson & Graebner, Pflanzenr. 31 (1907) 145. — Dahlgren, R.M.T., H.T. Clifford & P.F. Yeo, Families of the Monocotyledons (1985) 320–322. — Den Hartog, C., Sea-grasses of the World (1970) 10–11. — Eckardt, Th., in Engl., Syllabus ed. 12, 2 (1964) 499–512. — Hutchinson, J.B., Families of flowering plants II, Monocotyledons (1934) 50–51. — Markgraf, F., Ber. Deut. Bot. Ges. 54 (1936) 191–229. — Tomlinson, P.B., Anatomy of the Monocotyledons 7, Helobiae (Alismatidae) (1982) 384–421.

## PALYNOLOGY

(R.W.J.M. van der Ham)

The pollen grains of the *Cymodoceaceae* are filamentous monads (Ducker et al. 1978; Cox & Humphries 1993; Ackerman 1995). Those of *Amphibolis* are 3000–5000 µm long, those of *Cymodocea* c. 2000 µm, and those of *Halodule* c. 1000 µm. The pollen mother cells are not much elongate. At release from the tetragonal tetrad (microspores side by side) and during the free microspore period the microspores become progressively more elongate. Within the anther the pollen grains are coiled. This appears to be a characteristic of the *Cymodoceaceae* in contrast to the *Zosteraceae*, where the grains are arranged parallel to each other.

Pollen of the *Cymodoceaceae* is inaperturate. Blackmore et al. (1987) reported a single pollen tube for *Amphibolis antarctica* (multiple pollen tubes known in *Zosteraceae* and *Najadaceae*).

According to Ducker et al. (1978) the pollen of *Amphibolis* and *Thalassodendron* has no exine. A distinct, though undifferentiated intine is present. Its surface is sticky, being covered with lipid material and mucilage. Scanning electron micrographs show a ribbed, and at higher magnification finely reticulate pattern. However, as stated by Zavada (1983) pollen of *Thalassodendron* and *Halodule* has a thin unsculptured and unstructured sporopollenin layer (exine).

Filamentous pollen occurs in all members of three angiosperm families: the *Cymodoceaceae*, *Posidoniaceae* and *Zosteraceae*. A phylogenetic analysis (Cox & Humphries 1993) shows filamentous pollen to be a synapomorphy of these families. The *Cymodoceaceae* and *Posidoniaceae* are sister groups, and the *Zosteraceae* is their outgroup. *Amphibolis* and *Thalassodendron*, which have a similar pollen morphology (Ducker et al. 1978), are sister groups within the *Cymodoceaceae*.

*References:* Ackerman, J.D., Evol. Ecol. 9 (1995) 139–153. — Blackmore, S., C.A. McConchie & R.B. Knox, Cladistics 3 (1987) 333–347. — Cox, P.A. & C.J. Humphries, Bot. J. Linn. Soc. 113 (1993) 217–226. — Ducker, S.C., J.M. Pettitt & R.B. Knox, Austral. J. Bot. 26 (1978) 265–285. — Zavada, M.S., Bot. Review 49 (1983) 331–379.

## KEY TO THE GENERA

- 1a. Rhizome monopodial, herbaceous, with a short erect stem at each node. Leaf sheath persisting longer than the leaf blade. Anthers stalked . . . . . 2
- b. Rhizome sympodial, ligneous, with elongate, more or less branched, erect stems, arising from every fourth internode; roots 1–5 on the internode preceding the stem-bearing internode. Leaves with parallel nerves and denticulate apex. Leaf blade shed with its sheath. ‘Flowers’ enclosed by 4 leafy bracts. Anthers sessile, connate

- over their whole length, each crowned with one appendage. Style with 2 stigmata. False fruit composed of 1 or 2 fertilised ovaries surrounded by an enlarged fleshy bract . . . . . **Thalassodendron** (p.213)
- 2a. Leaves flat. Flowers solitary . . . . . 3
- b. Leaves subulate. 'Flowers' arranged in a cymose inflorescence . . . . . **Syringodium** (p. 211)
- 3a. Nerves 3. Anthers not attached at the same height on the stalk. Ovary with 1 undivided style . . . . . **Halodule** (p. 207)
- b. Nerves 7–17. Anthers attached at the same height on the stalk. Style divided into 2 stigmata . . . . . **Cymodocea** (p. 203)

### CYMODOCEA

*Cymodocea* König in König & Sims, Ann. Bot. 2 (1805) 96; Hartog, Sea-grasses of the World (1970) 160. — *Phycagrostis* [*Phycagrostis* Cavolini, Phuc. Anth. (1792) 13, nom. inval.] Willd., Sp. Pl. 4 (1806) 649; Kuntze, Rev. Gen. Pl. 2 (1891) 744. — *Cymodocea* sect. *Phycagrostis* Asch., Linnaea 35 (1868) 161; Benth. & Hook.f., Gen. Pl. 3 (1883) 1019 ('*Cymodocea* sect. *Phycagrostis*'). — *Cymodocea* subg. *Phycagrostis* Asch. in Neumayer, Anl. Wiss. Beob. Reisen ed. 1 (1875) 362; in Engl., Pflanzenr. IV.11, 31 (1907) 146. — Type species: *Cymodocea nodosa* (Ucria) Asch.

Dioecious. *Rhizome* creeping, herbaceous, monopodial with many vascular bundles in the cortical layer, and at each node with 1–5 more or less branched roots and a short erect stem bearing 2–7 leaves; internodes 1–6 cm long; scales scarious, ovate, with many tannin cells. *Leaf sheath* compressed, amplexicaulous or almost amplexicaulous, bi-auriculate and ligulate, 1.5–10 cm long, scarious flaps covered with numerous tannin cells, persisting longer than the leaf blade, leaving an open or a closed circular scar when shed, so giving the stem an annular appearance. *Leaf blade* linear, often narrowed at the base, with many tannin cells; margin entire, but serrulate or spinulose near the tip; nerves 7–17, all joining the intramarginal nerves at the apex; between each pair of nerves several very fine, parallel accessory veins; cross veins perpendicular; tip obtuse or sometimes emarginate, more or less distinctly toothed. '*Flower*' solitary and terminal, enclosed in a leaf similar to the others, a bud in the axil of the penultimate leaf developing into the prolongation of the main axis (sympodium). *Male 'flower'* stalked, consisting of 2 anthers, which are dorsally connate and attached at the same height on the stalk. *Female 'flower'* sessile or shortly stalked, consisting of 2 free ovaries each with a short style divided into 2 loriform stigmata. *Fruit* with a stony pericarp, semi-circular to semi-ovate or elliptic, laterally compressed, with dorsal ridges and a beak. — Fig. 4, 5.

Distribution — The genus contains 4 species and is widely distributed in tropical and subtropical seas of the Old World. In *Malesia* 2 species.

### KEY TO THE SPECIES

- 1a. Leaf scars closed. Leaves 2–4 mm wide; leaf sheath narrow, persistent, forming a scarious mass at the base of each shoot; nerves 9–15; leaf tip rounded to emarginate, faintly serrulate. Fruit semicircular, with dentate dorsal ridges . . **1. C. rotundata**

- b. Leaf scars open. Leaves 4–9 mm wide; leaf sheaths broad-triangular, not persistent; nerves 13–17; leaf tip obtuse, densely set with triangular teeth. Fruit elliptic, with 3 smooth dorsal ridges ..... **2. *C. serrulata***

### 1. *Cymodocea rotundata* Asch.

*Cymodocea rotundata* Ehrenb. & Hempr. ex Asch., Sitz.-Ber. Ges. Naturf. Fr. Berlin (1870) 84; Asch. in Engl., Pflanzenr. IV.11, 31 (1907) 147; Backer, Handb. Fl. Java 1 (1925) 50; Backer & Bakh.f., Fl. Java 3 (1968) 9; Hartog, Sea-grasses of the World (1970) 166, f. 47, 49b; Meñez, Phillips & Calumpang, Smithson. Contr. Mar. Sci. 21 (1983) 8, f. 3, 4 (map); Brouns, Science in New Guinea 12 (1986) 74, f. 5; Tomascik, Mah, Nontji & Moosa, Ecology of the Indonesian seas 2 (1997) 851, 854, f. 18.11 (map), 18.19, 18.21a. — *Phucagrostis rotundata* Ehrenb. & Hempr. [ex Asch., Linnaea 35 (1868) 160, nom. inval.] ex Kuntze, Rev. Gen. Pl. 2 (1891) 744. — Type: not seen (Red Sea).

*Cymodocea aequorea* auct. non König: Naves, Nov. App. (1882) 247.

*Cymodocea acaulis* Peter, Abh. Ges. Wiss. Gött. 13, 2 (1928) 13, 39, f. 1. — Type: not seen.

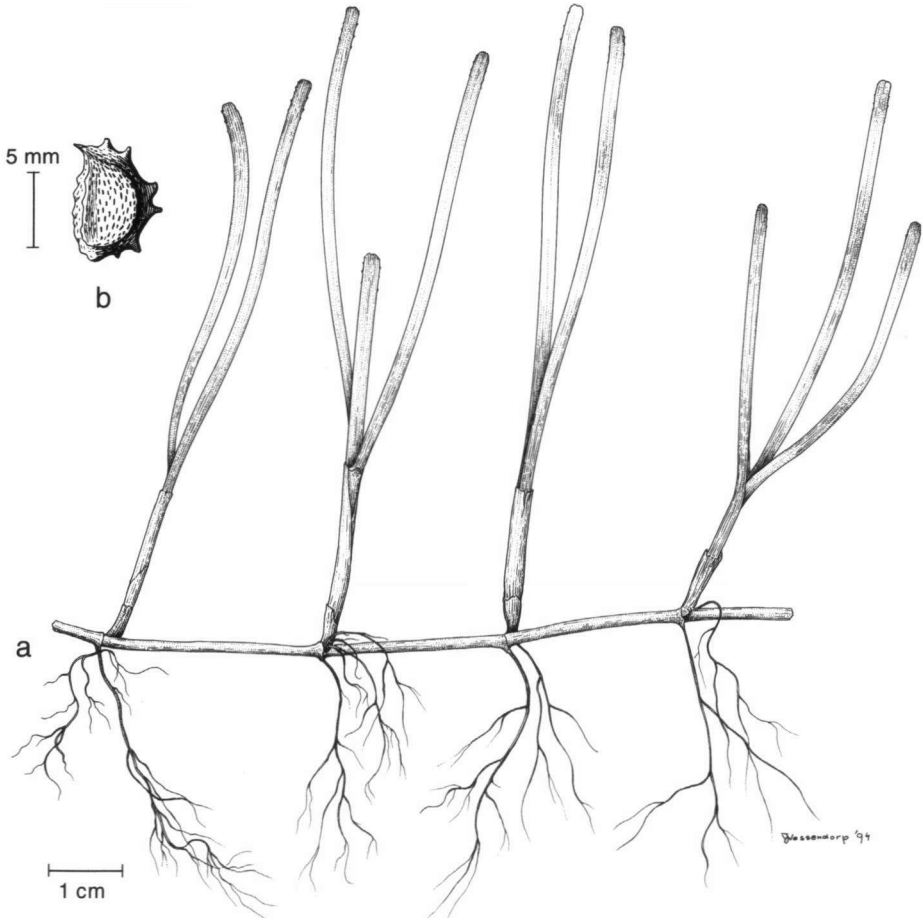


Fig. 4. *Cymodocea rotundata* Asch. — a. Habit; b. fruit.

Rhizome rather delicate, with at each node 1–3 irregularly branched, long roots and a short erect stem bearing 2–7 leaves; internodes 1–4.5 cm long; scales up to 1 cm long. *Leaf sheath* slightly obconical, pale purplish, 1.5–4(–5.5) cm long; auriculae acute; ligula 0.5 mm high, old sheaths forming a scarious mass, when shed leaving closed circular scars on the stem, giving it an annular appearance. *Leaf blade* linear, often somewhat falcate, 7–15 cm long and 2–4 mm wide, not narrowed towards the tip, entire, rarely somewhat spinulose; tip obtuse, faintly serrulate, sometimes slightly emarginate; nerves 9–15; between each pair of nerves 3 fine accessory veins; marginal nerves reaching the apical area; the midrib not projecting. *Male 'flower'* stalked, anthers 11 mm long, each crowned by a subulate process. *Female 'flower'*: ovary very small, gradually passing into the style, together 5 mm long; stigmata at least 30 mm long, spirally coiled. *Fruit* 1 or 2 together, sessile, semi-circular, laterally compressed, 10 mm long, 6 mm wide and 1.5 mm thick, with 3 dorsal, parallel ridges of which the median one is set with 6–8 conspicuous, acute teeth, and one ventral ridge bearing 3 or 4 teeth; pericarp sclerenchymatic, covered with numerous longitudinal tannin cells; beak apical, somewhat oblique, persistent, 2 mm long. — **Fig. 4.**

**Distribution** — *Cymodocea rotundata* is widely distributed along the coasts of the Indian Ocean and the western Pacific. It extends along the coast of Africa from the Red Sea as far south as Maputu and Madagascar. Further, it has been found along the southern coast of the Indian Peninsula, Andamans and Nicobars, and it extends through Malesia into the western Pacific (Bismarck Archipelago, Carolines, New Caledonia and Queensland) and its marginal seas (Gulf of Thailand, Vietnam, the Ryukyu Islands). It is widely distributed in *Malesia*: Riau Islands, Peninsular Malaysia, Java, Philippines, Borneo, Celebes, Lesser Sunda Islands, Moluccas, and New Guinea. It has not been recorded from Sumatra, probably due to under-collecting.

**Habitat & Ecology** — *Cymodocea rotundata* is most common at the lowest low-water mark, where it becomes uncovered during spring-ebbs only. It inhabits shallow terraces covered with coral sand. In this habitat the plants are small and widely spaced. The optimum habitat of the species is to be found on muddy flats, where the plants form very dense growths. In sandy habitats *C. rotundata* may be accompanied by *C. serrulata* and *Thalassia hemprichii*; on muddy substrata the species forms pure stands, or is associated with *Halodule pinifolia* or *H. uninervis*.

## 2. *Cymodocea serrulata* (R. Br.) Asch. & Magnus

*Cymodocea serrulata* (R. Br.) Asch. & Magnus, Sitz.-Ber. Ges. Naturf. Fr. Berlin (1870) 84; Asch. in Engl., Pflanzenr. IV.11, 31 (1907) 147; Backer, Handb. Fl. Java 1 (1925) 50; Hartog, Seagrasses of the World (1970) 171, f. 48, 49a; Meñez, Phillips & Calumpang, Smithson. Contr. Mar. Sci. 21 (1983) 8, f. 5, 6 (map); Brouns, Science in New Guinea 12 (1986) 74, f. 7; Tomascik, Mah, Nontji & Moosa, Ecology of the Indonesian seas 2 (1997) 851, 854, f. 18.11 (map), 18.20, 18.21b. — *Caulinia serrulata* R. Br., Prodr. Fl. Nov. Holl. (1810) 339. — *Posidonia serrulata* (R. Br.) Spreng., Syst. Veg. 1 (1825) 181. — *Kerneria serrulata* (R. Br.) Schult., Syst. Veg. 7 (1829) 170. — *Phucagrostis serrulata* (R. Br.) Kuntze, Rev. Gen. Pl. 2 (1891) 744. — Type: not seen.

*Cymodocea ciliata* (Forssk.) Asch., Linnaea 35 (1868) 162, pro minore parte, type excluded.

*Cymodocea asiatica* Makino, Bot. Mag. Tokyo 26 (1912) 211, pl. 17. — Type: not seen.

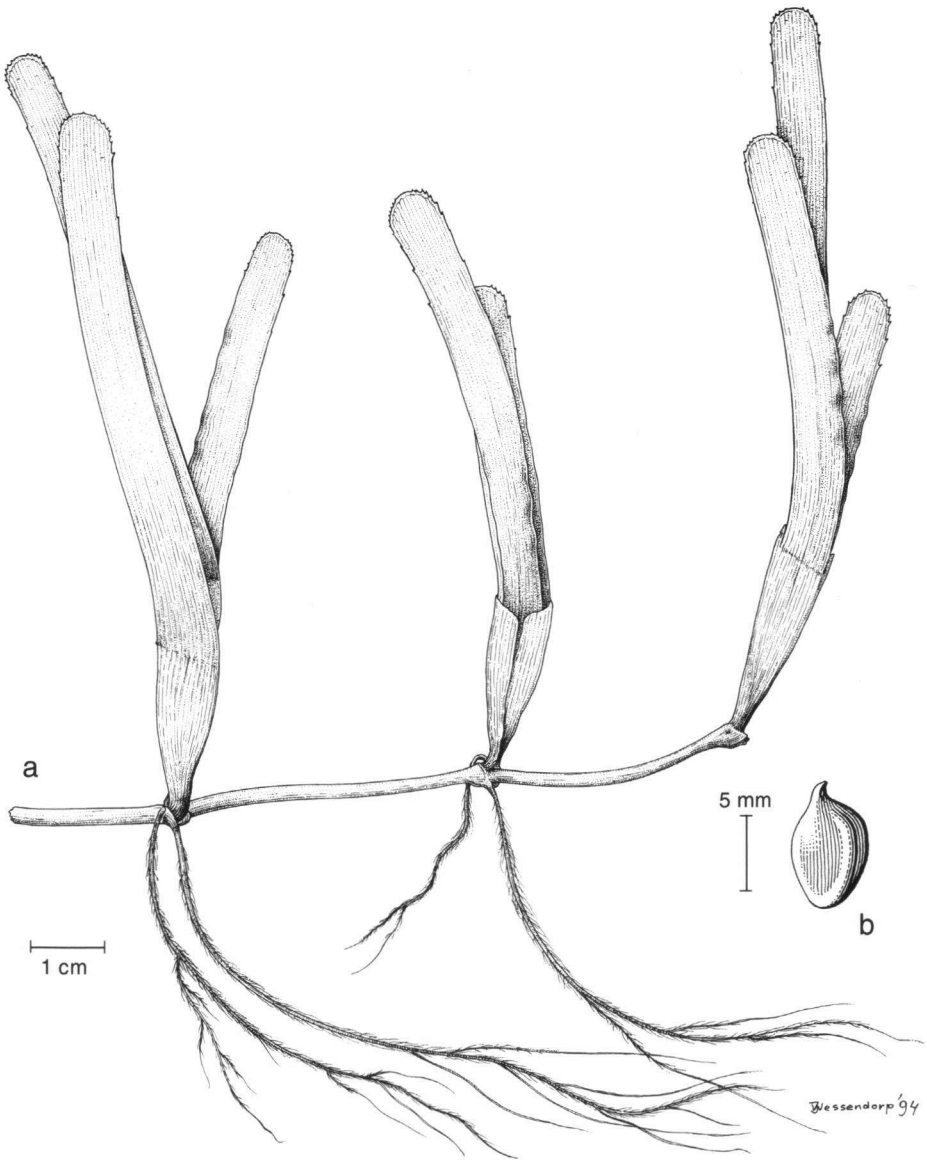


Fig. 5. *Cymodocea serrulata* (R. Br.) Asch. & Magnus. – a. Habit; b. fruit.

Rhizome robust, at each node with 2 or 3 sparsely branched roots and a short erect stem bearing 2–5 leaves; internodes 2–5.5 cm long. *Leaf sheath* broadly triangular, narrowed at the base, bright purple, 1.5–3 cm long; auriculae acute, 1 mm long; ligula 1 mm high; the sheaths leaving open circular scars on the stem when shed. *Leaf blade* linear to falcate, 6–15 cm long and 4–9 mm wide, narrowed at the base and slightly spinulose towards the apex; tip obtuse, serrate to dentate; teeth triangular; nerves 13–17, midrib



somewhat more conspicuous than the other nerves, not projecting; between each pair of nerves 3–4 fine accessory veins; marginal nerves not reaching the apical area. *Male* 'flowers' 2 per short shoot, with a stalk up to 20 mm; anthers yellowish, densely covered with tannin cells, c. 8 mm long, without a terminal process [McMillan, *Aquat. Bot.* 9 (1980) 291–295, f. 1–3]. *Female* 'flower' sessile; ovary 1.5 mm long, style 2–4 mm long, stigmata 23–27 mm long. *Fruit* sessile, elliptic in outline, laterally compressed, 7–9 mm long, 3–4.5 mm wide and 2 mm thick, with 3 dorsal, parallel, very blunt ridges; pericarp sclerenchymatic, dull; beak apical, straight, c. 1 mm long, sometimes with remnants of style and stigmata. — **Fig. 5.**

**Distribution** — *Cymodocea serrulata* is commonly distributed in the Red Sea and along the coasts of E Africa, as far south as Delagoa Bay and Madagascar. It extends through the tropical belt of the Indian Ocean (Seychelles, southern coast of India, Sri Lanka) and Malesia into the western Pacific as far as the Ryukyu Islands, New Caledonia and Queensland. In *Malesia* it has been recorded from Peninsular Malaysia, Java, Borneo, Philippines, Celebes, Lesser Sunda Islands, Moluccas, and New Guinea.

**Habitat & Ecology** — *Cymodocea serrulata* has its optimum development on mud-covered coral debris. On such a substratum it is mostly absolutely dominant. On muddy sand or coral sand it is also well-developed, but there it is only a component of a homogeneously mixed vegetation of *Thalassia hemprichii*, *Enhalus acoroides*, *Halodule uninervis* and *Halophila ovalis*. Although the coexistence of *C. serrulata* and *C. rotundata* has been recorded several times, this species combination is rare and reflects environmental conditions which are marginal to both species. *Cymodocea serrulata* mainly occurs around low-water mark and is stenohaline. According to Miki [*Bot. Mag. Tokyo* 48 (1934) 140] the northern limit of its area of distribution does not exceed the 21 °C February water isotherm.

## HALODULE

*Halodule* Endl., *Gen. Pl.*, Suppl. 1 (1841) 1368; Asch., *Linnaea* 35 (1868) 163, 187; Benth. & Hook. f., *Gen. Pl.* 3 (1883) 1019 ('*Halodula*'); Hartog, *Blumea* 12 (1964) 296; *Sea-grasses of the World* (1970) 146. — Type species: *Halodule uninervis* (Forssk.) Asch.

*Diplanthera* Thouars, *Gen. Nov. Madag.* 2 (1806) 3, non Gleditsch (1764); Asch. in *Engl., Pflanzenr.* IV.11, 31 (1907) 151. — Type species: *Diplanthera madagascariensis* Steud.

Dioecious. *Rhizome* creeping, herbaceous, monopodial, with 2 vascular bundles in the cortical layer, with at each node one or more unbranched roots and a short erect stem, bearing 1–4 leaves; internodes 0.5–6 cm long; scales scarios, ovate or elliptic, marked with more or less small, dark, longitudinal stripes and dots (tannin cells). *Leaf sheath* 1–6 cm long, amplexicaulous, bi-auriculate, ligulate; scarios flaps covered with numerous tannin cells, persisting longer than the leaf blade, when shed leaving a circular scar; these scars giving the stem an annular appearance. *Leaf blade* linear, entire, often narrowed at the base, with many tannin cells; nerves 3; midrib conspicuous, widened or furcate at the apex; lateral nerves intramarginal, inconspicuous, both ending in a usually well-developed lateral tooth; tip very variable in outline. 'Flower' solitary and terminal, enclosed in a leaf similar to the others, a bud in the axil of the penultimate leaf developing into the prolongation of the main axis (sympodium). *Male* 'flower' stalked, consisting of 2 anthers attached at different levels and joined dorsally by their lower parts;

pollen confervoid. *Female 'flower'* sessile, consisting of 2 free ovaries each with one long style. *Fruit* with stony pericarp, subglobose to ovoid, more or less compressed, with a short beak. — **Fig. 6.**

**Distribution** — The genus, which consists of 6–8 species, is widely distributed along the coasts of all tropical seas, in the Atlantic as well as in the Indo-Pacific. In *Malesia* 2 species.

**Habitat** — Small sea-grasses, forming extensive meadows, often together with other marine phanerogams on sandy as well as on muddy bottoms in shallow coastal waters.

#### KEY TO THE SPECIES

- 1a. Leaf tip rounded, more or less serrulate; lateral teeth faintly developed or absent; leaves 0.6–1.2 mm wide . . . . . **1. *H. pinifolia***  
 b. Leaf tip tridentate: median tooth obtuse (but in very narrow specimens often acute), shorter than or as long as the linear lateral teeth; leaves 0.25–3.5 mm wide . . . . .  
 . . . . . **2. *H. uninervis***

#### 1. *Halodule pinifolia* (Miki) Hartog

*Halodule pinifolia* (Miki) Hartog, *Blumea* 12 (1964) 309, f. 10; *Sea-grasses of the World* (1970) 158, f. 44; Meñez, Phillips & Calumpang, *Smithson. Contr. Mar. Sci.* 21 (1983) 13, f. 7, 8 (map); Brouns, *Science in New Guinea* 12 (1986) 71, f. 4; Tomascik, Mah, Nontji & Moosa, *Ecology of the Indonesian seas* 2 (1997) 854, f. 18.11 (map), 18.25. — *Diplanthera pinifolia* Miki, *Bot. Mag. Tokyo* 46 (1932) 787, f. 9; *ibid.* 48 (1934) 132, 135. — Type: *Miki*, Ryukyu Is., not seen.

Rhizome creeping, with 2–3 roots and a short erect stem at each node; internodes 1–3 cm long; scales ovate, 2.5–3 mm long. *Leaf sheath* 1–4 cm long. *Leaf blade* 5–20 cm long and 0.6–1.2 mm wide; midrib conspicuous, widening and sometimes furcate at the apex; intramarginal veins inconspicuous, both ending in a very small tooth; tip obtuse, set with more or less numerous small irregular serratures. *Male 'flower'* on a 10 mm long stalk; lower anther 2.5 mm long, upper anther 3 mm long, sometimes with small scales at the base (Miki, l.c.). *Female 'flower'* sessile; ovary ovoid, 1 mm long, style 13 mm long, lateral. *Fruit* ovoid, 2–2.5 mm long with a 1 mm long lateral beak.

**Distribution** — *Halodule pinifolia* is widely distributed in the eastern Indian Ocean (India, Sri Lanka) and in the western Pacific and its marginal seas, from Taiwan and the Ryukyu Islands through Malesia to Queensland, Fiji, the Tonga Islands and New Caledonia. In *Malesia* it is probably common. It has been recorded from Singapore, Java, Borneo, Philippines, Celebes (Makassar), the Lesser Sunda Islands, Moluccas, and New Guinea.

**Habitat & Ecology** — *Halodule pinifolia* occurs in the upper part of the sublittoral and the lower part of the eulittoral belt, on sandy and muddy bottoms in sheltered bays, in pools on coral reefs, but also in wave-beaten localities. It is a typical pioneer species which comes to dominance in places not suitable to other sea-grasses, or where the vegetation has been destroyed by mechanical disturbance. It does not seem to be able to compete with other species and, therefore, it occurs generally in monospecific growths. According to Miki (l.c.) the northern border of the area of *H. pinifolia* coincides with the 21 °C February water isotherm.

**2. *Halodule uninervis* (Forssk.) Asch.**

*Halodule uninervis* (Forssk.) Asch. in Boiss., *Fl. Orient.* 5 (1882) 24; Hartog, *Blumea* 12 (1964) 297, f. 1–3; *Sea-grasses of the World* (1970) 147; Meñez, Phillips & Calumpang, *Smithson. Contr. Mar. Sci.* 21 (1983) 13, f. 9, 10 (map); Brouns, *Science in New Guinea* 12 (1986) 71, f. 3; Tomascik, Mah, Nontji & Moosa, *Ecology of the Indonesian seas 2* (1997) 854, f. 18.11 (map), 18.24. — *Zostera uninervis* Forssk., *Fl. Aeg.-Arab.* (1775) cxx, 157. — *Diplanthera uninervis* Asch. in Engl. & Prantl, *Nat. Pflanzenfam., Nachtr.* 1 (1897) 37; in Engl., *Pflanzenr.* IV.11, 31 (1907) 152; Merr., *Philipp. J. Sc., Bot.* 10 (1915) 3; Ostenf., *Dansk. Bot. Ark.* 2, 6 (1916) 30; Backer, *Handb. Fl. Java* 1 (1925) 51; Miki, *Bot. Mag. Tokyo* 46 (1932) 783, f. 8. — Type: Red Sea, not seen.

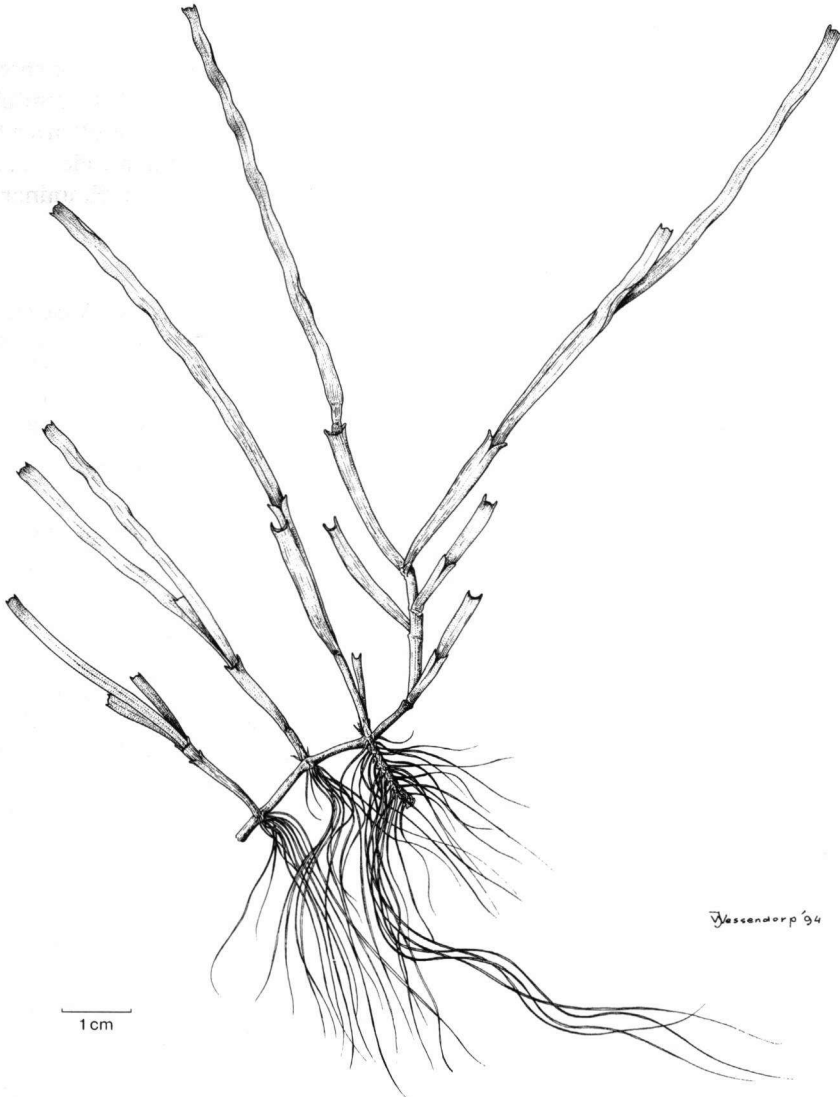


Fig. 6. *Halodule uninervis* (Forssk.) Asch. — Habit.

*Diplanthera tridentata* Steinh., Ann. Sc. Nat. II, 9 (1838) 98, pl. 4 B. — *Diplanthera madagascariensis* Steud., Nomencl. Bot. ed. 2, 1 (1840) 515. — *Halodule australis* Miq., Fl. Ind. Bat. 3 (1855) 227, nom. illeg. — *Halodule tridentata* (Steinh.) F. Muell., Census Austral. Pl. (1882) 121; Hartog, Blumea 12 (1964) 301, f. 4. — *Cymodocea australis* (Miq.) Trimen, Syst. Cat. Ceyl. Pl. (1885) 99. — Type: *Du Petit Thours*, Madagascar, not seen.  
*Ruppia* sp.: Zoll., Syst. Verz. (1854) 74.

Rhizome creeping, with 1–6 roots and a short erect stem at each node; internodes 0.5–4 cm long; scales ovate or elliptic, up to 6–7 mm long. *Leaf sheath* 1–3.5 cm long. *Leaf blade* 6–15 cm long and 0.25–3.5 mm wide, narrowed at the base, sometimes falcate; midrib conspicuous, widening and sometimes furcate near the apex; tip with 2 linear lateral teeth and an obtuse (but in very narrow specimens often acute) median tooth in which the midrib ends; median tooth as long as or shorter than the lateral teeth, rarely slightly longer, or not developed at all. *Male 'flower'* on a 6–20 mm long stalk; anthers 2–3 mm long, coloured red by numerous tannin cells; the upper anther attached 0.25–0.5 mm above the lower one. *Female 'flower'*: ovary ovoid, 1 mm long; style 28–42 mm long, terminal. *Fruit* subglobose-ovoid or globose, slightly appressed, 2–2.5 by 1.75–2 mm, with a 0.25–1 mm long apical beak. — **Fig. 6.**

**Distribution** — *Halodule uninervis* is widely distributed in the Indian Ocean and the western part of the Pacific. It is common along the coast of E Africa from the Red Sea as far as the province of Natal (S Africa), and it occurs also on Madagascar and the Seychelles. It is probably common along the southern coast of Asia, where it has been found in Oman, the Persian Gulf, India and Sri Lanka. The eastern part of the area extends from the Ryukyu Islands, Indochina and Thailand through Malesia to the tropical coasts of Australia; in the Pacific it has been found at least as far eastward as the Tonga Islands. In *Malesia* it has been recorded from Peninsular Malaysia, Java, Borneo, Philippines, Celebes, Lesser Sunda Islands, Moluccas, and New Guinea. There are no records from Sumatra and Borneo, probably due to under-collecting.

**Habitat & Ecology** — *Halodule uninervis* is one of the most eurybiontic tropical sea-grasses. It is essentially a sublittoral species, but it penetrates into the intertidal belt up to the mangrove swamps, while on the other hand it can descend to a considerable depth. It is a typical pioneer species, growing usually gregarious and being dominant in all kinds of habitats less suitable for other species. It can be found as a dominant on sandy as well as on muddy bottoms, in sandy pools on coral reefs and in creeklets and pools within the mangrove swamps, but also in estuaries and pools occasionally reached by sea water during exceptionally high tides or storm floods. In contrast to most pioneer species it is, however, able to maintain itself in a vegetation of more stenobiontic sea-grasses, as e.g. *Thalassia hemprichii*, *Cymodocea* species and *Syringodium isoetifolium*. According to Miki (l.c.) the species reaches its northern border along the 21 °C February water isotherm.

**Note** — The variability of the leaf width of the various populations is considerable and one can distinguish between wide-leaved and narrow-leaved populations which grow sympatric but never together. More detailed studies are necessary to establish whether these differences are only environmentally induced or whether they are genetically determined.

## SYRINGODIUM

*Syringodium* Kütz. in Hohenacker, 'Meeralgen' (Algae Marinae Exsiccatae) 9 (1860) no. 426; Dandy & Tandy, J. Bot. 77 (1939) 114; Hartog, Sea-grasses of the World (1970) 176. — Type species: *Syringodium filiforme* Kütz.

*Cymodocea* sect. *Phycoschoenus* Asch., Linnaea 35 (1868) 162; Benth. & Hook. f., Gen. Pl. 3 (1883) 1019. — *Cymodocea* subg. *Phycoschoenus* (Asch.) Asch. in Neumayer, Anl. Wiss. Beob. Reisen ed. 1 (1875) 363; in Engl., Pflanzenr. IV.11, 31 (1907) 149. — *Phycoschoenus* (Asch.) Nakai, Ord. Fam. etc. (1943) 211. — Type species: *Syringodium isoetifolia* (Asch.) Dandy.

Dioecious. *Rhizome* creeping, herbaceous, monopodial, with many vascular bundles in the cortical layer, at each node with one or more unbranched or slightly branched roots and a short erect stem, bearing 2–3 leaves; internodes 1–4 cm long; scales scarios, ovate, acute, with numerous tannin cells. *Leaf sheath* broad, 1.5–6 cm long, persisting longer than the blade, leaving open circular scars when shed, subamplexicaulous, bi-auriculate and ligulate; scarios flaps covered with numerous tannin cells; auriculae obtuse. *Leaf blade* subulate, often narrowed at the base, covered with numerous tannin cells, in cross section showing 1 central vascular bundle, 6–8 air channels and a varying number of pericentral vascular bundles. *Inflorescence* cymose, the lower branches dichasial, the higher ones monochasial, so forming an anthela of drepania. 'Flower' enclosed by a reduced leaf, the sheath of which is elliptic to ovate and inflated, up to 9 mm long and 3 mm wide, and whose lamina is only 5–20 mm long; towards the top of the inflorescence these leaves gradually decreasing in size. *Male 'flower'* stalked, consisting of 2 anthers which are dorsally connate at their lower parts and attached at the same height on the stalk; anthers without an apical process. *Female 'flower'* sessile, consisting of 2 free ovaries, each with a very short style which divides into 2 rather short stigmata. *Fruit* with stony pericarp, obliquely ellipsoid to obliquely obovoid, quadrangular in cross section and dorsally with an inconspicuous 4–7 mm long median ridge; rostrum short and bifid. — Fig. 7.

Distribution — Genus of two closely related species, *S. isoetifolium*, which inhabits the Indo-Pacific and *S. filiforme*, which is confined to the Caribbean and the Gulf of Mexico.

***Syringodium isoetifolium* (Asch.) Dandy**

*Syringodium isoetifolium* (Asch.) Dandy, J. Bot. 77 (1939) 116; Hartog, Sea-grasses of the World (1970) 177, f. 50, 51; Meñez, Phillips & Calumpong, Smithson. Contr. Mar. Sci. 21 (1983) 18, f. 11, 12 (map); Brouns, Science in New Guinea 12 (1986) 77, f. 8; Tomascik, Mah, Nontji & Moosa, Ecology of the Indonesian seas 2 (1997) 857, f. 18.11 (map), 18.26. — *Cymodocea isoetifolia* Asch., Sitz.-Ber. Ges. Naturf. Fr. Berlin (1867) 3; Linnaea 35 (1868) 163; in Engl., Pflanzenr. IV.11, 31 (1907) 149; Backer, Handb. Fl. Java 1 (1925) 50. — *Phucagrostis isoetifolia* (Asch.) Kuntze, Rev. Gen. Pl. 2 (1891) 744. — *Phycoschoenus isoetifolia* (Asch.) Nakai, Ord. Fam., etc. (1943) 211. — Type: not seen.

*Cymodocea aequorea* var. *Wight* ex Kunth, Enum. Pl. 3 (1841) 118 (for *Wight 2413*, excl. syn.).

*Rhizome* slender, with at each node 1–3 little branched or unbranched roots and a short erect stem bearing 2–3 leaves; internodes 1.5–3.5 cm; scales 5 mm long, perishing at an early stage. *Leaf sheath* 1.5–4 cm long, often tinged with red. Sheath of the re-

duced leaves in the inflorescence at most 7 mm long. *Leaf blade* 7–30 mm long, 1–2 mm wide, narrowed at the base; central vascular bundle surrounded by a ring of 6–8 air channels and a ring of 7–10(–15) pericentral vascular bundles, which are considerably narrower than the central one. *Male 'flower'* on a 7 mm long stalk; anthers ovate, 4 mm long. *Female 'flower'* sessile; ovary ellipsoid, 3–4 mm long, style 2 mm long; stigmata 4–8 mm long. *Fruit* obliquely ellipsoid, 3.5–4 mm long, 1.75–2 mm wide and 1.5 mm thick; rostrum 2 mm long, bifid. — **Fig. 7.**



**Fig. 7.** *Syringodium isoetifolium* (Asch.) Dandy — a. Flowering habit; b, c. female flower; d. male flower; e. fruit. — a  $\times$  1, b–e  $\times$  4. — Reproduced from Den Hartog, *Sea-grasses of the World* (1970) 180, f. 51.

Distribution — The species is widely distributed in the tropical part of the Indian Ocean and the western Pacific. It occurs from the Red Sea as far south as Delagoa Bay, in Madagascar, Mauritius and the Seychelles, in the Persian Gulf, in Sri Lanka and the southern coast of India and it extends from there through Malesia far into the western Pacific and its marginal seas. In the western Pacific it is known from Vietnam, the Ryukyu Islands, New Caledonia, Fiji, the Tonga Islands and tropical Australia. In *Malesia* the species is widely distributed: Peninsular Malaysia, Java, Borneo, Philippines, Lesser Sunda Islands, Moluccas and New Guinea. No records are known from Sumatra.

Habitat & Ecology — *Syringodium isoetifolia* occurs in very sheltered habitats where it is restricted to soft muddy and sandy bottoms. As its stiff shoots are not resistant to exposure the species is confined to the upper part of the sublittoral, where it forms submarine meadows, or more often occurs interspersed in sea-grass beds composed of *Cymodocea serrulata*, *C. rotundata*, *Thalassia hemprichii*, *Halodule uninervis* and *Enhalus acoroides*. In the intertidal belt it has been found sometimes in pools. According to Miki [Bot. Mag. Tokyo 48 (1934) 140] the northern border of the species coincides with the 21 °C February water isotherm.

### THALASSODENDRON

*Thalassodendron* Hartog, *Sea-grasses of the World* (1970) 186. — Type species: *Thalassodendron ciliatum* (Forssk.) Den Hartog.

Dioecious. *Rhizome* robust, up to 0.5 cm thick, ligneous, creeping, sympodial, with 2 erect, unbranched or little branched stems at every fourth internode. Roots usually 2–3, more or less branched, occurring only on the internode preceding the stem-bearing internode. Central cylinder of the rhizome consisting of a thick central vascular bundle and surrounded by a layer of parenchymatic tissue, containing many air channels, tannin cells and 2 concentric rings of vascular bundles. Inner vascular ring consisting of relatively thick bundles, outer ring consisting of rather scattered, narrow bundles, total number of vascular bundles c. 20. Cortex sclerenchymatic without vascular tissue. Epidermis collenchymatic, containing numerous tannin cells. Internodes up to 3 cm long. Stem and stem branches bearing terminally a cluster of leaves with numerous tannin cells. *Leaf sheath* compressed, 1.5–4.5 cm long, ligulate and auriculate, narrowed at the base, amplexicaulous, leaving a closed circular scar when shed. *Leaf blade* linear, with denticulate apex and a more or less spinulose margin, shed together with the sheath; nerves 13–27, parallel, connected by oblique cross veins; between each pair of nerves several fine accessory veins. '*Flower*' solitary and terminal on a short lateral shoot, subsessile, enclosed by 4 leafy bracts of which the 2 outer ones are identical and the 2 inner ones different in shape and nervation in the male and female plants. *Male 'flower'* consisting of 2 anthers attached at the same height and dorsally connate over their whole length, each crowned with one appendage. *Female 'flower'* consisting of 2 free ovaries, each with a short style divided into 2 loriform stigmata. *False fruit* composed of the 2 fertilised ovaries (one of which usually is abortive) and the fleshy inner bract; often germinating when still attached to the mother plant; seedling free floating. — Fig. 8.

Distribution — The genus consists of two species: *T. ciliatum* which is distributed in the tropical part of the Indo-Pacific, and *T. pachyrrhizum* which occurs only in a small extratropical area in Western Australia.

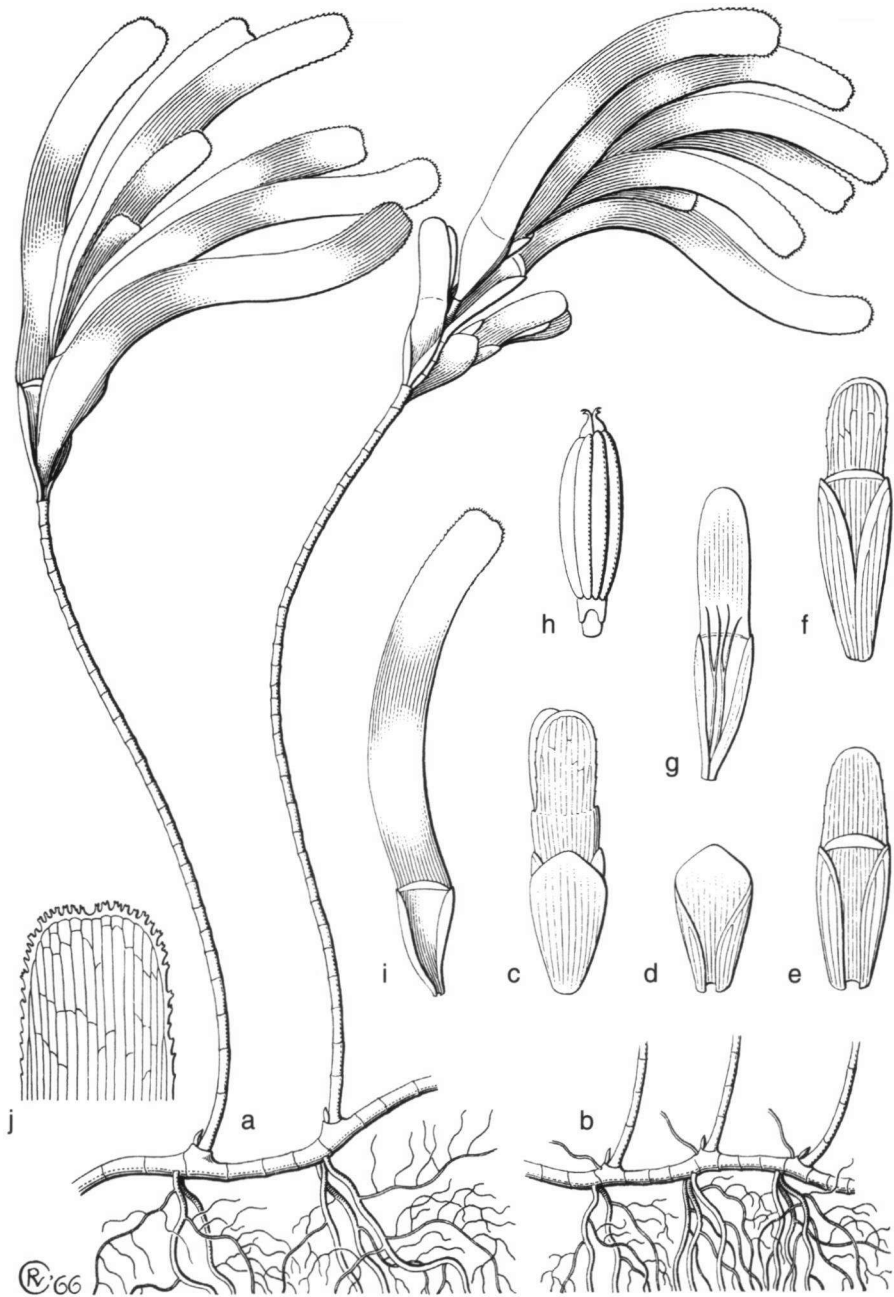


Fig. 8. *Thalassodendron ciliatum* (Forssk.) Hartog – a. Flowering habit; b. rhizome; c. cluster of 4 leafy bracts surrounding the female flower; d. bract I; e. bract II; f. bract III; g. bract IV, enclosing the two ovaries; h. male flower consisting of two connate sessile stamens; i. vegetative leaf showing ligula and open sheath; j. leaf tip with bi- and trifurcate denticulation. – a, b,  $\times 0.66$ ; c–g  $\times 1$ ; h  $\times 4$ ; j  $\times 2$ . – Reproduced from Den Hartog, *Sea-grasses of the World* (1970) 190, f. 52.



***Thalassodendron ciliatum* (Forssk.) Hartog**

*Thalassodendron ciliatum* (Forssk.) Hartog, *Sea-grasses of the World* (1970) 188, 273, f. 52; Meñez, Phillips & Calumpang, *Smithson. Contr. Mar. Sci.* 21 (1983) 18, f. 13, 14 (map); Brouns, *Aquat. Bot.* 23 (1985) 249; *Science in New Guinea* 12 (1986) 79, f. 9; Tomascik, Mah, Nontji & Moosa, *Ecology of the Indonesian seas* 2 (1997) 857, f. 18.11 (map), 18.27. — *Zostera ciliata* Forssk., *Fl. Aeg.-Arab.* (1775) 157. — *Thalassia ciliata* (Forssk.) König, König & Sims, *Ann. Bot.* 2 (1805) 97. — *Cymodocea ciliata* (Forssk.) Ehrenb. ex Asch., *Sitz.-Ber. Ges. Naturf. Fr. Berlin* (1867) 3, pro majore parte; *Linnaea* 35 (1868) 162, 185, pro majore parte; Asch. in *Engl. Pflanzenr.* IV.11, 31 (1907) 151, f. 33 A–B; Backer, *Handb. Fl. Java* 1 (1925) 50; Cohen, *S. Afr. J. Sc.* 36 (1939) 251, f. I–IV; Isaac, *Phytomorph.* 19 (1969) 44. — *Phucagrostis ciliata* (Forssk.) Ehrenb. & Hempr. ex Kuntze, *Rev. Gen. Pl.* 2 (1891) 744. — Type: *Forsskål*, Red Sea.

Rhizome robust, up to 0.5 cm thick; internodes 1.5–3 cm long. Stems 1–2, erect, 10–65 cm long, unbranched or little branched at every fourth internode; second stem usually not developed and present as a dormant bud. Roots 1–5, little or much branched, coiled, 0.5–2 mm thick and up to 8 cm long, on the internode preceding a stem-bearing internode. Scales enclosing the rhizome, 6 mm long, ovate, acute, dentate, dark brown, with numerous tannin cells, deciduous. *Leaf sheath* wide, compressed, 15–30 mm long, cream to pink, with obtuse auriculae; ligula obtuse, 10 mm wide and 2–2.5 mm high, often somewhat obliquely placed; leaf scars annular, closed, 2–8 mm apart. *Leaf blade* linear, falcate, 10–15 cm long and (6–)10(–13) mm wide, slightly narrowed at the base, green, in dried condition often dark brown; nerves 17–27, parallel, connected by rather oblique cross veins; margin almost entire except near the tip; tip rounded, often more or less emarginate, denticulate; apical teeth 0.5 mm, acute and sometimes bi- or trifurcate; teeth along the margin forming an irregular serration ('Flossenzähne', 'fin cells'). 'Flower' enclosed by 4 leafy bracts, which are green and often tinged with pink; the two outer bracts I and II identical in male and female plants, the inner bracts III and IV quite different in shape and nervation in the male and female plants; bract I usually consisting of the sheath only, although a small blade sometimes also develops, shed at an early stage; bract II consisting of a sheath and a blade which is 1/3–1/2 times the size of the sheath, ligulate. In the male plants bract III always shorter than bract II, and its sheathing flaps without veins; bract IV only 2 mm long, elliptic, membranous and with 1 median vein. In the female plants bract III of the same shape as bract II, ligulate, with veined sheathing flaps and becoming somewhat longer than bract II; bract IV fleshy, obscurely veined, differentiated into a sheath and a slightly longer blade, without a ligula, in full-grown condition as long as bract III, apex obtuse, smooth. *Male 'flower'* subsessile; anthers linear, 6–7 mm long (12–14 mm according to Isaac 1969), yellow and tinged with red (tannin cells), with short erect hair-like squamulae intravaginales at the base; when mature the anthers becoming released from the plants and floating at the surface, where the pollen is liberated; in still water the pollen is released when the anthers are still attached. *Female 'flower'*: ovary ellipsoid, 0.5–2 mm long; style 3–5 mm long, bearing 2 stigmata 30–40 mm long; the upper parts of the stigmata shed after fertilisation or loss of receptability. *False fruit* 3.5–5 cm long, oblong, consisting of 1 fertilised carpel (rarely 2) which is completely surrounded by the enveloping margins of the enlarged fleshy inner bract IV; when ripe free floating; development starting when still connected to the mother plant. — **Fig. 8.**

**Distribution** — The area of distribution of *T. ciliatum* consists of two separate parts. The first part comprises the Red Sea and the western part of the Indian Ocean. Along the eastern coast of Africa it is extremely common, and extends as far south as Zululand. Further it has been recorded from Madagascar and many island groups (Comores, Mascarenes, Seychelles, Aldabra, Maldives, Chagos Archipelago). The second part of the area comprises the eastern part of Malesia, the Solomon Islands and the eastern coast of Queensland; the species is apparently rather rare in this part of the area. In *Malesia* it has been found in Java, Philippines, Celebes, Lesser Sunda Islands, Moluccas and New Guinea.

**Habitat & Ecology** — *Thalassodendron ciliatum* occurs in the upper part of the sublittoral belt from mean low water spring down to at least 10 m depth. The species often occurs in wave-exposed sites at the outer side of the reefs. The uppermost plants rarely become uncovered by the tides. The species grows in circular patches at its upper limit, but in deeper water, in sheltered places, on sandy bottoms, on coral reefs and on sand-covered rocks it forms extensive and monotonous submarine meadows. The mat formed by the rhizome is at least 5–10 cm thick and is mostly covered with sand, but Brouns (1985) has found mats of 70 cm thickness. The plants are usually densely covered with epiphytic coralline algae. Other sea-grasses occur exceptionally together with *T. ciliatum*. The species lives usually in unisexual colonies; rarely do plants of both sexes grow together in one patch.