

2. Aquatic plant communities of poikilosaline waters

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The euryhaline plant group

In 1920, Arber formulated a set of four properties indispensable for a marine water plant. These properties are: (1), adaptation to life in a saline medium; (2), ability to grow when fully submerged; (3), possession of a secure anchoring system; and (4), hydrophilous pollination. In his monograph of the seagrasses of the world, den Hartog (1970) stated that this set of properties is insufficient for the delimitation of these marine angiosperms, because there is a second group of species which shares these properties with the seagrasses. This second group, which is here referred to as the euryhaline group, consists of a number of aquatic plant species occurring in various fresh waters, mixo- and hyperhaline brackish waters, and in continental waters of very different chemical composition and concentration. These plants can tolerate considerable fluctuations in the salt content, and their salinity range of occurrence is very wide in comparison to that of seagrasses (Bourn, 1935; St. John & Courtney, 1924; Davis & Tomlinson, 1974). These plants are also in other respects very tolerant, particularly to high temperatures. Their absence from the marine environment is striking; only under very special conditions one can find representatives of this euryhaline group in the sea. Probably this may be ascribed to the basic rule in ecology that a wide tolerance with regard to environmental fluctuations is coupled with a reduced capacity to compete with more stenobiotic taxa in more or less stable habitats (men being the only exception to this rule) (See Dahl 1956; den Hartog 1967).

From a taxonomic point of view the euryhaline

Table 2.1 Taxonomic composition of the euryhaline group of the Potamogetonaceae.

Subfamily	Genus
Ruppioideae	<i>Ruppia</i>
Zannichellioideae	<i>Zannichellia</i> <i>Althenia</i> <i>Pseudalthenia</i> <i>Lepilaena</i>
Potamogetonoideae	<i>Potamogeton</i> subgen. <i>Coleogeton</i>

group is rather restricted; all representatives belong to the family of the Potamogetonaceae *s.l.* Two subfamilies are completely confined to poikilosaline habitats, and in a third subfamily only a subgenus is involved. In fact, the whole group consists of 5 genera and 1 subgenus (Table 2.1). At the species level there are still many uncertainties and a reliable estimation of the number of species is not yet possible.

A review of the genera

1. *Ruppia*

The genus *Ruppia* is almost cosmopolitan in brackish and continental salt waters; there is even a number of freshwater records of this genus.

The taxonomy of the genus at the species level is still poorly understood, in spite of various local or more general monographic treatments (Ascherson & Graebner 1907, 1913; Fernald & Wiegand 1914; Setchell 1946; Luther 1947; Reese 1962, 1963;

Mason 1967; Gamberro 1968; den Hartog 1971).

For a long time it has been generally accepted that the genus was monotypic, i.e. consisting of one very variable species. Many taxa have been described at the variety level. Nowadays it appears that there are at least 7 species, but due to the wide variety of biotopes they occupy, geno- and phenotypic variation can only be separated by culture of the plants under controlled conditions. From an extensive study of herbarium material, it is now clear that there is one worldwide distributed species, *Ruppia maritima* L., characterized by the possession of a short peduncle. The other taxa, which possess long, spirally coiled or straight peduncles, are restricted to the temperate zone; some of them have been found in the tropics, but only at high altitudes.

2. *Zannichellia*

The genus *Zannichellia* is almost cosmopolitan, but was originally absent from Australia. Although some records of the genus in high salinity waters are known, its representatives occur generally in low salinity waters, up to 6‰ Cl', and some are characteristic of unstable freshwater habitats.

The taxonomy of *Zannichellia* suffers even more from old ideas than that of *Ruppia*, because even now the genus is considered to be monotypic (Ascherson & Graebner 1907, 1913; Reese 1963, 1967). Recent studies on European material, however, have shown that a number of taxa can be recognized on the basis of morphological, physiological and cytological characteristics (Luther 1947; Reese 1963, 1967; W. van Vierssen, personal communication). In Europe at least 4 taxa can be recognized, and it is by no means certain that the Asian, African and American representatives of *Zannichellia* are identical with these.

3. *Pseudalthenia*

The genus *Pseudalthenia*, also known as *Vleisia* (Tomlinson & Posluszny 1976; den Hartog 1980), accommodates only one species, *P. aschersoniana* (Graebner) den Hartog. It is restricted to the south-western point of Africa, where it inhabits so-called 'vleis', i.e. temporary estuarine lagoons (Reinecke 1964).

4. *Althenia*

The genus *Althenia* is monotypic, as far as is known today. Originally the genus was thought to be restricted to the western mediterranean coastal lagoons (Onnis 1967), but in the last 15 years records have been published from Iran (Dandy 1971), Turkey (den Hartog 1975), southern Russia and Central Asia up to the foothills of the Altai Mountains (Tvelev 1975), and South Africa (Obermeyer 1966). The genus has been found in typical brackish-water situations, but the occurrence in Central Asia and Iran is probably not confined to relic brackish waters (den Hartog 1974); it may also concern continental salt waters.

5. *Lepilaena*

The genus *Lepilaena* consists of at least 4 species (Willis, 1970; Aston, 1973), and is restricted in its distribution to temperate Australia and Tasmania. One of the species, *L. bilocularis* Kirk ex Petrie, occurs also in New Zealand (Moore & Edgar 1970). The species inhabit a wide range of brackish and athalassic habitats; some occur also under freshwater conditions, usually in temporary bodies of water, and there are also records of marine occurrence. This genus needs further taxonomic investigation. The chromosome number of *L. bilocularis* plants from New Zealand (Hair, Beuzenberg & Person 1967) appears to be different from those of a Victorian collection of this species (den Hartog, unpublished).

6. *Potamogeton*

The genus *Potamogeton* consists of two subgenera, one of which is strictly confined to fresh waters, where it reaches a great differentiation at the species level (Ascherson & Graebner 1907, 1913; Hagström 1916). The other subgenus, *Coleogeton*, is small, and consists of 5, but possibly more, species. One of these species, *Potamogeton pectinatus* L., has a worldwide distribution, and occurs in brackish, as well as continental salt waters, although not usually at salinities higher than 10‰ Cl', and also in unstable freshwater habitats, even in very oligotrophic soft waters. Two other species, *P. filiformis* Pers. and *P. vaginatus* Turcz., are more restricted in their geographical distribution; they

occur only in the boreal areas of the northern hemisphere. They share with *P. pectinatus*, however, the property that they inhabit extreme or physically unstable habitats. Nothing is known about the ecology of the other species.

Taxonomy at the species level

The lack of knowledge of the taxonomy at the species level is mainly due to the following factors:

- a. Great morphological variability of the plants, ascribed to the variability of environmental factors, under which the plants occur. Geno- and phenotypic variation were not distinguished.
- b. Uncritical study of herbarium material. Descriptions of taxa were often based on incomplete or immature material (e.g. unripe fruits). Several very useful characteristics were not recognized in the past.
- c. No studies of living plants were carried out.
- d. Local development of taxonomy, often without consultation and study of material from elsewhere, causing nomenclatural confusion.

At present it is possible to recognize taxa also on other than morphological characteristics, by using chromosome numbers, biometrical and statistical data, biochemical 'finger printing', etc. Culturing plants under controlled conditions may lead to a better understanding of the causes of the variability, and to better definitions of the taxa. In order to finalize the taxonomic status of the representatives of the eurysaline group, such studies are strongly recommended.

Common characteristics

The close taxonomic affinity of the various members of the eurysaline group, leads also to the recognition of a number of shared characteristics. All species are typical parvopotamids, i.e. they possess a creeping rhizome that usually is sympodial, but sometimes monopodial (*Ruppia*). The upright shoots are caulescent. The leaves are linear and usually distichously arranged, sometimes decussate and rarely verticillate. Due to the structure of the rhizome, all species are potential peren-

nials, but, as a consequence of the harsh ecological conditions to which they are exposed in their natural environment, most of the species, especially the finer ones, behave as annuals, and even show a tendency toward rhizome reduction.

The flowering shoots are always sympodial, except in the case of *Pseudalthenia* (under the name *Vleisia*) which produces a monopodial flowering shoot, the flowering branches themselves being sympodia (Posluszny & Tomlinson 1977). From a morphological point of view this genus forms a link to *Najas*, which is monopodial, but in a number of other characteristics rather similar to the Zannichellioideae.

The flowers are inconspicuous and very reduced. Pollination is hydrophilous, i.e. completely submerged or so-called semi-aquatic surface pollination takes place. In the latter case, pollen floats on the surface and the gynoecia are at least partially in contact with the surface. The latter mechanism is characteristic of *Potamogeton* sect. *Coleogeton* (with oblong pollen) and *Ruppia* (with boomerang-shaped or oblong pollen). *Lepilaena australis* Drumm. ex Harv. and *L. cylindrocarpa* (Koernicke ex Walp.) Benth. form a special case; in these species the male flowers, which are no more than the anthers, break off, rise to the surface, and release their spherical pollen which then sink and may be caught by the style of a female flower. In the Zannichellioideae the styles are long, while in *Ruppia* and *Potamogeton* sect. *Coleogeton* the styles are extremely reduced.

The fruits are sessile and arranged in small groups; in *Potamogeton* subgen. *Coleogeton* they occur more or less verticillate around the flowering axis. The development of a podogyne, which is in fact a part of the fruit in *Ruppia*, is well known; in the genus *Lepilaena* one species extends its pedicels after flowering; the infructescence obtains in this way a *Ruppia*-like aspect.

Phytosociological considerations

The plant communities in brackish and saline continental waters are mainly composed of representatives of the eurysaline group of aquatic plants. However, other plants may also take part in these communities. Eurysaline species of true freshwater

genera may intrude to some extent into the low salinity waters, and may even be quantitatively important, depending on environmental conditions, particularly salinity fluctuations. In Europe, the following species can be found together with representatives of the eurysaline group: *Myriophyllum spicatum* L., *Ranunculus baudotii* Godr., *Najas marina* L., *Vallisneria spiralis* L. and *Potamogeton pusillus* L. These species are usually local in their occurrence. In the other continents several other freshwater species show a similar behaviour.

In transitional areas with the sea, euryhaline seagrasses may also intrude into waters with a lower salinity; this concerns species of the genus *Zostera* in the temperate belt of the earth, while in the subtropics *Halodule* and *Cymodocea* species may coexist with species of the poikilosaline group. They may form mixed stands, but often the species form separate beds (den Hartog 1977).

However, the hard core of the plant communities in brackish and athalassic salt waters is formed by the representatives of the poikilosaline group. The only other plants which form an integrated component of these communities are various species of Charophyta. This algal class has developed a number of species with eurysaline character, e.g. *Lamprothamnium papulosum* (Wallr.) J. Ag. and *Chara canescens* Desv. & Lois. in Lois.

J. Tüxen (1960) has erected for these plant communities a special phytosociological class, the *Ruppieteae*. In the original version of this class, a very heterogeneous set of communities was accommodated because J. Tüxen meant it to contain all aquatic plant communities of the Baltic area, and did not consider their structure or life form. The idea that there is a group of plants with maximum development in neither fresh waters nor the sea was generally accepted. Therefore, den Hartog & Segal (1964) redefined the class in a more restricted sense.

Up to now one order, the *Ruppietalia*, has been described within the class, and only one alliance, the *Ruppion maritimae* Braun-Blanquet 1931. On the grounds of data on geographical distribution of the genera and species, a further differentiation can now be proposed. The plant communities of the class *Ruppieteae* have their optimum development in the warm temperate areas of both hemispheres. Towards the poles the number of taxa decreases, and in the tropics the whole class is only represented by one species, *Ruppia maritima* L. s.s. In the

tropics, other species of the eurysaline group occur only in waters at very high altitude. In the warm-temperate areas, however, diversity is higher, and the composition of the communities varies from continent to continent. The communities in the Americas and eastern Asia have the poorest development, as here only *Ruppia*, *Zannichellia* and *Potamogeton* subgen. *Coleogeton* are involved. The most common taxon is a *Ruppia* with a long, but nonspiraling peduncle, preliminary identified as *R. maritima* var. *longipes* Hagström, which seems intermediate between *R. cirrhosa* (Petagna) Grande and *R. maritima* s.s., and possibly is of hybrid origin. There are two endemic *Ruppia* species: *R. occidentalis* Watson in athalassic lakes in West Canada and the northwestern part of the U.S.A., and *R. filifolia* (Phil.) Skottsberg in the Andean chain, extending from Chile to Mexico. The taxa of *Zannichellia* have not been studied yet, but might be partially endemic.

In Europe, west and central Asia, mediterranean Africa and South Africa, the poikilosaline communities show striking similarities. The dominant *Ruppia* taxa are *R. maritima* and *R. cirrhosa*. Although *R. maritima* var. *longipes* has been described from Buchara (Hagström 1911), it has been very rarely found in the area under consideration. The genus *Althenia* occurs in the whole area, with the exception of the northern part of Europe, reaching its northernmost stations in southern Brittany. The genus *Zannichellia* is widely spread through the whole area; the distribution of taxa is however insufficiently known. In South Africa the genus *Pseudalthenia* has only been found in the immediate surroundings of the Cape Peninsula, and must be considered endemic.

Temperate Australia takes a very special position, because in the eurysaline communities two genera are represented with endemic species, viz. *Lepilaena* with 4 species and *Ruppia* with *R. maritima* s.s. and at least 3 endemic species. The genus *Zannichellia* has been recorded as an immigrant of the River Murray system (Willis 1970), and needs reinvestigation. In New Zealand, these communities occur in an impoverished form, with 2 *Ruppia* species and one *Lepilaena* (Moore & Edgar 1970). On the ground of these floristic differences, one can recognize three alliances, one for the American and East Asian communities, one for the Eurasian – African communities and one for the

communities of Australia and New Zealand. The two first-mentioned alliances have a number of species in common, but the latter alliance is from a floristic point of view of a much higher independence, and for this reason it can be accommodated in a separate order.

This results in the following hierarchical classification:

Class RUPPIETEA (J. Tüxen 1960) emend. den Hartog & Segal 1964.

Aquatic communities, poor in species, consisting of simple structured, monospecific or mixed beds of parvopotamid angiosperms, often together with Charophyta; in permanent or temporary, poikilohaline salt waters along the coast (brackish waters) as well as in continental salt waters, where the principal salts are sodium chloride, gypsum or magnesium sulphate; all over the world.

Character taxa: *Ruppia maritima* var. *maritima*, *Tetramyxa parasitica* Goebel (a plasmodiophorous parasite); *Potamogeton pectinatus* (shared with the class Potametea), *Lamprothamnium papulosum* (shared with Charetea).

The class comprises two orders with very similar structure, but with almost completely different floristic composition.

Order A: *Ruppialia* (J. Tüxen 1960) emend. den Hartog.

Character taxon: *Ruppia cirrhosa*, *R. maritima* var. *longipes*, *R. maritima* var. *brevirostris* (Agardh) Aschers. & Graebn.; *Zannichellia palustris* L. s.l.

This order comprises two geographically separated alliances.

Alliance 1: *Ruppion americanae* all. nov.

Character taxa: *Ruppia filifolia*, *R. occidentalis*.
Dominant taxon: *Ruppia maritima* var. *longipes*.

Widely distributed throughout the Americas.

On the ground of the dominance of *R. maritima* var. *longipes* in East Asian brackish waters, the communities of that area have to be preliminarily classified within this alliance. The Japanese species *Ruppia truncatifolia* Miki is insufficiently known.

Alliance 2: *Althenio-Ruppion* all. nov.*

Character taxon: *Althenia filiformis*.

Dominant taxon; *Ruppia cirrhosa*.

Widely distributed in Europe, West and Central Asia, and mediterranean Africa; a second area in South Africa, where *Pseudalthenia aschersoniana* can be considered an additional character taxon.

Order B: *Lepilaeno-Ruppialia* ord. nov.

Character taxa: *Ruppia megacarpa* Mason, *R. polycarpa* Mason, *R. tuberosa* Davis & Tomlinson, *Lepilaena bilocularis*, *L. australis*, *L. cylindrocarpa*, *L. preissii* (Lehm.) F. v. M.

This order is represented with one alliance in temperate Australia and in a somewhat impoverished state in New Zealand.

Alliance 3: *Lepilaeno-Ruppion*. all. nov.

With the characters of the order.

The monospecific communities in the tropics cannot be classified within one of the three described alliances, although they undeniably belong to the Ruppiaetea.

The various associations to be classified within the alliances cannot be dealt with here. They are the local units which vary from area to area. For Western Europe they have been described by Verhoeven (1980a).

Although the Ruppiaetea form a closely knit group of communities, it has to be stated here that the transition to freshwater communities is often gradual, particularly in gradient situations, because species such as *Potamogeton pectinatus* also play an important part in a number of communities characterized by the coexistence of parvopotamids, elodeids and myriophyllids in stagnant and running, shallow waters.

* The name *Ruppion maritimae*, first applied by Braun-Blanquet in 1931 and commonly used in phytosociological literature, can no longer be maintained. In the first place, opinion on the name-giving species *Ruppia maritima* has changed considerably, and in the second place the epitheton cannot even be maintained as an ecological indication, because communities of this alliance occur in brackish and athalassic waters. Verhoeven (1980a p. 12) proposed to use the name *Ruppion*, without any further indication. As, however, the name *Ruppion*, with or without epitheton, has always been regarded as a syntaxon of cosmopolitan distribution, it seems better to abandon the name completely, since three geographically separated alliances can be recognized.

The bipolar distributional pattern

It is striking that several species of the eurysaline group have an area of distribution split into a northern temperate and a southern temperate part, and are absent in the tropics. In the Americas, the Andean chain is an obvious link between the two areas, but between Eurasia and South Africa such a link does not exist. This remarkable distribution pattern is obviously of considerable geological age. The close relationship between the genera *Althenia* and *Lepilaena* points to a common ancestry; possibly this ancestor had a coherent distribution in brackish lagoons along the Tethys. Compare in this context of the area of the seagrass genus *Posidonia*, with several species in temperate Australia and one in the Mediterranean (den Hartog 1970).

Another hypothesis, which does not necessarily exclude the one just given, may be dispersal by birds. It is well-known that coots, swans and ducks (e.g. wigeon) feed extensively on the poikilosaline plants (Verhoeven 1978, 1980b), and may be agents of distribution. Flamingoes too are known to consume the fruits of *Ruppia* (McCann 1949). The present migration routes, as described by Moreau (1972), McClure (1974) and Dorst (1961), clearly connect the areas covered by the alliances described above, and show the isolation of temperate Australia and New Zealand in this respect. However, when the most-likely carrier species are considered, the evidence is insufficient. Migration of coots and flamingoes is insignificant, and swans and ducks do not migrate far to the south. The European wigeon reaches East Africa but does not cross the equator. According to their migration patterns, some waders, sand pipers and plovers appear to be more likely carriers, and they have moreover occasionally been observed feeding on *Ruppia* seeds washed ashore along ponds and lagoons. However, these seeds have not been recorded from stomach contents. According to Dorst (1961), migrating birds clean themselves thoroughly before they take to flight, and they fly with empty stomachs. The chance that seeds are transported by them is small, but not completely excluded.

It has to be borne in mind, however, that the present bird migration routes depend on present day geographical features, and that such features have changed during the geological history under the influence of orogenesis, glaciation and desertification.

Another point that needs clarification is the scarcity of representatives of the eurysaline group in the tropics. Possibly this may be explained by the ephemeral character of brackish or saline conditions in the tropics. In coastal lagoons subjected to a monsoon climate, marine communities are replaced by freshwater communities in a seasonal rhythm paralleling the dry and wet seasons; time is too short for the development of brackish water communities in the transitional periods. When marine waters become isolated they become either desalinated by extensive rainfall and turn rapidly into freshwater marshes, or hypersaline. The sparse records of *Ruppia maritima* in the tropics are all from hypersaline stations.

Future research

A classification of plant communities, be it local or on a mondial level, can never be a goal in itself. It can only serve as a first descriptive approach to the real goal, i.e. the knowledge of structure and function, and in fact the functioning of integrated ecosystems. Therefore, the fauna has also to be included in future studies, and the interrelations between all organisms within the biocoenoses have to be taken into account. When the fauna is considered, it will appear that from a taxonomical point of view the communities in the various brackish and athalassic waters of the world show considerably less similarity than do the plant communities which may be regarded as the frame of the biocoenosis. However, due to convergence of morphological characteristics of the participating taxa as a response to the special ecological conditions in poikilosaline environments, it may be expected also that the faunal component will show a considerable biological similarity. The study of the biological parallelism in the composition of the biotic part of the ecosystem must, therefore, be the next step towards understanding. On the basis of the parallelism in life forms, an idealized model can be constructed of the basic ecosystem, free of interference from all kinds of local peculiarities and disturbances. The biotic communities of poikilosaline waters are of a relatively simple architecture. Therefore, it should be possible to reach this goal with joint effort within a reasonable time.

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