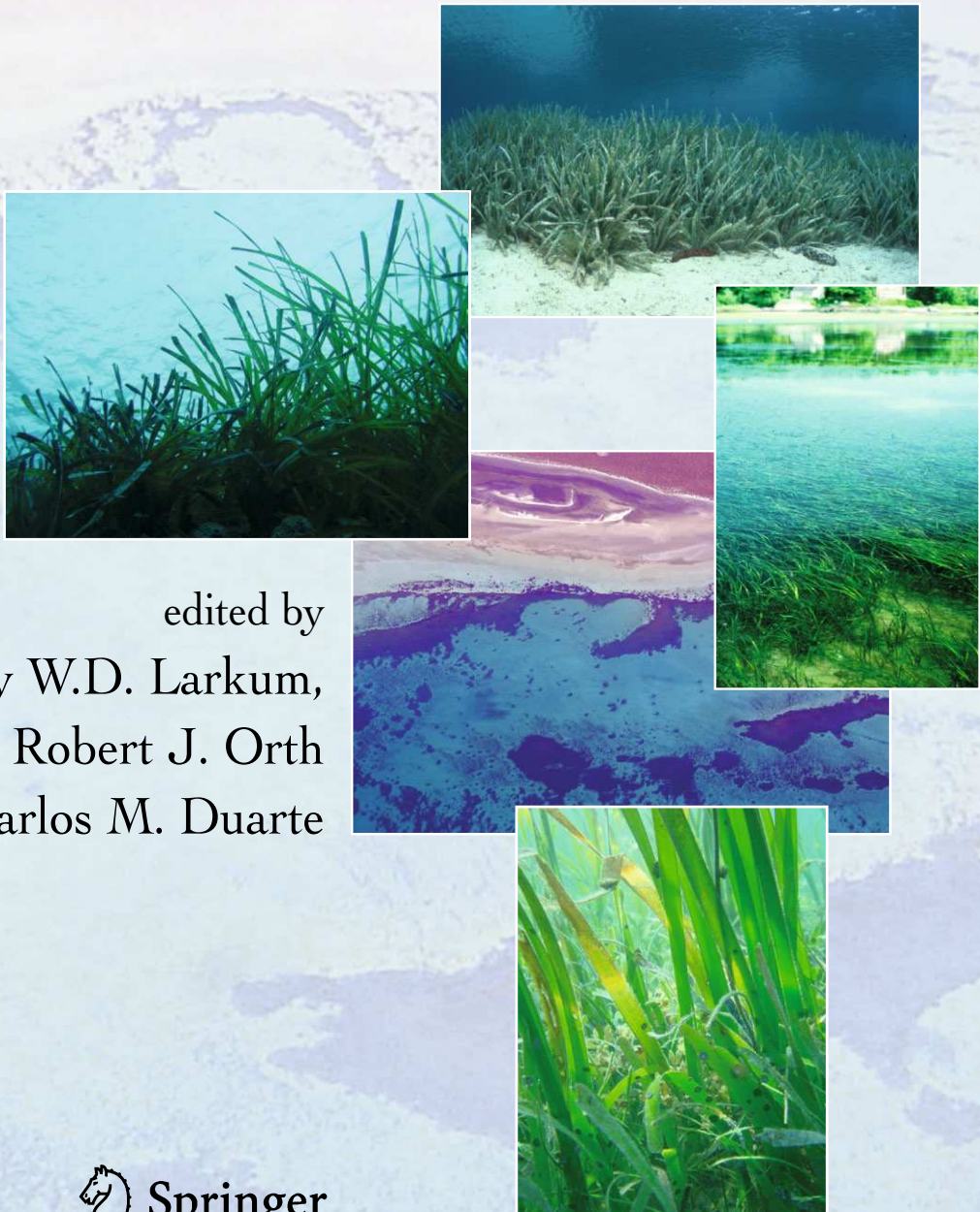


Seagrasses: Biology, Ecology and Conservation

edited by
Anthony W.D. Larkum,
Robert J. Orth
and Carlos M. Duarte



 Springer

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by

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Foreword

Seagrasses have captured the imagination of scientists only relatively recently. Marine algae or seaweeds have had a much more glorious history, extending back to the 18th Century. It is true that Aristotle described the seeds of *Posidonia oceanica* and that, much later, Carl von Linné (Linnaeus) recognized and named two species of seagrass in 1779: *Zostera marina* (1753) and *Posidonia (Zostera) oceanica* (1757). However this knowledge penetrated very little, despite the fact that the savant and grandfather of Charles Darwin, Erasmus Darwin wrote a stanza on *Zostera* in his Botanic Garden (Part V) in 1803 (see also Fig. 5, Chapter 25):

“Stretch’d on her mossy couch, in trackless
deeps,
Queen of the coral groves, *Zostera* sleeps;
The silvery sea-weed matted round her bed,
And distant surges murmuring o’er her head.”

There were certainly pioneers of seagrass biology early in the second half of the 19th Century (notably, P. Ascherson) and early 20th Century (e.g. C.H. Ostenfeld and W.A. Setchell). And while the pandemic decline of eelgrass in the 1930’s was widely noted along with loss of numerous ecosystem functions, seagrass science remained submersed for the next 40 years. It was not until the landmark publication of “Seagrasses of the World” by C. (Kees) den Hartog in 1970 that the taxonomy of seagrasses was in any way brought into line with systematic studies of most other plants over a century earlier. This was a seminal time as the advent of SCUBA diving led to a quantum leap forward in studies of the benthic components of the nearshore marine environment. A major result of this happy union of events was a sudden realization that seagrasses played a major role in nearshore ecosystems in all continents except Antarctica. This realization led to major funding initiatives such as the International Decade of Ocean Exploration, the launch of a journal in which seagrass biology played a major role (*Aquatic Botany*, 1975) and the launching of a series of Seagrass Workshops (the first in Leiden, 1973), which have focused the efforts of a growing cohort

of seagrass researchers around the world (Seagrass 2004 and International Seagrass Biology Workshop 6, in Townsville, Australia, had 170 delegates). In addition the recent publication of an introductory book on Seagrass Ecology (Hemminga and Duarte 2000), a Global Seagrass Methods book (Coles and Short, 2003) and a Global Seagrass Atlas (Green and Short, 2003) have given researchers and managers alike a new set of tools to facilitate the further understanding of seagrasses. However, despite this upsurge in seagrass science, much remains unknown in seagrass biology and ecology. Seagrass research has been concentrated in only a few areas of the world (Australia, Europe, United States) and with only a few of the 50+ species (e.g. *Zostera marina*, *Posidonia oceanica*, *Thalassia testudinum*), with many existing paradigms developed from even fewer species and areas (Duarte 1999).

The need for increased understanding today has taken on a new meaning, and urgency, as the rate of seagrass loss appears to be accelerating concurrently with the rapid urbanization of the coastal zone, where seagrasses are most abundant (Green and Short, 2003). The very survival of seagrasses, which have been present for over 100 million years, now depends on a renewed commitment by all parties – managers, scientists, politicians, and the general public – to form partnerships to conserve remaining seagrass beds and restore, where possible, lost seagrass habitat. This renewal can only be successfully accomplished with a clear understanding of how all seagrasses grow and survive and how various fauna utilize this habitat. Thus, we as editors, believe the contents of this book are timely in this regard as they set the stage for what we must do to insure seagrasses not just survive but thrive in the face of rapid urbanization of the coastal zone. We believe by examining where we were with seagrass science, what is occurring presently, and where we must go is critical to this survival. In this book, we have not just asked our authors to review their area of specialty, but more importantly they were asked to reassess and reformulate paradigms and set the stage for how the field **must** develop if seagrasses are to persist.

So what, taxonomically, are seagrasses? This question is tackled in Chapters 1 and 2. However, as will be seen in those pages the answer is not so easy as we would like. Seagrasses are certainly the only flowering plants that are found in the sea and they belong to the Monocotyledons. They belong to at least two families, the Potamogetonaceae and the Hydrocharitaceae, and maybe more. However, in contrast to freshwater and land plants, there are relatively few genera (ca. 12) and these are very diverse, indicating that seagrasses have had a multi-pronged origin. Furthermore, when it is realized that many of these genera have species, which grow in estuaries and coastal lagoons alongside other hydrophytes, the real difficulty in defining seagrasses becomes apparent. Should one include the Ruppiaceae in the list of seagrasses and, if one does, why exclude certain members of the Zanichelliaceae? These arguments are set out in Chapter 1 and 2; yet surprisingly questions remain. Suffice it to say that up to the present time a pragmatic assessment has been made by the seagrass community that seagrasses are those flowering plants that occur in estuaries or on continental sea margins – and *Ruppia* and *Zanichella* species are only allowed in under sufferance, as these can complete their life cycles outside marine waters.

And this discussion begs the question as to the definition of a seagrass? This again is a contentious question. Apart from the systematic questions posed in Chapters 1 and 2, there is the question of what morphological characteristics do seagrasses possess in common. As discussed in Chapter 3, it can be seen that most of the individual characteristics of seagrasses are possessed by other hydrophytes. Not even the ability to live in increased salinity is a unique feature of seagrasses. Certainly they all possess the ability to pollinate underwater and most reproduce underwater. Most are adapted to the wave-prone environment of the sea, with tough linear leaves and an underground rhizome system, but the widely distributed genus *Halophila* is an exception here. The characteristics most often cited as unique to seagrasses are as follows:

- Live in an estuarine or marine environment, and nowhere else.
- Pollinate underwater with specialized pollen.
- Produce seeds underwater which can be dispersed by both biotic and abiotic agents .

- Have specialized leaves with a very reduced cuticle and an epidermis which lacks stomata and is the main photosynthetic tissue.
- Have a rhizome or underground stem which is important in anchoring.
- Have roots that can live in an anoxic environment and are dependent on oxygen transport from the leaves and rhizome but are also important in the nutrient transfer processes.

The importance of seagrasses as it emerged over the last quarter of the 20th Century is in their key role on the shallow seaward margins of our continents. Seagrasses are now considered one of the important ‘ecosystem engineers’ (see Chapter 6) given their ability to change significantly numerous aspects of their environment. Their importance here is summarized in a set of axioms, which have become familiar to planners and conservationists, now often referred to as ‘ecosystem services’ (Costanza et al., 1997):

- Seagrasses are important primary producers, that is they convert sunlight and carbon dioxide efficiently into organic form;
- Seagrasses supply organic food to a variety of dependent food webs;
- Seagrasses stabilize the seabed in which they grow;
- Seagrasses structure the seabed on which they grow into a complex environment which provides places for many organisms to exist;
- Seagrasses act as the nursery ground for many commercially-caught species.

Are these axioms correct or are they “feel good” sayings that have been used to encourage the workers in the field. One of the recommendations to authors of chapters of this book was to challenge the current paradigms, and therefore the reader will find this reflected in many chapters. For example, the axiom that “seagrass ecosystems are driven by detritus” is challenged in Chapter 7 (Mateo et al.) where it is shown that production from epiphytic algae and benthic algae may well exceed that from the detrital production system of seagrasses.

Another area where science has made great progress is seagrass genetic structure. This is reflected in work on seagrasses and Chapter 2 (Waycott et al.) surveys the current status of seagrasses from this stand point. The result is a fresh approach to the taxonomy and systematizing of seagrasses. The

reader will find that several important changes are recommended here; and in some cases a species or even a genus (*Heterozostera*) has disappeared (and at higher levels important changes are recommended). These changes have not at this time been accepted by many taxonomists. This is reflected in the stance of Chapter 1 (den Hartog and Kuo). It will be many years before many of these differences are resolved. As both approaches have their shortcomings, there has been no attempt in this book to be prescriptive: where differences do occur the reader is advised of the different approaches and is left to make up her/his mind on the subject.

Seagrasses are, *par excellence*, the plants that evolved hydrophilous pollination but only recently has a mechanistic approach been undertaken. Ackerman (Chapter 4) reviews the nature of pollination mechanisms and the unique adaptations these plants have evolved to insure successful pollination. And with successful pollination emerges the production of a seed, the unifying theme in all angiosperm species. Yet little is known about seeds, seed ecology and seed dispersal processes in seagrasses. Orth et al., (Chapter 5) review the scant but growing body of literature for seagrasses but more importantly, attempt to integrate emerging issues in the terrestrial realm and their applicability to seagrasses.

Seagrasses influence numerous processes and these are highlighted in a number of excellent chapters. Marba et al. (Chapter 6) review the role of seagrass beds on coastal biogeochemistry, by first examining their effect on particulate and dissolved materials (i.e. organic matter, dissolved inorganic carbon, carbonates, gases) in the water column and sediments of coastal areas, and (2) by examining the processes involved in mineralization of organic matter and nutrient cycling in sediments colonised by seagrasses. Mateo et al. (Chapter 7) describe carbon fluxes in seagrass ecosystems. Koch et al. (Chapter 8) examine hydrodynamics at scales ranging from molecules to ecosystems. Romero et al. (Chapter 9) highlight nutrient dynamics. Borum et al. (Chapter 10) review current status of knowledge with respect to oxygen production, consumption and transport within seagrasses, and briefly discuss the potential coupling between seagrass oxygen dynamics and the occurrence of die-off events in seagrass beds. And finally, Duarte et al. (Chapter 11) address processes and mechanisms responsible for the dynamics of seagrass meadows.

Light and photosynthesis and their measurement are dominant themes from the earliest papers in seagrass ecology. Yet this field has been rapidly evolving with the development of new tools leading to new discoveries about light and its measurement and the basis of light capture and the photosynthetic mechanisms. A series of chapters allow for the reader to follow in progression the science of light penetration into marine waters (Zimmerman and Dekker, Chapter 12), the influence of seagrasses on light absorption and light reflection in shallow communities (Zimmerman, Chapter 13), the emerging role of remote sensing in seagrasses (Dekker et al., Chapter 15), and finally the importance of photosynthesis and the photosynthetic mechanisms of seagrasses (Larkum et al., Chapter 14).

Faunal and floral studies were also an important component in the early work by Japanese, American and European scientists and coincided with the many attempts to define community. This was followed by experimental work on the important interactions between plants and the many animals reported from seagrass beds. Borowitzka et al. (Chapter 19) review the literature on epiphyte diversity and abundance. Valentine and Duffy (Chapter 20) provide an important synthesis of the grazing world, both macro and meso-grazers, and their important direct and indirect interactions at varying spatial scales. Gillanders (Chapter 21) explores the latest developments in fisheries utilization, including new techniques for assessing habitat linkages (e.g. otolith chemistry) and how important seagrass beds are to fish production. Finally Heck and Orth (Chapter 22) succinctly summarize the previous generalizations that continue to be supported by recent work, and then focus attention on results that challenge the conventional wisdom on predator-prey interactions in seagrass meadows.

Research in the 1970's in Europe, United States and Australia showed the devastating negative influence of anthropogenic factors on seagrass distribution and abundance. Loss of seagrasses has continued at an alarming pace as human habitation of the coastal zone rapidly expands. Walker et al. (Chapter 23) detail aspects of more recent research demonstrating changes, both negative and positive, in seagrass distributions, as revealed by mapping and other detailed investigations. Ralph et al. (Chapter 24) provide an overview of the current understanding of how anthropogenic contaminants impact seagrasses, the ecophysiological responses of seagrasses and finally

describe how modeling can be used to manage contaminant loads (specifically nutrients) in the process of seagrass recovery. Kenworthy et al. (Chapter 25) examine the current state of seagrass science within the viewpoint of conservation biology, discussing areas where seagrass science is developing a conservation biology approach, identifying priority research topics for conservation science in the future, citing examples where science and conservation biology are being applied in the seagrass biome, and finally recommending a course of action based on the principles of conservation biology to reverse the global trend of fragmentation, local extinction, and general degradation of the seagrass biome. Finally, Bell et al. (Chapter 26) bring into focus a new approach to studying seagrasses in relation to the entire landscape, by first providing a brief review of concepts and techniques associated with a landscape approach, then evaluating how information collected from studies in seagrass systems compares to that from analogous terrestrial systems/landscapes. Finally, they discuss some potential areas of future research in the field of seagrass landscape ecology, recommending conceptual and methodological improvements.

Last, a significant amount of research has been conducted on three genera, *Thalassia*, *Posidonia* and *Zostera*, which together account for much of the world's seagrass meadows. Three knowledgeable

groups of scientists have attempted to synthesize the important aspects of significant research on these three genera with the hope that research in the other nine genera will follow suit.

The science of seagrasses has made tremendous strides in the last two decades but much remains ahead. We hope the chapters in this book both provide the necessary background on what brought each topic to where it is today and indicate where future research needs to go to advance the field to the next level. If we have accomplished that, then we, as editors, will feel we have done our job in this book.

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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 **Ruppiales** (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 stenobiotic 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 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 actinomorphic, 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 *rbcL* (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 spathe 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 spathe 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, *rbcL*) 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 *matK* 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. Regrettably, 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 *matK* 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. iwataensis* 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 quadrilobular, 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 complicated. 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 as 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 is 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. ostensfeldii* 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 actinomorphic 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 spathe 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 pro-

truding 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 *rbcL* gene sequence. Independent molecular research by Tanaka et al. (1997) using the *rbcL* 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 *rbcL* 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. hawaiiiana*. 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. hawaiiiana* 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