Chapter 1

Taxonomy and Biogeography of Seagrasses

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I. Introduction

Seagrasses are aquatic angiosperms, which are confined to the marine environment. The term seagrass (with several linguistic variants in the Germanic language group) refers undoubtedly to the grass-like habit of most of its representatives. The term has been long used by fisherman, hunters, farmers, and other inhabitants of the coastal areas of several European countries, i.e. areas where only species occur with long linear leaves. Ascherson (1871) probably was the first researcher to introduce the term into the scientific literature.

The seagrasses form an ecological group, and not a taxonomic group. This implies that the various seagrass families do not necessarily have to be closely related.

The taxa regarded as seagrasses belong to a very limited number of plant families, all classified within the superorder Alismatiflorae (Monocotyledonae) (Dahlgren et al., 1985), also generally known as the Helobiae (Tomlinson, 1982). The subclass Alismatanae (Kubitzki, 1998) is with respect to its contents identical with Alismatiflorae. Three out of four families consist exclusively of seagrasses, viz. the **Zosteraceae**, the **Cymodoceaceae**, and the **Posidoniaceae**. In the past these families generally have been classified as subfamilies of the **Potamogetonaceae** (Ascherson and Graebner, 1907; den Hartog, 1970). Further studies have shown that the latter family appeared to be too heterogeneous (Tomlinson, 1982; Dahlgren et al., 1985), and had to be split. So, apart from the Potamogetonaceae *sensu stricto*, all of the former subfamilies were upgraded to the family level. In fact some authors had already long ago recognized the special identity of these families, e.g. Dumortier who described the Zosteraceae as early as 1829 as an independent family beside the Potamogetonaceae *sensu stricto*, and the Zannichelliaceae. A fourth family, the **Hydrocharitaceae**, contains three genera that are considered seagrasses, but the other 14 genera in this family are confined to fresh-water habitats (Cook, 1990, 1998).

Apart from the families mentioned above which have altogether 12 marine genera there are no other genera that are fully confined to the marine environment. In other aquatic plant families so far only two species have been found that occur exclusively in marine habitats, viz. *Ruppia* aff. *tuberosa* of the family **Ruppiaceae**, and *Lepilaena marina* of the family **Zannichelliaceae** (Kuo and den Hartog, 2000). The inclusion of these two species within the seagrasses is still a matter of debate. Descriptions of these families and genera have been included in the treatment of the monocotyledonous flowering plants edited by Kubitzki (1998) (Hydrocharitaceae by Cook; Ruppiaceae and Najadaceae by Haynes, Holmberg-Nielsen and Les; Potamogetonaceae and Zannichelliaceae by Haynes, Les and Holm-Nielsen; Cymodoceaceae, Posidoniaceae and Zosteraceae by Kuo and McComb). Furthermore, brief descriptions of all presently described seagrass species, as well as a key for the identification of them, have been provided by Kuo and den Hartog (2001).

Arber (1920) formulated a set of four properties, which in her opinion were considered to be

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indispensable for a marine water plant. These properties can be listed as follows: (i) the plants must be adapted to life in a saline medium; (ii) the plants must be able to grow when fully submerged; (iii) the plants must have a secure anchoring system; and (iv) the plants must have a hydrophilous pollination mechanism. It is obvious that seagrasses fulfil these requirements; they are able to achieve their vegetative as well as their generative cycle, when fully submerged in a saline medium. This set of properties is, however, not complete, as there are several other taxa of aquatic plants that also satisfy the four criteria listed by Arber, although they do not normally occur in marine habitats; nevertheless, they do even better in fact than the seagrasses where salinity tolerance is concerned (den Hartog, 1970). They form the ‘eurysaline’ group (den Hartog, 1981), an ecological group of aquatic plants, that is characteristic for waters with an unstable salinity, such as mixo- and hyperhaline brackish waters, continental salt waters where the dominant anion can be chloride, sulfate or even hydrocarbonate (therefore the term ‘saline’ is used, to distinguish it from ‘haline’ which refers to chloride dominated waters with a marine character); some of these taxa can occur in hard fresh water, and there are observations of some of them from extremely oligotrophic fresh waters. It is also known that representatives of this group can withstand very large and very sudden fluctuations in environmental parameters, such as salinity and temperature, and in contrast to the true seagrasses their seeds are resistant to protracted desiccation. Although the representatives of this group may be found in coastal areas their general distribution is not maritime; their altitudinal range is from sea level up to 4000 m in mountains. The eurysaline group consists of taxa from three monocotyledonous families, the **Ruppiaceae** (with the genus *Ruppia*), the **Zannichelliaceae** (with the genera *Zannichellia*, *Lepilaena*, *Althenia*, and *Pseudalthenia*), formerly classified as subfamilies of the Potamogetonaceae, and the **Potamogetonaceae** *sensu stricto* of which only *Potamogeton* subgen. *Coleogeton* (by some authors considered to be an independent genus, *Stuckenia*) is involved. Several other aquatic plant families have developed species with a rather wide salt tolerance, e.g. *Najas marina* in the Najadaceae (which recently has been shown to be part of the Hydrocharitaceae), and *Ranunculus baudotii* in the Ranunculaceae, a dicotyledonous family. So the true seagrasses are characteristic for homoiohaline marine habitats, while the members of the eurysaline group occur in poikilosaline waters. It appears, that these eurysaline species can live under marine circumstances, but are usually not able to compete successfully with the seagrasses. According to den Hartog (1970) it is probably a basic rule in ecology that a wide tolerance for environmental fluctuations is coupled with a reduced capacity to compete with more stenobiontic taxa under more or less stable circumstances. The capacity to compete successfully with other organisms in the marine environment is thus another basic property of seagrasses.

It has to be pointed out that not all seagrasses are stenohaline to the same degree. Particularly some members of the genera *Zostera*, *Cymodocea*, *Halodule*, and *Halophila* may penetrate to some extent into estuaries, and these are the same ones that extend up to the middle of the intertidal zone. This means in practice that under estuarine conditions and in the intertidal belt true seagrasses and eurysaline water plants may meet, just as further upstream eurysaline species may come into contact with fresh-water plants. In the Baltic (Samuelsson, 1934; Luther, 1951a,b) and in the Black Sea (Milchakova, 1999), which both show a reduced salinity and a considerable salinity gradient, mixed stands of seagrasses and eurysaline aquatics have been commonly recorded.

It is our intention to present here the taxonomy of the seagrasses at the family and the genus level, including also descriptions of the families of the poikilosaline group which have a true marine representative. The author’s names of the species, accepted as valid, are given in the ‘List of the seagrass species of the world’ (see Appendix A p. 22–23).

II. Key to the Angiosperm Families Containing True Marine Species

1a. Leaves differentiated into a sheath and a blade, without a ligule, or a blade with a clear petiole. 2
1b. Leaves differentiated into a sheath and a blade, with a ligule. 3
2a. Flowers dioecious, (sometimes monoecious) with a trimerous perianth. Pollen spherical, free or arranged within a moniliform string. . . . . Marine **Hydrocharitaceae**
2b. Flowers monoecious, in pairs on a peduncle, each with two anthers and 4-many ovaries, but

without a perianth. Pollen boomerang-shaped, free. . . . . **Ruppiaceae**

3a. Inflorescence cymose, with the branches ending in 'spikes'. Flowers actinomorphous, bisexual, consisting of three stamens with large connectives and one ovary with a sessile, disc-shaped stigma. Tannin cells present . . . **Posidoniaceae**

3b. Flowers simple, unisexual, consisting of 1 or 2 ovaries or a single stamen, arranged within a specialized inflorescence or just single or in pairs. Stamens with reduced connectives. Ovary bearing a style with 1, 2, or 3 stigmata. Tannin cells present or absent. 4

4a. Flowers, unisexual or bisexual, arranged in two rows on one side of a flattened spadix enclosed in a spathe. Stamens consisting of two extrorsely dehiscent thecae, connected by a ridge-like connective. Ovary horizontally placed, with a short thick style and two stigmata shed after flowering. Tannin cells absent. . . . . **Zosteraceae**

4b. Flowers unisexual, solitary, in pairs or as a cluster on a common pedicel, terminating a short branch. Tannin cells present or absent. 5

5a. Leaves with 3-many nerves and numerous tannin cells. Flowers unisexual, without a perianth, solitary or in pairs, or arranged within a cymose inflorescence. Male flowers sessile or stalked consisting of two, dorsally connate anthers. Pollen filiform. Ovaries in pairs with 1, 2, or 3 filiform styles. Tannin cells present. . . . . **Cymodoceaceae**

5b. Leaves very narrow, with only one central nerve, without tannin cells. Flowers terminal. Male flower consisting of a stalked anther, often with a small scaly perianth. Female flower consisting of 1–8 free carpels on a joint pedicel, surrounded by a scaly perianth. Styles peltate or feathery. Pollen spherical. Tannin cells absent . . . . **Zannichelliaceae**

III. Seagrasses: General Taxonomy

Zosteraceae

Zosteraceae Dumortier, Anal. Fam. Pl. (1829) 65, 66; nom. cons.
Typus: *Zostera* L.

Monoecious or dioecious marine plants. Rhizome creeping, herbaceous, monopodial or sympodial; when monopodial with two vascular bundles in the cortical layer and at each node two 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 4–10 vascular bundles in the cortical layer and at each node two unbranched roots and an erect stem with distichously arranged leaves and without roots at its nodes. Leaves linear, differentiated into a sheath and a blade with a ligule. Leaf sheath compressed, amplexicaulous, ligulate, either membranous and tubular or open and then auriculate with scarious flaps. Leaf blade linear, with 3–9(-11) parallel nerves and with several accessory bundles between every two of these; nerves connected by perpendicular cross-veins, margin entire, sometimes slightly denticulate or provided with a fringe of uncolored, 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 two more or less overlapping, auriculate flaps, enclosing a sessile or stalked spadix on the dorsal side of which in *Zostera* and *Heterozostera* the male flowers (stamens) and female flowers (gynoecia) are alternately arranged. Stamens consisting of two free, bilocular, extrorsely length-wise dehiscent, deciduous thecae connected by a reduced ridge-like connective, without a filament; pollen confervoid. Retinacula intramarginal, one beside each stamen, sometimes absent (*Zostera* subgen. *Zostera*); on the female spadices of *Phyllospadix* alternating with the gynoecia. Gynoecium consisting of a superior, horizontally placed, ellipsoid or crescent-shaped ovary with a short thick style and two stigmata of which the distal parts are shed after fertilization; ovule 1, orthotropous, pendulous. Fruit indehiscent, ovoid or ellipsoid with scarious pericarp or else crescent-shaped with the pericarp differentiated into a soft exocarp and a hard fibrous endocarp. Seed 1, ovoid or ellipsoid; embryo macropodous consisting for the larger part of the hypocotyl, which is ventrally grooved; in this groove the short, straight, tubular cotyledon which serves as a sheath for the plumula; primary root usually not developing; endosperm absent. Tannin cells absent.

The family consists of three genera, viz. *Zostera*, *Heterozostera*, and *Phyllospadix.*

There is no doubt about the monophyletic status of the family Zosteraceae. This has already been concluded by Tomlinson (1982) on merely anatomical and morphological grounds. A further confirmation comes from molecular phylogenetic studies of the families of the subclass Alismatidae, using chloroplast *rbc*L (Les et al., 1997; Procaccini et al., 1999a). Les et al. (1997) demonstrated that the Zosteraceae are more closely related to the Potamogetonaceae and the Zannichelliaceae than with the other seagrass groups. These studies, however, did not support the recognition of *Heterozostera tasmanica* as representing a distinct genus, but accepted it as a distinct species within the subgenus *Zosterella* (Les et al., 1997, 2002). Based on the *matK* gene sequence data, Tanaka et al. (2003) also show a similar result. On the other hand, Kato et al. (2003) proposed to divide the Zosteraceae into three genera: *Phyllospadix*, *Zostera* and *Nanozostera*, the genus *Nanozostera* containing two subgenera, *Zosterella* and *Heterozostera*. In this case, by priority *Heterozostera,* which was established more than 30 years earlier, should be used as the generic name instead of *Nanozostera*. There is nothing known about the possible ancestors of the family. Originally it was thought that *Archeozostera* (Koriba and Miki, 1931, 1960) from the Cretaceous of Japan was a protozosterid (den Hartog, 1970), but Kuo et al. (1989) have shown convincingly that *Archeozostera* is not a seagrass at all, and possibly not even a plant.

Key to the Genera

1a. Rhizome monopodial, herbaceous, with two vascular bundles in the cortical layer; a short lateral branch at each node. 2

1b. Rhizome sympodial, but sometimes monopodial, often ligneous, with 4–10 vascular bundles in the cortical layer. Stems erect, not branched, with distichous leaves . . . . ***Heterozostera***

2a. Monoecious. Spadix always enclosed within the spathal sheath. Retinacula, if present, membranous, not nerved, smaller than the ovaries or stamens. Peduncle of the spathe partly coalescent with the axis from which it springs. Fruit ovoid or ellipsoid. Rhizome with elongate internodes, and with two, or more, long, thin roots at each node. Vegetative parts not sclerenchymatic. Leaf-blades thin, translucent; margin entire or rarely slightly denticulate. Sheaths deciduous; sometimes some scaly basal parts remaining. . . . . ***Zostera***

2b. Dioecious (rarely monoecious). Spadix, when mature, projecting out of the spathal sheath. Retinacula coriaceous, one-nerved, larger than the ovaries or stamens. Peduncle free. Fruit crescent-shaped. Rhizome with very short, thick internodes, and with two or more thick roots at each node. Vegetative parts usually strongly sclerenchymatic. Leaf-blades coriaceous, with 'fin cells' along the margin. Basal parts of the sheaths decaying with age into bundles of very fine, woolly fibres . . . . ***Phyllospadix***

Zostera L. Sp. Pl. ed. 1 (1753) 986.
Type species: *Zostera marina* L.

The genus consists of two well-distinguished subgenera, *Zostera* and *Zosterella*.

In subgen. *Zostera* the rhizome has the fibre bundles in the outermost part of the cortex, and there are always two groups of roots at each node; the leaf-sheaths are tubular and rupturing with age; the generative shoots are terminal and retinacula are absent. In the old literature this subgenus is referred to as subgen. *Alega*; according to the rules of botanical nomenclature the correct name is subgen. *Zostera*, as it contains the type of the genus. In subgen. *Zosterella* (Ascherson) Ostenfeld (type species *Z. nana* Mertens ex Roth = *Zostera noltii* Hornemann) the fibre bundles occur in the innermost layers of the outer cortex of the rhizome; the leaf-sheaths are open with two membranous flaps; the generative shoots develop lateral and in the inflorescences the retinacula are always present. Recently, Tomlinson and Posluszny (2001) upgraded the latter subgenus to a genus in its own right, *Nanozostera*, mainly because they considered the differences between this taxon and the subgenus *Zostera* of the same order as its differences with *Heterozostera*. Meanwhile Kuo (2005) has discovered that the genus *Heterozostera* is also not homogeneous from a morphological point of view.

The subgenus *Zostera* is widely distributed in the northern temperate coastal waters of the Atlantic and the Pacific. Up to now four species have been accepted (den Hartog, 1970), but a further analysis may show that this number is too low. At present

Z. marina has been recorded from both sides of the northern Atlantic and both sides of the northern Pacific. The species *Z. caespitosa* and *Z. caulescens* are restricted to the Asiatic side of the Pacific; *Z. asiatica* described from the north-eastern Pacific may be identical with the wide-leaved form of *Z. marina*, earlier described as *Z. latifolia* and *Z. oregona*. The record of *Z. asiatica* by Phillips and Willey-Echeverria (1990) for the Pacific coast of North America may refer to *Z. latifolia* or *Z. oregona*. Regrettably the few distinguishing characters intergrade, and hamper the definition of clear-cut taxa. Backman (1991) recognized five varieties of *Z. marina* along the Pacific coast of North America, and formally described these. However, he also did not discuss the relationship of these varieties, if any, with the taxa related to *Z. marina*, earlier described from the same area, such as *Z. oregona, Z. latifolia* or *Z. pacifica*, nor is there any indication that his *Z. marina* var. *typica* has any relation to the original specimens of this species that was described from Europe. In Europe *Z. marina* is also not a sharply defined species. There occur perennial, biennial, and annual populations. The annual form has been recorded by some authors as a separate species, *Z. angustifolia*; others consider it at the variety level or as an example of the variability of the species, because of the lack of reliable distinguishing morphological characters. Van Lent and Verschuure (1994) found that there is a continuum between the annual and perennial populations; some appear to be truly annual, in others part of the plants appears to be biennial, i.e. at least surviving the winter season; and a third group of populations is permanently green. These differences in life cycle were found in a small area in the same estuary in The Netherlands. It has also to be mentioned, that various populations along the European coast show considerable differences in their temperature and salinity tolerance. Further taxonomic research in this subgenus is necessary.

The subgenus *Zosterella* is widely distributed in the warm temperate coastal waters of the seas of the northern and the southern hemisphere, with some incursions in tropical waters and one species extends into the cold temperate zone. In the Atlantic, including the Mediterranean only one species, *Z. noltii* occurs. It has been recorded also from the land-locked Caspian Sea and the Aral Sea. In the northern Pacific the subgenus is represented also by only one species, *Z. japonica*, which extends from the Siberian east coast down to Vietnam. Quite recently this species has colonized the Pacific coasts of Canada and the USA. In the southern hemisphere *Z. capensis* occurs from the Cape Province up to Kenya. In temperate Australia three species occur, *Z. muelleri, Z. mucronata,* and *Z. capricorni*, which more or less exclude each other geographically. *Z. muelleri* inhabits the coasts of Victoria, Tasmania and the eastern part of South Australia, *Z. mucronata* is restricted to the eastern coasts of South Australia and the southern and south-western part of Western Australia, and *Z. capricorni* is distributed along the eastern coast of Australia up to Papua New Guinea. Moreover, it occurs in New Zealand, together with *Z. novazelandica*.

Les et al. (2002) carried out a phylogenetic study on the Australian and New Zealand Zosteraceae using DNA sequences from nuclear (ITS) and plastid (*tmk* intron, *rbc*L) genomes (see also Waycott et al., Chapter 2). These molecular studies did not support the distinctness of *Zostera capricorni, Z. mucronata, Z. muelleri*, and *Z. novazelandica* as four discrete species, but indicated that some isolation by distance had occurred. The *mat*K gene sequence data of Tanaka et al. (2003) also show that *Z. muelleri, Z. capricorni, Z. novazelandica*, and *Z. mucronata* belong to the same lineage. However, Tanaka et al. (2003) also unexpectedly found *Z. capensis* is not associated with the other above mentioned *Zostera* species but belongs to the same lineage as *H. tasmanica*. In the meantime, Les et al. (2002) further conducted a cladistic analysis of 31 morphological, vegetative and reproductive characters, based on data from 15 previous publications of seven species of *Zostera* subgen. *Zosterella*, to conclude that there are no morphological differences between these species. Based on molecular and cladistic evidence Les et al. (2002) recommended that all Australian *Zostera* species should be merged taxonomically as a single species, which in that case by priority should be called *Z. muelleri*, and not *Z. capricorni*, as proposed by Les et al. (2002), as this latter species has been described nine years later. Regretfully, this error has already been applied in the most recent literature (Green and Short, 2003). On the other hand, Kato et al. (2003) retained all described *Zostera* and *Heterozostera* species but wrongly placed these species under the genus *Nanozostera*. As discussed above a taxonomic mistake has been made by choosing *Nanozostera* instead of *Heterozostera*.

In our opinion the three Australian species are in general well distinguished by morphological differences in their leaf-tip and nervation. The shape of the leaf apex, in spite of having considerable variation, still is one of most important vegetative characters for identification of these *Zostera* species. Further *Z. capricorni* has leaves with five longitudinal nerves, while the other two species have only three. An other important fact is, that the three species have each a different area of distribution with only marginal overlap. In these areas of overlap intermediate forms occur, but these may be the result of hybridization. We certainly do not deny that the species are closely related. Robertson (1984) noticed also that a broad spectrum of intergrades occurs and recommended further basic taxonomic work to elucidate the *Z. mucronata–Z. muelleri–Z. capricorni* complex. Turner et al. (1996) also could not decide the species status of their studied *Zostera* material from New Zealand.

However, Les et al. (2002) echoed Robertson's (1984) suggestions recommending 'common garden experiments to be conducted among these species' to see whether those leaf tip and other morphological characters are the result of environmental conditions, or are genetically determined, or both. Until such fundamental data are available, we recommend here that at least *Z. muelleri, Z. capricorni*, and *Z. mucronata* should continue to be recognized. McMillan (1982) investigated five *Zostera* species, amongst which four members of the subgenus *Zosterella*, and found that each species presented a different isozyme pattern.

Further, it should be noted that three out of 31 characters separate *Z. noltii* and *Z. japonica* (see Les et al., 2002), but the *mat*K tree shows a close affinity of these two species, which have disjunct distributions (Tanaka et al., 2003).

Robertson (1984) recognized two ecotypes of *Zostera muelleri* from south-eastern Australia, one in the intertidal belt of sheltered bays, and a more robust estuarine form in lagoons and more or less land-locked waters, which is almost permanently submerged. She stressed that numerous intergrades occur between them. Similar observations have been made for other *Zostera* species, e.g. *Z. noltii* in western Europe, Mauritania, and the Mediterranean, *Z. capricorni* in New South Wales, and *Z. capensis* in South Africa.

Phyllospadix Hooker, Fl. Bor. Am. 2 (1838) 171

Type species: *Phyllospadix scouleri* Hooker

The genus contains five species, all occurring along the northern temperate coasts of the Pacific. The genus is rather homogeneous, although two groups of species can be recognized. One group consists of the two species, *P. scouleri* and *P. torreyi*, and occurs along the west coasts of Canada, the USA, and Baia California. It is characterized by having rhizome nodes with 6–10 roots (in two rows), leaves with only three nerves (*P. japonicus* belonging to the other group also has three nerves), and generative axes consisting of one to several internodes and bearing one or more pedunculate spathes. The second group has three species, distributed in cold temperate waters in eastern Asia (*P. iwatensis* and *P. japonicus*) and North America from the Aleutic Islands southward to Oregon (*P. serrulatus*). In these three species the rhizome nodes have only two roots, and the generative axes are reduced to short pedunculate spathes.

Tsvelev (1981) erected a special section, *Phyllospadix* sect. *Sagitticarpus*, to include *P. torreyi*, because its inflorescence produces numerous spathes, without considering the infrageneric classification of the other species of the genus. Although we can recognize within the genus two species groups there is in our opinion no reason to subdivide *Phyllospadix* into sections or subgenera. If these groups have to be formally upgraded to the section level, the group which contains the type species should be named in accordance with the rules of the botanical nomenclature *P*. sect. *Phyllospadix* and *P*. sect. *Sagitticarpus* is in that case a superfluous synonym.

Further, it should be mentioned here that Tsvelev (1981) described two new species, *P. juzepczukii* and *P. ruprechtii* from eastern Russia and California respectively. Unfortunately, we have not been able to see material from these species. It appears that the leaves of *P. juzepczukii* have only three nerves, as in *P. japonicus*, and these taxa may possibly be identical, but in that case the species would show a very remarkable disjunct area of distribution. As far is known to us *P. japonicus* is restricted to the Honshu coast of the Japanese Sea, but is absent from Hokkaido, Korea and China. *P. juzepczukii* seems to be widely distributed in the northern Far East. It is clear from the diagnosis of *P. ruprechtii* that this species is synonymous with *P. scouleri*. Finally, Dawson et al. (1960) have found some 3-nerved, almost perfectly cylindrical leaf fragments of a *Phyllospadix* specimen along the coast of Baia California, Mexico.

Heterozostera (Setchell) den Hartog, Sea-grasses of the world (1970) 114
Type species: *Zostera tasmanica* Martens ex Ascherson (= *Heterozostera tasmanica* (Martens ex Ascherson) den Hartog)

The genus has been originally erected to classify the rather aberrant *Z. tasmanica.* All previous researchers (den Hartog, 1970; Tomlinson, 1982; Les et al., 1997; Tomlinson and Posluszny, 2001) treated *Heterozostera* as monotypic and having distinct vegetative wiry erect stems and more than two vascular strands in the rhizome cortex. More material has now become available for study and the concept of the monotypic genus has to be reconsidered. The most recent revision of *Heterozostera* demonstrates that it is represented by three distinct taxa in Australia, and a fourth in South America (Kuo, 2005). All three Australian species have numerous cortical vascular bundles in the rhizome cortex, but only one of them possesses 'wiry erect stems'. Within the genus two distinct species groups can be distinguished which possibly have to be ranked as sections or subgenera. It is interesting to mention that Les et al. (2002) observed a low level of molecular divergence (ITS and *tmK*) between the *Heterozostera* population from eastern (one collection) and western (four collections) Australia. Due to a lack of morphological evidence (which they did not consider) to support this molecular finding, they concluded that this molecular difference was due to a relatively prolonged geographical isolation of the two populations rather than as clear evidence of a speciation event.

Cymodoceaceae

Cymodoceaceae N. Taylor in N. Amer. Fl. 17 (1909) 31; nom. cons.
Typus: *Cymodocea* König

Dioecious marine plants. Rhizome creeping, either herbaceous, monopodial, and rooting at the nodes (*Cymodocea*, *Syringodium*, *Halodule*) 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 three 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 two 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 two free ovaries each with either a long style (*Halodule*) or a short style, which is divided into 2 or 3 loriform stigmata. Ovule 1, suborthotropous, 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 four cuneate spreading lobes grow out (*Amphibolis*) or consisting of a fleshy bract which encloses the fertilized 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*).

The family contains five genera: *Halodule*, *Cymodocea*, *Syringodium*, *Thalassodendron*, and *Amphibolis.*

From a morphological point of view the family is homogeneous, and monophyletic. In the past it has often been combined with the Zannichelliaceae, e.g. by Hutchinson (1934). The five genera are all well distinguished and there is no controversy about their status as is the case in the Zosteraceae. The family is old, as there are several fossil records of members of the genus *Cymodocea* from Eocene and Miocene deposits. *Thalassocharis* from the Cretaceous of The Netherlands and Germany has been considered as being a seagrass by Voigt and Domke (1955) and den Hartog (1970) did not reject this conclusion, but remarked that the stiff compact stems and the absence of aerenchymatic tissue show that *Thalassocharis* was not yet very well adapted to life in the aquatic environment. Kuo and den Hartog

(2000) did not regard *Thalassocharis* as a seagrass anymore.

In spite of the great differences in the morphology and the anatomy of their reproductive structures as well as their modes of pollination, Les et al. (1997) treated the families Cymodoceaceae, Posidoniaceae and Ruppiaceae together as one phylogenetic unit, the 'Cymodoceaceae complex', to distinguish it from the other seagrass groups such as the Zosteraceae and the marine Hydrocharitaceae.

Within the family two groups of genera can be recognized. *Halodule, Cymodocea,* and *Syringodium* have a monopodial rhizome, are herbaceous, and have leaf-blades that are shed before the leaf-sheaths. *Thalassodendron* and *Amphibolis* have a sympodial, ligneous rhizome, and the leaf-blades are shed with the sheaths as single units; further, these two genera show vivipary. There is, however, in our opinion no reason to give these groups a formal taxonomic status.

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
1b. Rhizome sympodial, ligneous, with elongate, more or less branched, erect stems at certain nodes. Leaf-blade shed with its sheath. Anthers subsessile. 4
2a. Leaves flat. Flowers solitary. 3
2b. Leaves subulate. 'Flowers' arranged into a cymose inflorescence. . . . . ***Syringodium***
3a. Nerves 3. Anthers not attached at the same height on the peduncle. Ovary with one undivided style . . . . ***Halodule***
3b. Nerves 7–17. Anthers attached at the same height on the peduncle. Style divided into two stigmata. . . . . ***Cymodocea***
4a. Rhizome with two unbranched or little branched stems at every fourth rhizome node; roots 1–5 on the node preceding the stem-bearing one. Leaves with parallel nerves and denticulate apex. 'Flowers' enclosed by four leafy bracts. Anthers connate over their entire length, each crowned with one appendage. Style with two stigmata. False fruit composed of 1 or 2 fertilized ovaries surrounded by the enlarged inner bract . . . . ***Thalassodendron***
4b. Rhizome with 1–2 branching roots at each node and at a distance of (1-) 4–8 nodes one profusely branched stem. Leaves entire, with pseudoparallel nerves, and a bidentate apex. 'Flowers' enclosed by normal leaves. Anthers connate with their lower parts, each crowned with 2–3 appendages. Style with three stigmata. 'Fruit' consisting of one fertilized ovary with four pectinate, spreading lobes arising just above its base; viviparous. . . . . ***Amphibolis***

Halodule Endl., Gen. Pl. suppl. 1 (1841) 1368.
Type species: *Diplanthera tridentata* Steinheil (= *H. uninervis* (Forssk.) Ascherson).

The typification of *Halodule* has been complicate. Du Petit Thouars (1806) was the first to describe the genus from Madagascar under the name *Diplanthera*, but he unfortunately did not add a species name to his material. Steinheil (1838) described the material as *D. tridentata*. Steudel (1840) referred to the same material and named it, without a description, *D. madagascariensis*. He recognized a second species, *D. indica* that turned out to be *Halophila ovalis*. From Steudel's work it becomes also obvious, that the genus name *Diplanthera* has been used also for other genera in very different families. Endlicher (1841) referred to the material of Du Petit Thouars (1806) and the work of Steinheil (1838) as he founded the genus *Halodule*, but regrettably he failed also to transfer the species name to the new genus. Miquel (1855) was the first to describe a species in the genus as *H. australis*, for material from Indonesia, similar to Steinheil's species; therefore, the new epithet was superfluous. It took till 1882, before this material was properly named.

The genus consists of seven species. The main characters used for the identification of the species are the shape of the leaf tip and the width of the leaves (den Hartog, 1970). There are too few data of the generative structures, and the degree of variation of these is not yet clear; at present they cannot be used to identify the taxa. Moreover, they are not known for several taxa.

H. uninervis commonly occurs in the tropical Indo-West Pacific with a narrow- and a wide-leaved form. It is possible that these two forms represent different taxa; in that case the name *H. uninervis* is linked to the wide-leaved form, while the narrow-leaved form should be named *H. tridentata* (Steinheil) F. von Mueller. In the West Pacific a second species, *H. pinifolia*, occurs as well; in the

Indian Ocean it is less common and restricted to India. In the Caribbean *H. wrightii* is widely distributed from Cuba and the smaller Antilles; along the coast of South America it crosses the mouth of the Amazon River, and extends southward along the coast of Brazil (De Oliveira et al., 1983). Other localities of this species are on the Atlantic coast of Africa, e.g. in Mauritania, Senegal, and Angola; it is expected that in future more locations will be discovered. It is remarkable that populations satisfying the diagnosis of this species have been found in Kenya. In southern Brazil the species is replaced by *H. emarginata*. Finally *H. beaudettei* occurs in the Gulf of Mexico, and less frequently in the Caribbean. It extends along the Atlantic coast of the USA northward up to North Carolina. This species has been found also along the Pacific coast, from Panama up to Mexico, where it reaches its northernmost locations in the Sea of Cortes. In the USA *H. beaudettei* is traditionally referred to as *H. wrightii*, but it relates in no way with the true *H. wrightii* which has been described after material from Cuba. The remaining two species are only known from one collection, *H. ciliata* from Pacific Panama, and *H. bermudensis* from the Bermuda Islands.

Although the identification characters show some variability at present no other means for identification are available. Studies of chromosome numbers, isozymes, and molecular analyses may be helpful to establish definitively the validity of the present species. The only chromosome count available, as far is known, suggests that possibly polyploidy is involved (den Hartog et al., 1979). McMillan (1980, 1982) found differences in the isozyme composition of East African and Texan *Halodule* populations, but provided no morphological descriptions of the used material.

Cymodocea König in König & Sims, Ann. Bot. 2 (1805) 96; nom. cons.
Type species: *Cymodocea aequorea* König (= *C. nodosa* (Ucria) Ascherson)

The genus, consisting of four species, has a mainly tropical distribution. *C. rotundata* and *C. serrulata* have a more or less similar pattern of distribution along the coasts of the tropical Indo-West Pacific. *C. nodosa* occurs in the subtropical Mediterranean and extends its area in the Atlantic northward to Portugal and southward to Senegal; further it is common on the Canary Islands. The fourth species, *C. angustata*, is endemic to the north-western part of Australia.

The distribution of this genus has been much wider in the past. In the Avon Park formation, a late Middle Eocene deposit in Florida, well preserved remains of seagrasses were found; among them were two species of *Cymodocea* (Lumbert et al., 1984). *C. floridana* differs from the present-day species, but is close to *C. angustata*. The second species appears to be preserved less completely; its leaf-blade is rather similar to that of *C. nodosa*. Fossil fruits have been found often in various deposits along the Mediterranean (Ruggieri, 1952). Another species, *C. micheloti,* has been recorded from the Miocene of Sulawesi (Celebes), Indonesia (Laurent and Laurent, 1926). This species is identical with the present-day *C. serrulata*.

Syringodium Kützing in Hohenacker, "Meeralgen" (Algae Marinae Exsiccatae) 9 (1860) no. 426
Type species: *Syringodium filiforme* Kütz.

This genus contains two species. *S. isoetifolium* is widely distributed in the coastal waters of the Indian Ocean and the western Pacific; along the west coast of Australia it penetrates far into the temperate zone and occurs even south of Perth. *S. filiforme* is restricted to the Gulf of Mexico and the Caribbean, and it has been recorded from Bermuda.

Thalassodendron den Hartog, Sea-grasses of the World (1970) 186
Type species: *Zostera ciliata* Forsskål (= *Thalassodendron ciliatum* (Forssk.) den Hartog)

This genus contains two species. *T. ciliatum* is widely distributed in the tropical Indo-West Pacific. In the Indian Ocean it is dominant on the reefs of the coasts of East Africa, many of the oceanic islands, and along the Red Sea. It does hardly occur along the northern coasts, as it absent from Pakistan, India, Sri Lanka, and BanglaDesh. In the western Pacific its occurrence is scattered, the northernmost locality being in the South Chinese Sea, the southernmost in Queensland. The other species, *T. pachyrhizum*, has a small area of distribution in the temperate south-western part of Western Australia, where it occurs on exposed reefs in the open ocean.

A fossil species, *T. auricula-leporis* has been described from the Middle Eocene Avon Park formation, Florida (Lumbert et al., 1984); its rhizome, however, does not show the regular features of the still living representatives of the genus; probably does it belong to an extinct genus of the Cymodoceaceae.

Amphibolis C. Agardh, Spec. Alg. 1 (1823) 474
Type species: *Amphibolis zosteraefolia* C. Agardh (= *A. antarctica* (Labill.) Sonder et Ascherson.

According to Ducker et al. (1977, p. 68) the genus *Amphibolis* was erected by C. Agardh (1823, p. 474) as a green alga with two species, *A. bicornis* (1823, p 474), and *A. zosteraefolia*, (1823, p. 475) from New Holland. Later, Agardh (1824, p. 192) recognized *A. zosteraefolia* as synonymous with *Ruppia antarctica* Labill., which was originally described by Labillardière (1806) as a flowering plant from the shore of Western Australia. Ducker et al. (1977) selected *A. zosteraefolia* instead of *A. bicornis* as the type of the *Amphibolis,* because, according to them, the type specimen of *A. zosteraefolia* has the unique grappling apparatus of which Agardh made the first description.

This genus is fully restricted to the temperate south and west coasts of Australia. It consists of two species. *A. antarctica* is distributed from Victoria and Tasmania in the east along the whole southern and western coast of Australia north to Carnarvon. The area of distribution of *A. griffithii* is more restricted; it occurs from Spencer Gulf in South Australia to the Geraldton area in Western Australia.

Posidoniaceae

Posidoniaceae Hutchinson, Fam. Fl. Pl. 2 (1934) 41; nom. cons.
Typus: *Posidonia* König

In earlier versions of the International Code of Botanical Nomenclature the name of the family has been ascribed to Lotsy (1911); he indeed used the name but did not add a formal description of the family.

Monoecious, perennial marine plants. Rhizome creeping, herbaceous, monopodial, with branched roots at the nodes; cortex with dark-colored secretory tannin cells. Scales covering the rhizome sheath-like, partly or completely amplexicaulous, scattered with fine brown dots (tannin). Erect lateral shoots ending in bundles of distichously arranged leaves. Leaf-sheath amplexicaulous or subamplexicaulous, biauriculate, ligulate. Leaf-blade linear with parallel nerves. Sheath as well as blade with numerous dark dots and stripes (tannin), the latter parallel with the nerves. Inflorescence cymose, pedunculate. Flowers hermaphrodite or masculine. Perianth absent. Stamens 3, sessile, consisting of a broad connective with at each side an extrorsely dehiscent, bilocular theca. Pollen confervoid. Gynoecium containing one orthotropous, parietal, pendulous ovule. Stigma irregularly lobed. Fruit with fleshy pericarp. Seed filled completely by the embryo; embryo straight, consisting for the greater part of a large, fleshy hypocotyl with an apical 4-polyphyllous plumula. Hypocotyl with numerous tannin cells. Primary root present or absent.

The family contains only the genus *Posidonia*, the history of which goes back to the Cretaceous.

Posidonia König in König & Sims, Ann. Bot. 2 (1805) 95; nom. cons.
Type species: *Posidonia caulini* König (= *P. oceanica* (L.) Delile)

The genus *Posidonia* has a rather remarkable pattern of distribution; one species, *P. oceanica*, is completely restricted to the Mediterranean; the other eight species of the genus occur in the waters of temperate Australia (Cambridge and Kuo, 1979; Kuo and Cambridge, 1984). Although there is no need to split the genus into sections or subgenera three groups can be recognized. *P. oceanica* forms a group in itself, because of the development of a significant primary root from the embryo. In the Australian species there is no development of a primary root at all. Among them two groups can be distinguished.

P. australis, *P. angustifolia*, and *P. sinuosa* form together the *P. australis*-group (Cambridge and Kuo, 1979). These species are found in relatively sheltered coastal waters where they can form extensive monospecific beds. They have thin, rather flexible, short leaves, relatively large air lacunae and rather few fibre bundles; their roots are rather fine and much branched. Their leaf-sheaths are short, so the meristems are not very deeply buried.

In contrast the five species of the *P. ostenfeldii*-group (*P. ostenfeldii, P. robertsoniae, P. denhartogii, P. coriacea*, and *P. kirkmanii*) grow in the open ocean and in high energy coastal sublittoral habitats (Kuo and Cambridge, 1984). They are characterized by very long, thick, tough, leathery leaves, with narrow air lacunae and an abundance of fibre bundles in the subepidermal layer and in the mesophyll. The leaf-sheaths are very long, up to 25 cm, and the meristems are deeply buried in the substrate (20–30 cm); the roots are very long and sparsely branched, showing wrinkled expanded thickenings up to 3 mm thick.

Recently, Campey et al. (2000) re-evaluated the species boundaries of the members of the *P. ostenfeldii* species complex in one locality, and found that there is a continuous variation of the character traits within the complex, suggesting the existence of a morphological continuum between the species; they also did not find any allozyme variation. According to them *P. coriacea* and *P. robertsoniae* are not separate species, and have to be regarded as synonyms.

Hydrocharitaceae

Hydrocharitaceae Juss., Gen. Pl. (1789) 67; nom. cons.: pro parte (excluding the dicotyledons *Nymphaea*, *Nelumbio*, *Trapa, Proserpinaca*, and the monocotyledon *Pistia* which were included in the original description of the family).
Typus: *Hydrocharis* L.

Monoecious or dioecious, annual or perennial aquatic plants, having either a creeping monopodial rhizome with unbranched roots at the nodes, and distichously, rarely tristichously, arranged leaves, or an erect main axis (which may be highly contracted) with roots at the base, and spirally arranged or verticillate leaves. Leaves submerged, sometimes floating or partly emerged, linear, lanceolate, elliptic, ovate or orbicular, either sessile and then sometimes sheathing at the base, or differentiated into a leaf-blade and a petiole, always without a ligula; nerves more or less parallel, straight or curved, connected by perpendicular or ascending cross-veins. Stipulae sometimes present. Squamulae intravaginales present. Flowers actinomorphous or, rarely, slightly zygomorphous (*Vallisneria*), with a true, trimerous perianth, unisexual, and then sometimes with rudiments of the other sex, or bisexual, sessile or pedicellate, solitary or arranged in a cymose inflorescence, enclosed by a spathe. Spathe consisting of two free or partly to completely connate spathal leaves (bracts), pedunculate or sessile. Perianth consisting of 1 or 2 whorls of 3 segments. Stamens (2-) 3-several, arranged in one or more whorls; anthers basifixed, bi- or quadrilocular, longitudinally dehiscent; filaments more or less slender, sometimes absent. Pollen globose, sometimes released in moniliform chains (*Halophila, Thalassia*). Gynaecium paracarpous. Ovary inferior, linear, ellipsoid or ovoid, consisting of (2-) 3-15 carpels, unilocular; between ovary and perianth often a long, filiform hypanthium. Placentas parietal either protruding nearly to the centre of the ovary, or obsolete. Styles (2-) 3-15, often more or less split into two stigmatic branches. Ovules several, orthotropous to anatropous, erect or pendulous, with two integuments. Fruits indehiscent, opening by decay of the fleshy or membranous pericarp; or, rarely stellately dehiscent (*Thalassia*). Seeds several, fusiform, ellipsoid, ovoid or globose. Embryo straight, either with the hypocotyl and the cotyledon not distinctly separated and with a very inconspicuous plumula at the base of a lateral groove; or with a well differentiated hypocotyl and cotyledon and a large well developed plumula. No endosperm.

The family contains 17 genera, of which *Thalassia*, *Halophila*, and *Enhalus* are fully marine.

Thalassia as well as *Halophila* have been regarded to be sufficiently different from a morphological point of view to erect special subfamilies for them; some authors considered them even as separate families. Nakai (1943), for example, erected the family Thalassiaceae for the genus *Thalassia*, because of its ‘confervoid’ pollen (in fact strings of spherical pollen), its distichous linear leaves, its quadrilocular, laterally dehiscent anthers, and its superior ovary (an incorrect observation as the ovary is inferior). Nakai (1943) erected also the family Halophilaceae to contain the genus *Halophila*, because of its ‘confervoid’ pollen (strings of pollen as in *Thalassia*), its opposite, stipulate, petiolate, pinnately nerved leaves, its bilocular extrorse anthers, and its inferior ovary. In our opinion the family status is not really warranted for these genera; the subfamily status within the Hydrocharitaceae expresses in fact sufficiently the special position as well as the relationship of these taxa.

The status of a possible arrangement of the remaining 15 genera within subfamilies is still open to debate. Ascherson and Gürke (1889) and Eckardt (1964) distinguished two, Dandy in Hutchinson (1934) only one, and Dahlgren et al. (1985) three subfamilies, while Tomlinson (1982) refrains from giving an opinion on this subject. Cook (1998) does not arrive at a formal classification, but distinguishes three groups, (1) the *Limnobium*-group, (2) the *Vallisneria*-group, and (3) the *Elodea*-group and the more or less alone standing genus *Blyxa*, that according to him could be considered to represent the archetype of the family. Cook places the seagrass *Enhalus* in the *Vallisneria*-group, but according to him, in spite of the reductions in many morphological and anatomical characteristics, it shows features that indicate intimate affinities to the *Limnobium*-group. Nakai (1943) regarded *Enhalus* as representing a family on its own, the Enhalaceae, mainly because it is a 'planta maritima'; this family is untenable, but unfortunately validly published in accordance with the rules of botanical nomenclature. On morphological grounds the seagrass *Enhalus* seems to be clearly related to the fresh-water genus *Vallisneria*, and has been classified by den Hartog (1970) within the subfamily **Vallisnerioideae**. Les et al. (1997) suggest another arrangement of the Hydrocharitaceae based on the *rbc*L gene sequence. Independent molecular research by Tanaka et al. (1997) using the *rbc*L and *mat* K gene sequences indicates that *Najas*, generally classified as a family of its own (Najadaceae), is an in-group of the Hydrocharitaceae, and thus would lose its special status. Further, they demonstrated that the three marine genera, *Enhalus, Halophila*, and *Thalassia* form a monophyletic grouping, but the recognition of all marine Hydrocharitaceae as a separate monophyletic family is not strongly supported by the *rbc*L data. Therefore, Les et al. (1997) concluded that these genera must be retained as a single taxon, e.g. as a subfamily, within the Hydrocharitaceae rather than as a distinct marine family. In our opinion the three marine genera have in common that they fit the morphological basic plan of the Hydrocharitaceae and possess a set of physiological properties to deal with life in the marine environment. Apart from these basic characters the three marine genera show hardly any similarities. The molecular data probably indicate that the adaptation to the marine conditions in the three genera has followed a similar pattern and that probably the same physiological mechanisms are involved. For this reason we keep to the view that the two marine subfamilies **Thalassioideae** and **Halophiloideae** should be maintained and that *Enhalus* belongs to the **Vallisnerioideae**.

Key to the Marine Genera

1a. Very coarse plants with a thick rhizome and strap-shaped leaves; leaf margins with very coarse nerves, after decay remaining as persistent strands. Flowers with three petals and three sepals. Male spathe with numerous flower-buds which become detached just before flowering, the flower then floating freely at the water surface. Pollen spherical, free. Female flower on a long peduncle, which spirally contracts after pollination. Tannin cells present . . . . . ***Enhalus***

1b. Moderately coarse or even very delicate plants with more slender rhizomes. Male spathe containing only one flower, shed after anthesis. Pollen spherical, arranged into moniliform strings. Tannin cells present or absent.

2a. Leaf-bearing branches arising from the rhizome at distances of several internodes; each internode covered by a scale. Leaves distichous, linear; nerves parallel. Spathal leaves partly connate. Styles 6–8, each divided into two stigmata. Parietal placentas protruding far into the centre of the ovary. Fruit stellately dehiscent. Tannin cells present . . . . ***Thalassia***

2b. Leaf-bearing branches arising from the thin rhizome at each node. Leaves petiolate, in pairs, in pseudo-whorls or distichously arranged; with a pinnate nervation. Spathal leaves free. Styles 3–6, not divided. Parietal placentas protruding only slightly into the ovary. Fruit dehiscent by decay of pericarp. Tannin cells absent . . . . ***Halophila***

Enhalus L.C. Richard, Mém. Inst. Paris 12, 2 (1812) 64,71,74.
Type species: *Enhalus koenigi* Rich. (= *E. acoroides* (L. *f*.) Royle)

Enhalus is a monotypic genus, widely distributed along the coasts of the Indian Ocean and the tropical part of the western Pacific.

Thalassia Banks ex König in König and Sims, Ann Bot. 2 (1805) 96
Type species: *Thalassia testudinum* Banks ex König

This genus contains two well-defined species. *T. hemprichii* is widely distributed in the coastal waters of the Indian Ocean and the western Pacific. *T. testudinum* is restricted to the Gulf of Mexico and the Caribbean, and it has been recorded from Bermuda.

Fossil leaf material of *T. testudinum* has been found in the Avon Park deposits from the Middle Eocene of Florida (Lumbert et al., 1984).

Halophila Du Petit Thouars, Gen. Nov. Madag. 2 (1806) 2
Type species: *Halophila madagascariensis* Steudel, validated by Doty & Stone, 1967.

The typification of *Halophila* has been a weary affair, because the original author of the genus did not describe the species on which the genus was based. Steudel (1840, p. 515) published the name *H. madagascariensis* without a description of the species, thus not validly, but the geographical indication makes it clear that he must have referred to the material of Thouars; at that time there were no other collections of *Halophila* from Madagascar in the Paris herbarium. Doty and Stone (1967) validated the name after 127 years. In 1970 den Hartog considered this species still as a synonym of *H. ovalis*, which is based on *Caulinia ovalis* from Australia (K, BM), and did not give *H. madagascariensis* even the status of a subspecies. After a new study we now agree that the two taxa indeed show some differences. There is, however, another option for the typification of the genus, as *H. ovata* was the first species described and illustrated within the genus.

In the genus *Halophila* five sections have been described, based on differences in the gross vegetative morphology of the plants. These sections do not show differences with respect to the structure of the flowers; the variation in the number of styles, for example, may differ between populations of the same species. Differences in the way of arrangement of the flowers into inflorescences seem more characteristic at the species level; the same holds for monoecy and dioecy.

Most species can be classified within the typical section, *Halophila* sect. *Halophila*. This section contains all *Halophila* species with one pair of petiolate leaves born on short erect lateral shoots. It is the morphologically most diverse group and its geographical distribution coincides with that of the whole genus. The species of this section occur in various habitats and show a large morphological variability; some of these variants can be treated as independent taxa in their own right. Currently, there are ten described species: *Halophila ovalis* (consisting of four subspecies), *H. madagascariensis, H. ovata, H. minor, H. australis, H. johnsonii, H. decipiens, H. capricorni, H. stipulacea,* and *H. hawaiiana.* These species and the subspecies of *H. ovalis* have recently been briefly redescribed, with the exception of *H. madagascariensis* (Kuo and den Hartog 2001).

Most of the species of the section *Halophila* are restricted in their occurrence. Only *H. decipiens* is widely distributed occurring in both the northern and the southern hemisphere, along the tropical and subtropical coasts of the Indian, the Pacific, and the Atlantic Oceans, but the species has not been recorded so far from the Mediterranean.

H. ovalis is widely distributed in the tropical Indo-West Pacific and penetrates in some areas beyond the tropics, e.g. in Western Australia, and in Japan as indicated by Miki (1934). *H. minor* has also a wide area of distribution, from East Africa to the western Pacific, but it does not extend beyond the tropics. *H. stipulacea*, is very common along the eastern coasts of Africa, in the Red Sea and the Persian Gulf, and also occurs on Madagascar and along the west coast of India. This species has invaded the Mediterranean via the Suez Canal and is there still expanding its area of distribution (Den Hartog, unpublished). *H. australis* has a wide distribution in the temperate seas of southern Australia, *H. capricorni* is restricted to the Coral Sea, and *H. ovata* occurs only in the northern part of the western Pacific (Saipan, Guam, Yap, Manila Bay) (Kuo 2000). *H. johnsonii* is the rarest species as it is restricted to one area in Florida.

It appears that various morphologically distinct species in this section could not be distinguished by a recent molecular study (Waycott et al. 2002). McDermid et al. (2003) reported that several morphological variations with little genetic variation occur in populations of *H. hawaiiana* from different islands of the Hawaiian Archipelago. Procaccini et al. (1999b) found that the recently established populations of *H. stipulacea* on Sicily exhibited both significant morphological variations with depth and site as well as high genetic polymorphism, but these variations appeared to show no correlation. These authors suggested that this phenomenon might be influenced by environmental conditions and through vegetative or other means of asexual reproduction; however, they did not specify which environmental factors and did not make an effort for collecting or observing reproductive materials from different populations.

The section *Spinulosae* Ostenfeld is characterized by having much elongated, stiff erect lateral shoots bearing up to 20 pairs of distichously arranged sessile leaves at the nodes. The section consists of only one species, *H. spinulosa*, which is morphologically fairly homogeneous. Japar Sidik et al. (2000) reported, however, that there are some populations in Malaysia where the leaves are tristichously arranged. The species is common in Malaya, and extends via Indonesia where it is rare, to New Guinea and tropical and subtropical Australia. There are no records of the species from Thailand and Vietnam; the most northern record is from Luzon, Philippines.

The section *Microhalophila* Aschers. is characterized by the possession of distinct erect lateral shoots, which bear on the top a pseudo-whorl of 4–10 sheathing petiolate leaves. It contains one delicate species, *H. beccarii*, which shows some slight morphological variation. This species is widely distributed along the southern shores of the South Chinese Sea, the Gulf of Thailand, the Gulf of Bengal, and the Indian coast of the Arabian Sea. So far, it has not been recorded from Indonesia and Australia. It reaches its northern limit in south China and Taiwan. The species is usually associated with mud flats and mangrove communities and often exposed at low tide.

The fourth section of the genus, sect. *Americanae* Ostenfeld is characterized by having distinct erect lateral shoots with two scales about half way up and a pseudo-whorl of 4–8 leaves at the top. It contains two morphologically fairly distinct dioecious species, *H. engelmanni*, which occurs in the Gulf of Mexico and the northern Caribbean (Cuba), and *H. baillonii*, which has been recorded from the southern Caribbean, the Pacific coast of Central America, and from Brazil.

The fifth section of the genus, sect. *Tricostatae* Greenway, consists of fragile plants with herbaceous, elongated erect lateral shoots bearing at each node a rosette of (2-) 3 leaves. The section contains only one annual, dioecious species, *H. tricostata,* which is restricted in its occurrence to north-eastern Australia.

Ruppiaceae

Ruppiaceae Horaninov, Prim. Lin. Syst. Nat. (1834) 46; nom. cons.
Typus: *Ruppia* L.

In earlier editions of the International Code of Botanical Nomenclature the name of the family was ascribed to 'Horaninov ex Hutchinson, Fam. Fl. Pl.2 (1934) 48'.

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 ligule; leaf-blade with only a midrib; margins smooth, but near the leaf-tip irregularly serrulate; on either side of the midrib a wide air lacuna. 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 two 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 two opposite stamens and 4-numerous 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 podogyne develops at the base of each carpel after fertilization, 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.

The family contains only one genus, *Ruppia*.

Ruppia L. Sp. Pl. (1753) 127.
Type species: *Ruppia maritima* L.

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 salinities up to three times the salinity of the sea. It has also been found under marine conditions, but only in very sheltered places, where also very large temperature fluctuations may occur. 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.

Circa 10 species are known. As a consequence of the 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 recognized 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 to the problem was to consider the genus as containing one very variable species. This has given cause to the uncritical 'traditional' identification of specimens of this genus as *R. maritima*. Studies based on the investigation of living plants, herbarium material and chromosome analyses in Europe (Reese, 1962; Verhoeven, 1979), Australia (Jacobs and Brock, 1982) and New Zealand (Mason, 1967) have shown that this is not correct. It is obvious that the genus is in an urgent need of revision on a world scale. This revision should not only be based on herbarium material, but also on the study of living material cultured under various ecological circumstances; further chromosome and isozyme studies should be included.

The genus *Ruppia* has been classified in the past in various ways; 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 and Brock (1982) the differences with *Potamogeton* are not sufficient to warrant a separate position within the Potamogetonaceae *sensu stricto*. Les et al. (1997) have shown that molecular *rbc*L data indicate that *Ruppia* is phylogenetically much closer to *Posidonia* than to *Potamogeton*.

The only exclusively marine species of the genus has not yet been formally described, and is indicated as *R*. aff. *tuberosa* (den Hartog, in preparation)

Zannichelliaceae

Zannichelliaceae Dumortier, Anal. Fam. Pl. (1829) 59, 61; nom. cons.
Typus: *Zannichellia* L.

Monocious or dioecious, annual or rarely perennial aquatic herbs. Rhizome creeping, sympodial, often poorly developed, herbaceous, rooting at the nodes. Roots not branched, 1-several per node. Scales on the rhizome membranous, caducous. Erect shoots arising from each node, sympodial, branching profusely and producing flowers arranged in a rather complex inflorescence. Leaves distichously arranged, sometimes alternate or in a pseudo-whorl, linear, green, without tannin cells, with a single central vein, on each side of it with 1–2 parallel air channels; margin entire; leaves with a ligule, sheathing at the base, or without a ligule, but with free stipules at the base of the leaves (*Zannichellia*). Tannin cells absent. Flowers terminal. Male flower with or without perianth, with one stamen consisting of 2–12 longitudinally dehiscent, sporangiate cells, with or without connective appendages. Stamens generally submerged, but in at least one species emerging above the water surface. Pollen spherical. Female flower consisting of a cup-shaped structure, the cupula, with 1–8 sessile or shortly pedicellate free carpels. Cupula consisting of three tepals, which are free (*Lepilaena, Althenia*), or united to form a closed tube (*Zannichellia, Pseudalthenia*). Carpels with a short (*Zannichellia, Pseudalthenia*) or a long style (*Lepilaena, Althenia*); stigma funnel-shaped or peltate with a smooth, lobate, or feathery appearance. Ovule 1, anatropous, pendulous. Fruit an achene, with a hard endocarp, a soft mesocarp and a membranous exocarp, and a terminal beak. In some species a short podogynium is developed after fertilization, forming an integral part of the fruit without an abscission zone. Fruit wall smooth or tuberculate. No endosperm.

The family has a world wide distribution, and consists of four genera. The taxonomy of the family at the genus level has been worked out by Tomlinson and Posluszny (1976). *Zannichellia* has a very wide distribution, almost covering the area of the family, and has been recorded from sea level up to the high Andes and the Himalayas. The species of this genus occur in brackish as well as hard fresh water, in standing ponds and lakes as well as in streams, but do not inhabit marine sites. Most of these species are also tolerant to large temperature fluctuations, and their seeds can stand protracted desiccation. In the past the genus has been considered to consist of one extremely variable species, *Z. palustris*. This has often led to an uncritical 'traditional' identification of plant material of this genus. It has, however, turned out that a number of well-defined species can be recognized. In Europe at least six species occur (Van Vierssen, 1982; Van Vierssen and Van Wijk, 1982; Uotila et al., 1983; Talavera et al., 1986), and more species are expected to be recognized, as the material from the Ponto-Caspian area and Central Asia has been subjected to a critical study. Haynes and Holm-Nielsen (1987) described a species from the Andes. The genus is urgently in need of a revision. *Althenia*, with one or two, but possibly more species, is distributed from the Mediterranean area to Central Asia, and has further been recorded from South Africa. It occurs in saline waters of salt marshes along the coast, but is also widely distributed in continental salt waters. The genus *Pseudalthenia* (also known under the name *Vleisia*) is monotypic and is restricted in its occurrence to a few brackish-water environments in the Cape Province of South Africa. *Lepilaena* is the only genus in this family with a true marine species.

Lepilaena Drummond ex Harvey, J. Bot. Kew Gard. Misc. 7 (1855) 57
Type species: *Lepilaena australis* Drummond ex Harvey

The genus contains at least six species which all are widely distributed in temperate Australia; one of these, *L. bilocularis*, is shared with New Zealand. Robertson (1986) gives a key to the presently described species of the genus. Its representatives occur in all kinds of brackish water habitats, but also in continental salt waters; further they inhabit hard fresh water environments such as shallow lakes and ponds, and are often found in temporary pools. A still undescribed species has been collected in a shallow temporary soft water environment in south-western Australia. One species, *L. marina*, has been found so far only in sheltered marine environments; in vegetative condition this species can be confused with *L. bilocularis*. Marine records of the latter almost certainly refer to *L. marina*, e.g. the records by den Hartog (1970).

IV. Biogeography

The first attempt to analyze the geographical distribution of the seagrasses was by Ascherson (1871), who produced also the first world map of their distribution. At present this paper has only historical value, as taxonomy of the seagrasses and knowledge of their distribution has increased enormously since, not least by the continuous efforts of Ascherson himself to obtain material from all over the world, and to publish updates (Ascherson, 1875, 1906). His work has been continued by the publication of the fine essays by Ostenfeld (1915) and Setchell (1920, 1935). Ostenfeld published also a number of detailed maps of the areas of distribution of the seagrass species known at that time in the prestigious series 'Pflanzenareale' (Ostenfeld, 1927a, marine Hydrocharitaceae; 1927b, marine Potamogetonaceae, i.e. representatives of the Zosteraceae, Posidoniaceae and Cymodoceaceae). In his monograph den Hartog (1970) described the areas of all known species, based on the collections available at that time, and produced maps of the distribution of all 12 genera. These maps show also perfectly that the pattern of seagrass distribution, already suggested by Ascherson (1906), has become more and more prominent. Later publications show a further increase in knowledge; Lüning (1990, p. 204) amended the genus maps of den Hartog. Larkum and den Hartog (1989) discussed the evolution of seagrass genera and events that gave rise to their current distribution. Regrettably the species maps given by Green and Short (2003) in their world atlas of seagrasses (2003 Appendix 3) are not always fully accurate.

Seven genera appear to be mainly distributed along tropical coasts, viz. *Thalassia*, *Halophila*, *Syringodium*, *Halodule*, *Cymodocea*, *Thalassodendron* and *Enhalus*. The first four genera have representatives in the tropical Atlantic as well as in the Indo-Pacific. The other three genera are restricted to the Indo-West Pacific. However, with respect to *Cymodocea, Halophila* and *Thalassodendron* the picture is somewhat more complicated. One of the *Cymodocea* species, *C. nodosa*, has a more warm-temperate distribution in the Mediterranean, and fans out into the Atlantic along the Iberian Peninsula and the north-western coast of Africa where it just passes the Tropic of Cancer. *Halophila*, with 15 described species the most species-rich genus of the seagrasses, has developed a warm-temperate species, *H. australis*, occurring along the southern shores of Australia, and the widespread Indo-West Pacific species, *H. ovalis*, extends its area in East Asia far beyond the tropics. *Thalassodendron* has one species with a wide distribution in the tropical Indo-West-Pacific and a second species with a very small area of distribution along the warm-temperate south-western coast of Australia. In all other cases where tropical species cross the Tropic of Cancer (e.g. in the northern Red Sea, and the Ryukyu Islands) or the Tropic of Capricorn (*Syringodium isoetifolium* along the Australian West coast) warm currents make this possible. It is striking that the tropical Atlantic seagrass flora has no genera of its own, although it is well distinguished at the species level. The only supraspecific taxon characteristic for the tropical Atlantic, with one outlying record for Pacific Central America (den Hartog, 1960), is *Halophila* sect. *Americanae*.

Five genera are mainly distributed along the world's temperate shores, viz. *Zostera*, *Phyllospadix*, *Heterozostera*, *Posidonia* and *Amphibolis*. Two of these genera have their distribution in the northern as well as in the southern hemisphere. *Zostera* subgen. *Zosterella* has representatives in temperate Australia, New Zealand, southern Africa, as well as in eastern Asia and along the Atlantic and Mediterranean coasts of Europe, and northern Africa. *Z. noltii* is the only species occurring in the continental relict seas of western Asia (Caspian Sea and Aral Sea). It is striking that up to very recently this subgenus has been absent from the Atlantic as well as the Pacific coasts of the Americas. *Zostera* subgen. *Zostera* is restricted to the northern Pacific and the northern Atlantic, and also occurs in the Mediterranean and the Black Sea. *Posidonia* is the second genus with a bipolar distribution, but in contrast to *Zostera* the northern hemisphere distribution is restricted to one species in the Mediterranean, and in the southern hemisphere it occurs with eight species in Australia. *Heterozostera* and *Amphibolis* are restricted to temperate Australia, apart from a small area occupied by the endemic *H. chilensis* in Chile. Only some species of *Zostera* subgen. *Zosterella* penetrate here and there within the tropics.

The Arctic Sea has no species of its own, although the cold temperate species *Zostera marina* crosses the Arctic Circle in Europe as well in the northern Pacific. Antarctica is devoid of seagrasses.

In spite of shipping, fishing, culturing marine organisms, and other human activities over the centuries, the areas of distribution of the seagrasses are still reasonably intact. The only changes which are of an anthropogenous nature relate to *Z. japonica* which has been accidentally introduced in Pacific North America and is still expanding its area (Harrison, 1976; Bigley and Barreca, 1982), and *Halophila stipulacea* which has passed through the Suez Canal and has conquered the eastern Mediterranean. Of course, within the known areas large changes in abundance of species have taken place, of which many are indicated in the atlas of Green and Short (2003).

In the reviews by Larkum and den Hartog (1989) and Kuo and den Hartog (2000) it is already stated that the origin of the seagrasses is still very unclear. Fossil material is extremely rare. Most of the fossils thought to be seagrass appeared not to be seagrass at all. The original material of *Archeozostera*, described from the Cretaceous of Japan, appeared after a profound study by Kuo et al. (1989) not to be a seagrass and probably not even a plant. There was already some doubt about *Thalassocharis*, described from the Cretaceous of Westfalen (Germany) and Maastricht (The Netherlands), as the stems had no seagrass morphology; the absence of air lacunae leads to the conclusion that it is not an aquatic plant. The only seagrass genus of which the Cretaceous origin can be confirmed appears to be *Posidonia*. *P. cretacea* Hos. et v. d. Mark, described from Germany, is not very well known, but recently a very fine specimen, consisting of a bundle of leaf-sheaths fully comparable with the 'shaving brush' of the mediterranean *P. oceanica*, has been collected from the Cretaceous of Maastricht.

Other seagrass fossils are known from the Eocene of the Basin of Paris; these have been assigned to *Posidonia parisiensis* (Brongt.) Fritel, *Cymodocea serrulata* and *C. nodosa* (den Hartog. 1970; Larkum and den Hartog, 1989). An other set of Eocene seagrass fossils has been collected from the Avon Park formation in Florida, viz. *Thalassodendron auricula-leporis* den Hartog, *Cymodocea floridana* den Hartog and *Thalassia testudinum* (Lumbert et al. 1984). It is remarkable that most of these Eocene fossils can be identified as, or are morphologically very similar to, presently still extant species. *C. floridana* shows a striking resemblance to *C. angustata*, which has a very small area of distribution in northwestern Australia (Kuo and den Hartog, 2000). The Eocenous *Thalassodendron* species is rather different from the modern species, and may be classified into a genus of its own. Beautifully preserved fossils of *C. serrulata* have been collected from the Miocene of Sulawesi (formerly Celebes) as *C. micheloti* (Laurent and Laurent, 1926).

From these few confirmed fossils it can be concluded that seagrasses already developed at an early stage of the evolution of the angiosperms. Taking into consideration that at present three exclusive seagrass families can be recognized, and a fourth family with two seagrass subfamilies, the possibility may not be excluded that the evolutionary transition from terrestrial plants to fully submersed marine plants may have taken place just as many times. Les et al. (1997) concluded after a phylogenetic analysis that among the seagrasses three lineages can be recognized giving evidence that these lineages independently entered the marine environment. These lineages are (i) the Zosteraceae, (ii) the Cymodoceaceae complex consisting of the Posidoniaceae, the Cymodoceaceae and the Ruppiaceae, and (iii) the Hydrocharitaceae.

The Ruppiaceae and the Zannichelliaceae occur in waters with a very diverse chemical composition, such as brackish and continental salt waters, but also in hard fresh waters. *Ruppia* species sometimes occur in the marine environment, particularly in the intertidal zone of muddy or sandy flats where seagrasses are absent; after the introduction of *Zostera japonica* in North America *Ruppia* decreased markedly. In temperate Australia *Lepilaena* (Zannichelliaceae) occurs with *Ruppia* in brackish waters. Both genera have developed one species that is fully restricted to very sheltered marine conditions, and these two species generally form together a community. These species are probably the most recent seagrasses in the evolutionary history.

It is apparent from the very limited fossil record that the distribution of the seagrasses must have been quite different from the present situation, as is demonstrated by the fossil occurrence of *Cymodocea* and a *Thalassodendron*-like species in North America, genera presently absent from America.

Another fact is that fossil material of Zosteraceae has not been found in Cretaceous or Tertiary deposits, but only in Quaternary layers; the presence of *Z. noltii* in the Caspian and Aral Seas shows, however, that on the ground of the history of these seas *Zostera* must have been in existence already in the Miocene. Larkum and den Hartog (1989) have attempted to use all kinds of geological data to work out the history of the Australian seagrass flora. The great handicap for this approach remains the lack of fossil material. Of the 12 presently living seagrass genera some fossil remains of only four are known, and this is insufficient to elaborate in a reliable way the areas of origin of the various families. One would expect that thick seagrass deposits, as presently known from *Posidonia* species and *Thalassodendron ciliatum*, must have been formed also in the past. Therefore, it is recommended that seagrass researchers should more cooperate with paleontologists when marine geological deposits are explored.

V. Conclusion and Outlook

We acknowledge the important contribution made by molecular technology [*rbc*L, *mat*K (plastid DNA) and ITS (nuclear DNA) gene sequences] in our understanding of phylogenetic relationships of seagrasses, particularly at the higher levels for which this approach has been developed (the reader is referred to Waycott et al., Chapter 2, for an in-depth review of this topic). However, this powerful tool may not always be suitable for defining the species and cannot replace the morphological characters generally used for species identification. To consider taxa which cannot be separated by the present molecular techniques as ‘phenotypic plasticity’ of a wider molecularly defined ‘biological species’ is not really a solution of the problem; new advanced techniques may show that they are indeed different. There is a great need to correlate the molecular data to morphological and physiological data.

In this connection we refer to the works of McMillan, who studied isozymes (McMillan, 1980, 1982, 1991; McMillan and Williams, 1980) and sulfated flavonoids (McMillan et al., 1980; McMillan, 1983, 1986) in many seagrass species, but he generally did not give morphological descriptions of the material used, with the exception of the taxa within the genus *Halophila*. In the latter case the isozyme and flavone patterns seem characteristic at the species level, but unfortunately the number of observations is low. More research is necessary, as McMillan and Williams (1980) clearly state.

Admittedly the number of useful morphological characters that can be used to identify the seagrass species is very limited due to the relatively simple morphological and anatomical features in both the vegetative and the reproductive organs of seagrasses; this holds in fact for many other aquatic plants as well (see Chapter 3, Kuo and den Hartog). So, another powerful tool, that of the cladistic analysis, which often is employed in terrestrial plant taxonomy may not be very suitable for seagrass taxonomy, as demonstrated by Les et al. (2002).

It is true that the currently available knowledge of seagrass taxonomy, in particular where the definition of species is concerned, is not always adequate and requires an urgent improvement. Basic morphological and anatomical studies on as many samples as possible from wide geographic areas and growing under as many different habitat conditions as possible should be conducted. It is very important that good documentation of morphological and anatomical variations within the species from the various study areas becomes available; it has to be encouraged that samples of material used for molecular, physiological, phytochemical and morphological research are deposited in the recognized herbaria for future study and to improve the descriptions of species. Without such fundamental studies, the queries on identification of variable species such as those of *Zostera, Halodule,* and *Halophila* will continue to persist. A stable taxonomy is a necessary base for all botanical research. Therefore, it is also recommended that, if possible, type material of the various taxa is included in the analyses.

Finally we have come to the conclusion, in agreement with Tomlinson (1982), that there are no special morphological characters that distinguish the seagrasses from other aquatic plants. The only character in which most of them differ from the other aquatic plants is the filiform pollen (Zosteraceae, Posidoniaceae, Cymodoceaceae) or the strings of spherical pollen (*Thalassia, Halophila*); however, we do not see what the special advantage of these may be for life in the marine environment.

The seagrasses as well as the aquatics of the eurysaline group, obviously, differ from the other aquatic plants by their ability to live in waters with a high salinity. It is at present still not clear how they cope with this situation. The fact that the seagrasses inhabit generally the homoiohaline waters, where the environmental conditions are relatively stable, and the eurysaline species the poililosaline waters where they are generally subjected to large fluctuations in salinity, indicates that these plants must have evolved very special physiological mechanisms to deal with these problems. So far very little is known about these mechanisms; it is not even clear whether there is only one mechanism or whether each family involved has developed its own way to deal with salinity, as the families are not closely related. These mechanisms are certainly firmly fixed in the genomes of these plants. Therefore, we recommend a thorough study of the physiology of both the seagrasses and the eurysaline aquatics in order to solve this basic problem.

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Appendix: A List of the Seagrass Species of the World

The list presents all taxa recognised as seagrasses. Eurysaline taxa which may be found in brackish water and occasionally under marine conditions have not been incorporated.

Zosteraceae

1. Zostera Linnaeus

Zostera subgenus **Zostera**

1. *Zostera marina* Linnaeus
2. *Zostera caespitosa* Miki
3. *Zostera caulescens* Miki
4. *Zostera asiatica* Miki

Zostera subgenus **Zosterella** (Ascherson) Ostenfeld

5. *Zostera noltii* Hornemann
6. *Zostera japonica* Ascherson et Graebner
7. *Zostera capensis* Setchell
8. *Zostera capricorni* Ascherson
9. *Zostera muelleri* Irmisch ex Ascherson
10. *Zostera mucronata* den Hartog
11. *Zostera novazelandica* Setchell

Phyllospadix W.J. Hooker

12. *Phyllospadix scouleri* W.J. Hooker
13. *Phyllospadix torreyi* S. Watson
14. *Phyllospadix serrulatus* Ruprecht ex Ascherson
15. *Phyllospadix iwatensis* Makino
16. *Phyllospadix japonicus* Makino

? *Phyllospadix juzepczukii* Tsvelev (see footnote*)

Heterozostera (Setchell) den Hartog

17. *Heterozostera tasmanica* (Martens ex Ascherson) den Hartog
18. *Heterozostera polychlamis* Kuo
19. *Heterozostera nigricaulis* Kuo
20. *Heterozostera chilensis* Kuo

Cymodoceaceae

Halodule Endlicher

21. *Halodule uninervis* (Forsskål) Ascherson
22. *Halodule beaudettei* (den Hartog) den Hartog
23. *Halodule wrightii* Ascherson
24. *Halodule bermudensis* den Hartog
25. *Halodule ciliata* den Hartog
26. *Halodule pinifolia* (Miki) den Hartog
27. *Halodule emarginata* den Hartog

Cymodocea König in König et Sims

28. *Cymodocea nodosa* (Ucria) Ascherson
29. *Cymodocea rotundata* Ehrenberg et Hemprich ex Ascherson
30. *Cymodocea serrulata* (R. Brown) Ascherson et Magnus
31. *Cymodocea angustata* Ostenfeld

Syringodium Kützing in Hohenacker

32. *Syringodium filiforme* Kützing in Hohenacker
33. *Syringodium isoetifolium* (Ascherson) Dandy

Thalassodendron den Hartog

34. *Thalassodendron ciliatum* (Forsskål) den Hartog
35. *Thalassodendron pachyrhizum* den Hartog

Amphibolis C. Agardh

36. *Amphibolis antarctica* (Labillardière) Sonder et Ascherson
37. *Amphibolis griffithii* (J.M. Black) den Hartog

Posidoniaceae

Posidonia König in König et Sims
38. *Posidonia oceanica* (Linnaeus) Delile
39. *Posidonia australis* J.D. Hooker
40. *Posidonia sinuosa* Cambridge et Kuo
41. *Posidonia angustifolia* Cambridge et Kuo
42. *Posidonia ostenfeldii* den Hartog
43. *Posidonia robertsoniae* Kuo et Cambridge
44. *Posidonia coriacea* Cambridge et Kuo
45. *Posidonia denhartogii* Kuo et Cambridge
46. *Posidonia kirkmanii* Kuo et Cambridge

Hydrocharitaceae

Vallisnerioideae

Enhalus L.C. Richard
47. *Enhalus acoroides* (Linnaeus *f*.) Royle

Thalassioideae

Thalassia Banks ex König in König et Sims
48. *Thalassia hemprichii* (Ehrenberg) Ascherson in Petermann
49. *Thalassia testudinum* Banks ex König in König et Sims

Halophiloideae

Halophila Du Petit Thouars

Halophila sect. **Halophila**
50. *Halophila ovalis* (R. Brown) J.D. Hooker
 ssp. *ovalis*
 ssp. *bullosa* (Setchell) den Hartog
 ssp. *linearis* (Den Hartog) den Hartog
 ssp. *ramamurthiana* Ravikumar et Ganesan
51. *Halophila ovata* Gaudichaud in Freycinet
52. *Halophila minor* (Zollinger) den Hartog
53. *Halophila australis* Doty et Stone
54. *Halophila hawaiiana* Doty et Stone
55. *Halophila madagascariensis* Steudel ex Doty et Stone
56. *Halophila johnsonii* Eiseman in Eiseman et McMillan
57. *Halophila stipulacea* (Forsskål) Ascherson
58. *Halophila decipiens* Ostenfeld
59. *Halophila capricorni* Larkum

Halophila sect. **Microhalophila** Ascherson
60. *Halophila beccarii* Ascherson

Halophila sect. **Spinulosae** Ostenfeld
61. *Halophila spinulosa* (R. Brown) Ascherson

Halophila sect. **Tricostatae** Greenway
62. *Halophila tricostata* Greenway

Halophila sect. **Americanae** Ostenfeld
63. *Halophila engelmanni* Ascherson
64. *Halophila baillonii* Ascherson ex Dickie in J.D. Hooker

Ruppiaceae

Ruppia Linnaeus
65. *Ruppia* aff. *tuberosa* (den Hartog, in prep., not yet formally described)

Zannichelliaceae

Lepilaena Drummond ex Harvey
66. *Lepilaena marina* E.L. Robertson in Womersley

*See the discussion under "**Phyllospadix** Hooker". The authors of this chapter have not had the opportunity to study material of this species. Its description, however, is insufficiently clear to distinguish it from other species of *Phyllospadix*. For this reason we have not given it a number in the list.