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THE SEA-GRASSES OF THE WORLD

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ORIGIN, EVOLUTION AND GEOGRAPHICAL DISTRIBUTION OF THE SEA-GRASSES

Although this paper is primarily meant to be a taxonomic treatment of the marine Angiosperms, some other aspects will be discussed, such as the requirements for life in the sea and the origin, fossil record and geographical distribution of these plants. For the ecological aspects I want to refer to my earlier paper (DEN HARTOG, 1967) on the ecology of sea-grass communities in which growth-forms, zonation and succession of the sea-grasses as well as the structure and function of their ecosystem were discussed.

a. Requirements for life in the sea.

According to ARBER (1920) there are four properties which are indispensable for a marine water plant. In the first place, it must be adapted to life in a saline medium. Secondly, it must be able to grow when completely submerged. Thirdly, it must have at its disposal an anchoring system which is sufficiently developed to withstand wave action and tidal currents. Finally, it must have the capacity for hydrophilous pollination, since "any aerial method must be doomed to failure, except in halcyon weather in a non-tidal sea". In other words, the plants must be able to achieve their vegetative as well as their generative cycle in a saline medium, while completely submerged, and must be securely anchored in the substratum or be attached to the substratum. It is obvious that sea-grasses possess the first two properties. Furthermore, they possess more or less strong rhizomes and show a tendency for gregarious growth; this fulfills the third requirement. Finally, all sea-grasses satisfy the fourth requirement, as they are well-equipped for hydrophilous pollination.

Entirely submerged pollination takes place in most genera. Adaptations to this type of pollination are the long styles of *Halophila* and *Halodule*, the long stigmata of *Cymodocea*, *Syringodium*, *Amphibolis* and *Thalassodendron*, the elongate hypanthia of *Thalassia* and *Halophila*, and the disc-shaped, lobate or laciniate stigma of *Posidonia*. Moreover, the confervoid shape of the pollen-grains of all marine representatives of the *Potamogetonaceae* may be regarded as an adaptation increasing their floating capacity. The Hydrocharitaceous *Halophila* and *Thalassia* have spherical pollen-grains, but as these are arranged in coherent, moniliform chains a similar result is reached.

Semi-aquatic surface pollination, whereby the pollen drifts on the water surface and the styles are at least partially in contact with the water surface, has been recorded for *Phyllospadix* and *Zostera*, although entirely submerged pollination occurs just as often in these genera.

Among the marine Angiosperms *Enhalus acoroides* is the only species which shows aerial surface pollination. Hereby the pollen as well as the styles remain dry. The species is further peculiar in having large globular pollen-grains and by the fact that its male flowers break off in the spathe and rise to the surface, where they have a short but independent existence. The latter feature is also known from some other *Hydrocharitaceae*, e.g. *Vallisneria* species and *Elodea nuttallii* (Planch.) St John, and is also shown by *Lepilaena australis* Drummond ex Harv. in Hook., a representative of the *Potamogetonaceae*. The flowering biology of *Enhalus* is completely adapted to the tidal cycle.

Most sea-grasses are dioecious and those which are monoecious show proterogyny (*Zostera*, *Heterozostera*, *Halophila decipiens*). Thus cross-fertilization is a rule.

Although all sea-grasses satisfy the 4 criteria of Arber, there are a few other taxa which also fulfill these conditions, viz. *Zannichellia*, *Lepilaena*, *Althenia*, *Ruppia* and *Potamogeton* subgen. *Colcogeton* (with *P. pectinatus* L.), all of which are representatives of the *Potamogetonaceae*. The range of salinity which they can tolerate is even greater than that of the sea-grasses, as they are to be found in fresh water, in mixohaline and hyperhaline brackish waters and in continental salt waters. As far as the chemical composition of the salt water is concerned they are not quite so restricted as the sea-grasses. *Ruppia*, for example, occurs not only in waters where NaCl is the dominant salt but also in waters where Na₂SO₄, MgSO₄ or CaSO₄ dominate. *Zannichellia* and *Potamogeton pectinatus* have been recorded from waters where Na₂CO₃ is the dominant salt. Furthermore, all these taxa can tolerate very sudden and very large fluctuations in the salt content. From an ecological point of view they are in fact ubiquitous. These extremely euryhaline taxa, nevertheless, seldom penetrate into the purely marine environment, although their salt tolerance certainly does not prevent them from doing so. They sometimes occur together with the most euryhaline sea-grasses in brackish waters, such as estuaries and lagoons, but are generally restricted to poikilohaline waters.

The fact that these taxa, in spite of their enormous tolerance with respect to salinity, are apparently unable to inhabit the marine environment permanently must be ascribed to a low competition capacity. It is probably a basic rule in ecology that a wide tolerance with regard to environmental fluctuations is coupled with a reduced capacity to compete with more stenobiontic taxa in more or less stable habitats.

b. Origin of the marine Angiosperms

In her discussion of the requirements which have to be fulfilled by plants in order to be able to thrive in the marine environment, ARBER (1920) followed the then prevailing opinion that the marine Angiosperms had penetrated the sea from the fresh water. This opinion is still held by some authors (SCULTHORPE, 1967). It is based on the following facts:

1. Both the *Potamogetonaceae* and the *Hydrocharitaceae* are typical water-plant families, and are widely distributed in fresh water. 2. Not a single marine Angiosperm is closely related to a terrestrial plant.

These facts indicate, according to Arber, that the sea-grasses have evolved from ancestors which were already adapted to life in the water. She even suggested that the transition from fresh water to sea water may have been bridged in the following sequence: fresh-water species → salt-tolerant fresh-water species → brackish-water species → marine species. The *Potamogetonaceae* and *Hydrocharitaceae* are supposed by her to have passed through all the stages of this series, while other families, e.g. the *Ceratophyllaceae*, the *Callitrichaceae*, the *Naiadaceae*, the *Ranunculaceae* and the *Halorrhagidaceae* did not go further than producing a few salt-tolerant fresh-water species. Arber concluded her essay with the following optimistic expectation: "Conceivably in future ages, if the evolution of fresh-water plants proceeds on its present lines, a greater number may reach the specialised stage of hydrophilous pollination, and some of these may colonise the sea, thus democratising the narrow and exclusive circle of the marine Angiosperms."

My own ideas about the origin of the marine Angiosperms are diametrically opposed to the above opinion. Although it is tempting to regard the small group of the sea-grasses as a side-track in the development of the large group of fresh-water plants, there are several arguments which can be put forward to prove just the opposite. The fact that the *Potamogetonaceae* and the *Hydrocharitaceae* are mainly distributed in fresh water may be true at species level; however, a completely different picture arises when one considers the distribution of the subfamilies belonging to these families. The family of the *Potamogetonaceae* is rather heterogeneous and can be subdivided into 6 subfamilies. Three of these, the *Zosteroideae*, the *Posidonioideae* and the *Cymodoceoideae* with together 9 genera, are completely marine. The *Zannichellioidae* with 3 genera and the *Ruppioideae* with 1 genus are salt-tolerant to a high degree, but are unable to thrive permanently under marine conditions. The *Potamogetonoideae* with 2 genera are restricted to fresh water, with the exception of *Potamogeton* subgen. *Coleogeton*, which has an ecological range similar to that of the *Zannichellioidae* and *Ruppioideae*.

The family of the *Hydrocharitaceae* consists of 3 subfamilies of which the *Thalassioideae* and the *Halophiloideae*, both with one genus, are completely marine. Of the 13 genera of the subfamily *Vallisnerioideae* only one genus, *Enhalus*, is marine; the other twelve are undisputedly fresh-water genera with an occasional salt-tolerant representative.

Another argument can be advanced from the fossil records. Fossil remains, referred to as sea-grasses, have been described in the works of BRONGNIART (1828, 1849), BUREAU (1886), SAPORTA & MARION (1878), UNGER (1847, 1851), WATELET (1866), etc., mainly under the names *Zostrites* and *Caulinites*. They are listed for the greater part in Ascherson's

monograph of the *Potamogetonaceae* (1907, p. 33, 39, 151). SCHENK (in ZITTEL, 1890, p. 379) rightly remarked with respect to the fossils described as *Naiadaceae* and *Potamogetonaceae* that these families are "in demselben Verhältniss reich an Arten, als diese fraglich sind, sowohl hinsichtlich ihres Werthes als Arten, wie ihres Werthes als Glieder der Gruppe." While admitting that a part of the material had been correctly identified, he remarked that many of the fossil remains are too fragmentary or too badly preserved to allow even their recognition as monocotyledons. He suggested the possibility that some remains described as pine-needles or as *Poacites* could just as well be remains of *Naiadaceae* or *Potamogetonaceae*.

Fortunately this uncertainty does not apply to all fossil sea-grass material. There is sufficient fossil evidence for stating that sea-grasses were already developed at an early stage in the history of the Angiosperms.

Thanks to the later studies of FRITEL (1910, 1914), L. & J. LAURENT (1926) and STOCKMANS (1932) it can now be considered certain that at least three sea-grasses occurred in the Basin of Paris during the Eocene, viz. 1. *Posidonia parisiensis* (Brongt.) Fritel (= *Caulinites parisiensis* Brongt. = *Posidonia perforata* Saporta & Marion). 2. *Cymodocea serrulata* (R.Br.) Aschers. & Magnus (= *Corallinites micheloti* Watelet = *Cymodocea micheloti* Laurent), and 3. *Cymodocea nodosa* (Ueria) Aschers. fossilis (Brongt.) Laurent (= *Culmites nodosus* Brongt. = *Caulinites nodosus* Unger = *Zosterites marinus* Unger = *Cymodoceites nodosus* Fritel).

Cymodocea nodosa has also been recorded from Pliocene and Quaternary layers in Emilia, Italy; here even the fruits were found (RUGGIERI, 1952). Beautifully preserved fossils of *Cymodocea serrulata* have been described and illustrated by L. & J. LAURENT (1926) from the Miocene, north-east of Makassar, Celebes.

It is noteworthy that these Tertiary fossils all belong to still existing genera and that at least two of them can be identified with still existing species.

More interesting for my purpose are the fossils from the Cretaceous. A well developed sea-grass flora must already have existed at that time, as well preserved fossils of at least two genera have been found, viz. *Archeozostera* and *Thalassocharis*. Little is known about *Posidonia cretacea* Hos. & v. d. Mark, also recorded from the Cretaceous.

Well preserved imprints of *Archeozostera* have been found in several localities in Japan (KORIBA & MIKI, 1931, 1960; OISHI, 1931). The general habit of these plants is very dissimilar to that of the present sea-grasses. The short, stiff leaves are distichously arranged along an upright stem and do not seem to be differentiated into a blade and a sheath. The erect stems contain several air lacunae. The upper part of the erect stem consists of a cymose system (rhipidium, according to KORIBA and MIKI, 1960) of inflorescences. There are a number of spathes consisting of rather long leaves with involute margins clasping a spadix. According to Koriba and Miki this spadix bears at one side one row of fruits and is attached

to the spathe. The latter feature, however, may be due to the fossilization process. It is possible that the structure of the rhizome is sympodial.

Koriba and Miki regarded the genus as being related to the *Zosteroidae* on account of the one-sided arrangement of the fruits on the spadix and the cymose system of inflorescences. However, the genus differs from this group on two points; the leaves are not differentiated into a blade and a sheath and then there is this supposed coalescence of the spathe and spadix. As the spadix is enclosed by the spathe, these authors also saw a relationship with the *Araceae* and they concluded that *Archeozostera* was intermediate between the *Araceae* and the *Zosteroidae*, although the adaptation to the aquatic habitat was less pronounced than in the last-mentioned group. On account of the stiff and undifferentiated leaves I agree with their view that the adaptation to aquatic life was not so advanced but I reject the supposed relationship with the *Araceae*. A spadix enclosed by a spathe is a normal feature in the *Zosteroidae* and occurs also in the *Aponogetonaceae* and in the families of the *Spadiciflorae*. In my opinion *Archeozostera* is a protozosteroid.

Even more interesting is the occurrence of *Thalassocharis* in the Cretaceous of Limburg (the Netherlands) and Westfalen (Germany). Material of this genus has been preserved in the form of imprints and of silicified remains, and has been studied thoroughly by VOIGT & DOMKE (1955). The genus is characterized by a sympodial rhizome and erect stems with distichously arranged leaves. It can be classified under the *Cymodocoidae* on account of the structure of the leaf-scars and the occurrence of tannin cells. In *Th. westfalica* Hos. & v. d. Mark the erect stems are at least 36 cm long and ca. 2½ cm thick ("daumenstark" according to Voigt & Domke). *Th. bosqueti* Debey ex Miquel is considerably less coarse. A section of the stem of *Th. bosqueti* reveals that the central cylinder contains ca. 20 vascular bundles and that the cortical tissue is differentiated into an inner and an outer ring. The inner ring appears to be divided into sectors, the rather wide strips of parenchyma being separated by narrow radial lamellae of coarser cells. In the parenchyma scattered vascular traces occur. The outer ring consists of small, thick-walled, more or less collenchymatic cells, which probably were lignified. The most striking feature is without doubt the complete absence in the stem of intercellular lacunes or air channels, which are so characteristic for the recent aquatic plants. 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.

Among the recent *Cymodocoidae* there are 2 genera characterized by sympodial rhizomes and stiff, erect stems, viz. *Amphibolis* and *Thalassodendron*. In both genera the inner cortical ring contains numerous air channels, but the outer cortical ring consists of small, thick-walled, lignified cells. These genera may have been derived from *Thalassocharis*-like ancestors. The other 3 genera of the subfamily do not have a peripheral

lignified ring and are completely herbaceous. Furthermore, in these genera the structure of the axes is no longer sympodial but monopodial, except for the inflorescences.

On the base of these (regrettably few) fossil data I think it is not too hazardous to accept that the marine Angiosperms have evolved from salt-tolerant shrub-like terrestrials with sympodial rhizomes and cymose inflorescences and which were able to stand submersion in salt water to some degree. These shrubs must have occurred in the upper part of the intertidal belt, *i.e.* in the habitat where nowadays the mangrove trees and their undergrowth, and several *Gramineae* (*Spartina*, *Puccinellia*, *Sporobolus*) and *Chenopodiaceae* (*Arthrocnemum*, *Atriplex*, *Halimione*, *Suaeda*, *Salicornia*, *Tecticornia*) are found. By changing over from their original, probably anemophilous system of pollination to hydrophilous pollination it would have been possible for these plants to extend their area into the shallow coastal waters. In this respect it is noteworthy that the most primitive of the recent sea-grass genera, *viz.* *Amphibolis* and *Thalassodendron*, are the only sea-grasses showing vivipary, a feature which is characteristic for many mangrove species.

It is improbable that plants such as *Archeozostera* and *Thalassocharis*, which were still so little adapted to life in the water, can have evolved from also little adapted fresh-water ancestors. They would never have succeeded in passing the difficult route from the fresh water via the brackish water to the sea. In my opinion the Angiosperms originally invaded the sea and the fresh water quite independently along different lines.

The *Zosteroideae*, the *Cymodoceoidae* and the *Posidonioideae*, the three marine subfamilies of the *Potamogetonaceae*, must have evolved directly from terrestrial ancestors. In the fresh water the *Potamogetonoideae* probably developed from the same terrestrial stock as these three marine subfamilies. This subfamily, which is adapted to more or less unstable environmental conditions, possibly underwent a further change in arid areas, where fresh waters become concentrated to salt waters of greatly varying chemical composition and subject to large salinity fluctuations, and so the *Ruppioideae* were split off. These, equipped with a great tolerance to poikilohalinity, were also able to penetrate brackish waters, but further extension into the marine environment was prevented by competition with the stenohaline sea-grasses.

The marine *Cymodoceoidae* also showed a further evolution. They penetrated the brackish water and reached the fresh water. This pathway has been taken in the course of time by many groups of organisms. In the fresh water a secondary development took place, resulting in the splitting off of the subfamily *Zannichellioidae* and of the family *Naiadaceae*, the first of which is ecologically similar to the *Ruppioideae*.

It should be mentioned here that I regard the terrestrial *Juncaginaceae*, which have so many characters in common with the *Potamogetonoideae* (see also MARKGRAF, 1936), as a product of the same ancestral stock.

A separate development of the marine and fresh-water subfamilies of the *Hydrocharitaceae* also has to be accepted. Only the position of the genus *Enhalus* is not clear, as it is quite isolated within the heterogeneous fresh-water subfamily *Vallisnerioideae*; it is, however, considerably more primitive than its closest relative, *Vallisneria*, the only genus in this subfamily which can tolerate brackish water to some extent.

c. Geographical distribution of the sea-grasses

The present picture of the sea-grass distribution appears to be rather complete, although there are still areas from which any records, positive or negative, will be welcome. This is true in particular for the extreme northern part of the Pacific and for South America. SETCHELL (1935b) recorded the find of a leaf-blade of an unknown *Zosteroid* species near Montevideo, but the beds of that species have still to be discovered. The records of *Heterozostera tasmanica* from Chile and of *Halophila baillonis* from Brazil are still based on a single collection. In other regions surprises cannot be excluded, when one considers the recent discovery of *Zostera americana* along the Pacific coast of the U.S.A., of *Halophila ovata* in Kenya and Australia, and of *Halophila baillonis* along the Central American Pacific coast.

The great age of the sea-grasses is reflected in the geographical distribution of the recent genera. There are 7 genera which can be regarded as characteristic for the tropical seas and 5 genera which are more or less confined to the temperate seas. The first category consists of the 3 marine genera of the *Hydrocharitaceae*, viz. *Enhalus* (fig. 8), *Thalassia* (fig. 9) and *Halophila* (fig. 10), and the 4 genera *Halodule* (fig. 4), *Cymodocea* (fig. 5), *Syringodium* (fig. 6) and *Thalassodendron* (fig. 7) of the subfamily *Cymodoceoideae*. It must, however, be mentioned that some of these genera contain species which have extended their area into subtropical or even warm-temperate seas, e.g. *Halophila ovalis* and *Syringodium isoetifolium*, while others have developed species which are restricted to subtropical waters, e.g. *Cymodocea nodosa*, *C. angustata* and *Thalassodendron pachyrhizum*.

The tropical sea-grasses are concentrated in 2 large areas. By far the richer is the Indo-West Pacific area, where all 7 genera occur. The other area, comprising the Caribbean and the Pacific coast of Central America, has 4 genera in common with the Indo-West Pacific, viz. *Halodule*, *Syringodium*, *Thalassia* and *Halophila*, but lacks genera peculiar to it. In fact it has only one endemic supraspecific taxon, viz. *Halophila* sect. *Americanae*. On the species level the similarity between the two areas is smaller. *Halophila decipiens* has a pantropical distribution and *Halodule wrightii* occurs in the Atlantic as well as in the Indian Ocean. Except for these two species the Indo-West Pacific and the Caribbean area have no species in common.

The disjunct distribution of the tropical sea-grasses can only be understood when the division of the earth in sea and land during earlier geolog-

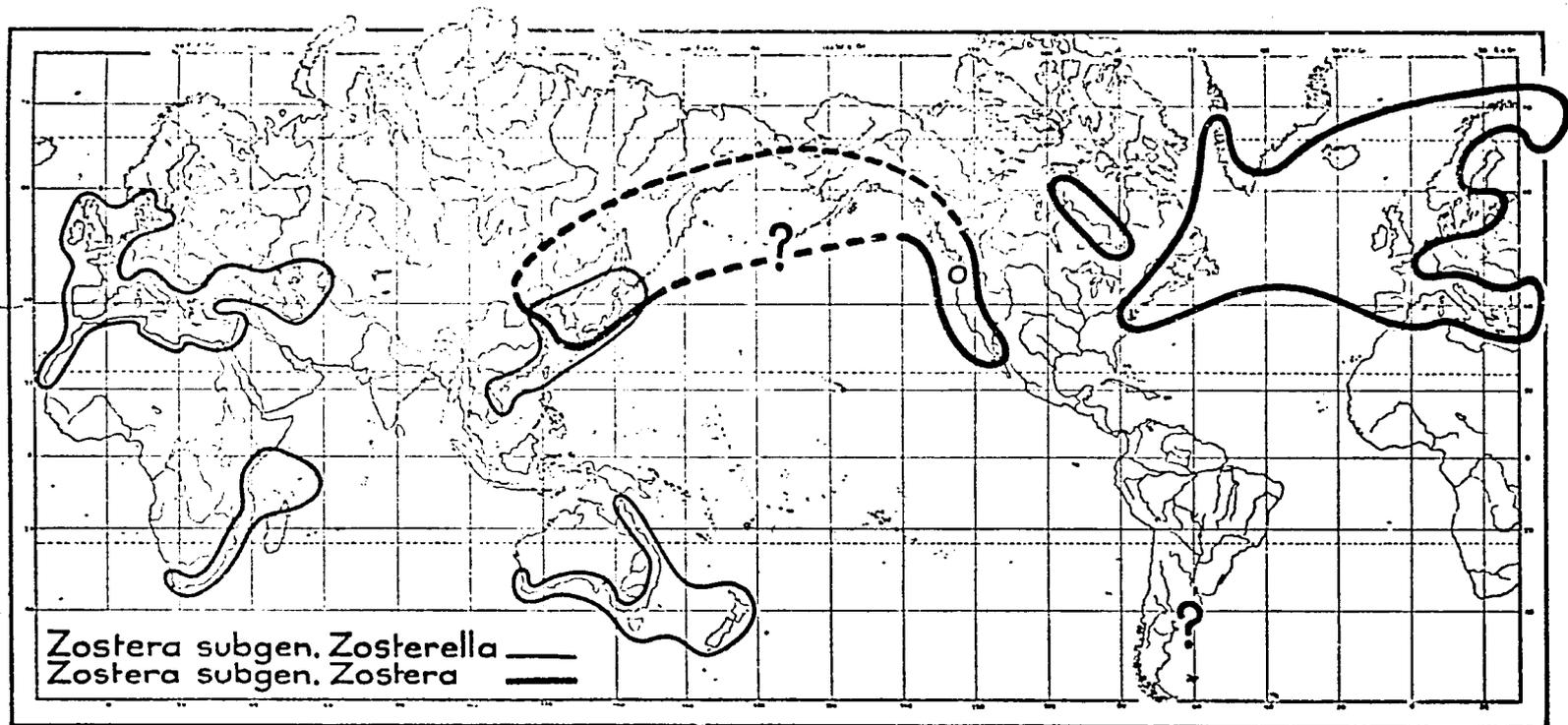


Fig. 1. The geographical distribution of *Zostera* subgen. *Zostera* and subgen. *Zosterella*. The distribution of the subgen. *Zostera* in the Bering Sea and the Sea of Okhotsk is insufficiently known. The inclusion of the Aral Sea within the area of distribution of the subgen. *Zosterella* is based on records by Zenkevitch (1963). The question-mark near Argentina indicates the record by Setchell (1935b) of an unidentified zosteroid species.

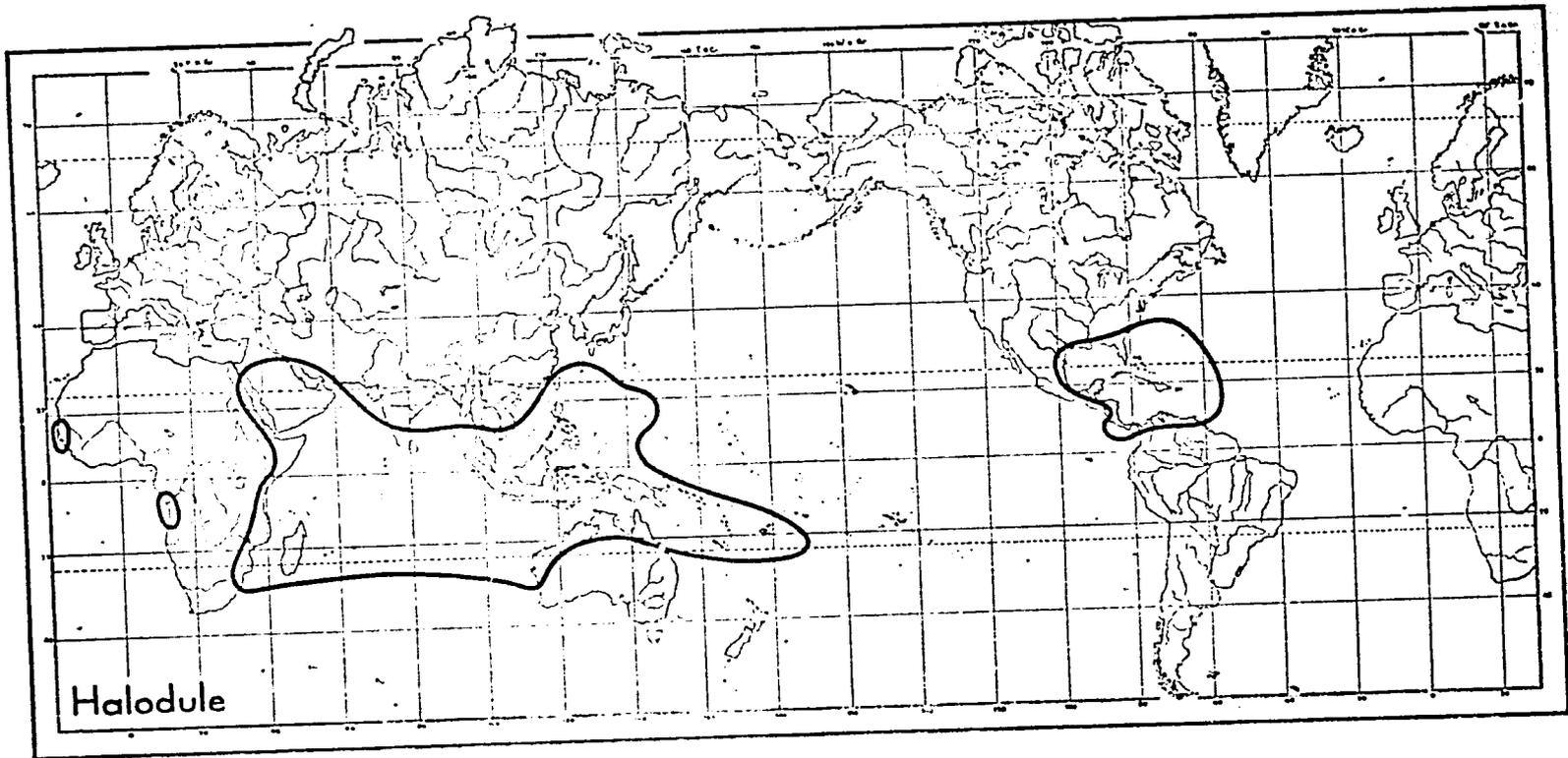


Fig. 4. The geographical distribution of the genus *Halodule*.

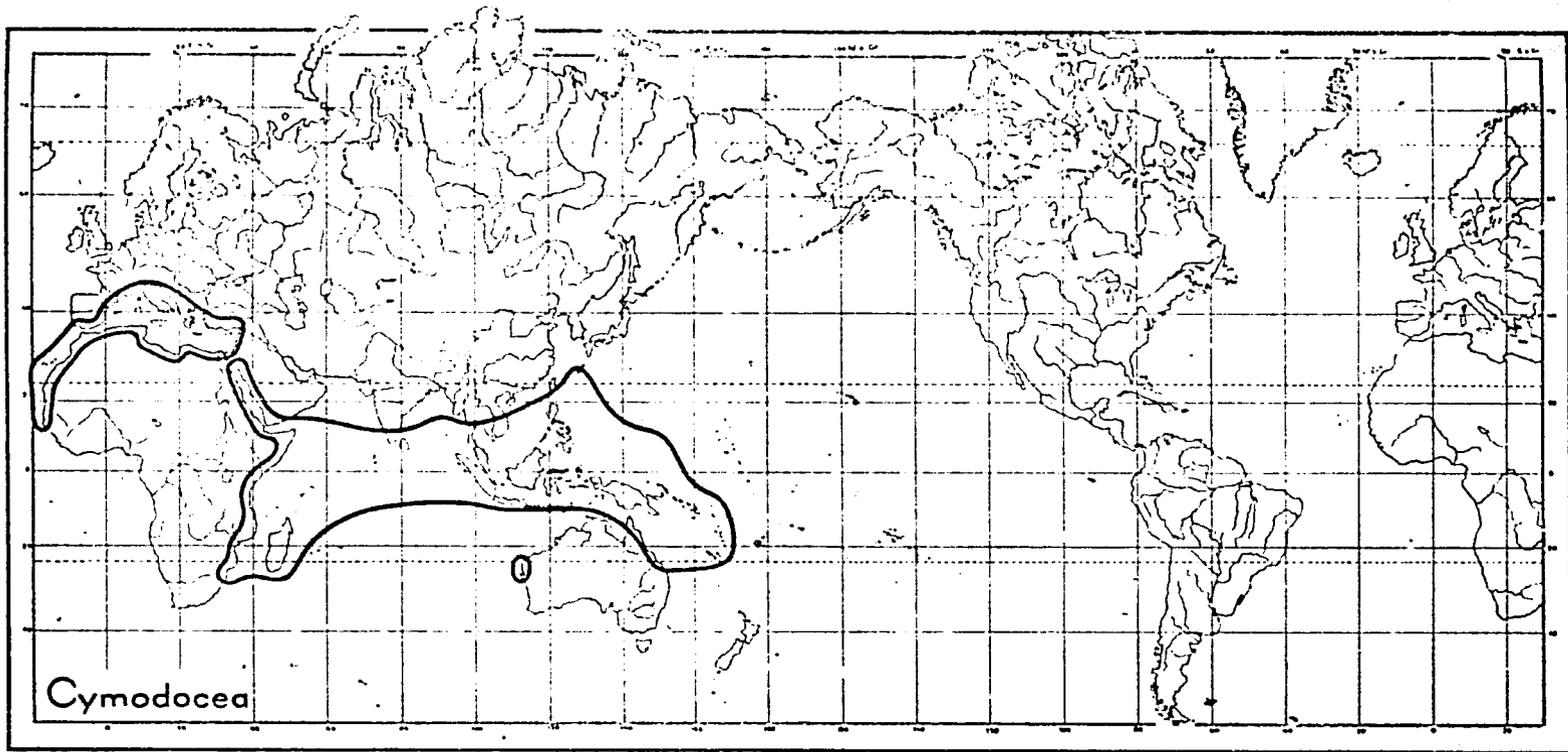


Fig. 5. The geographical distribution of the genus *Cymodocea*.

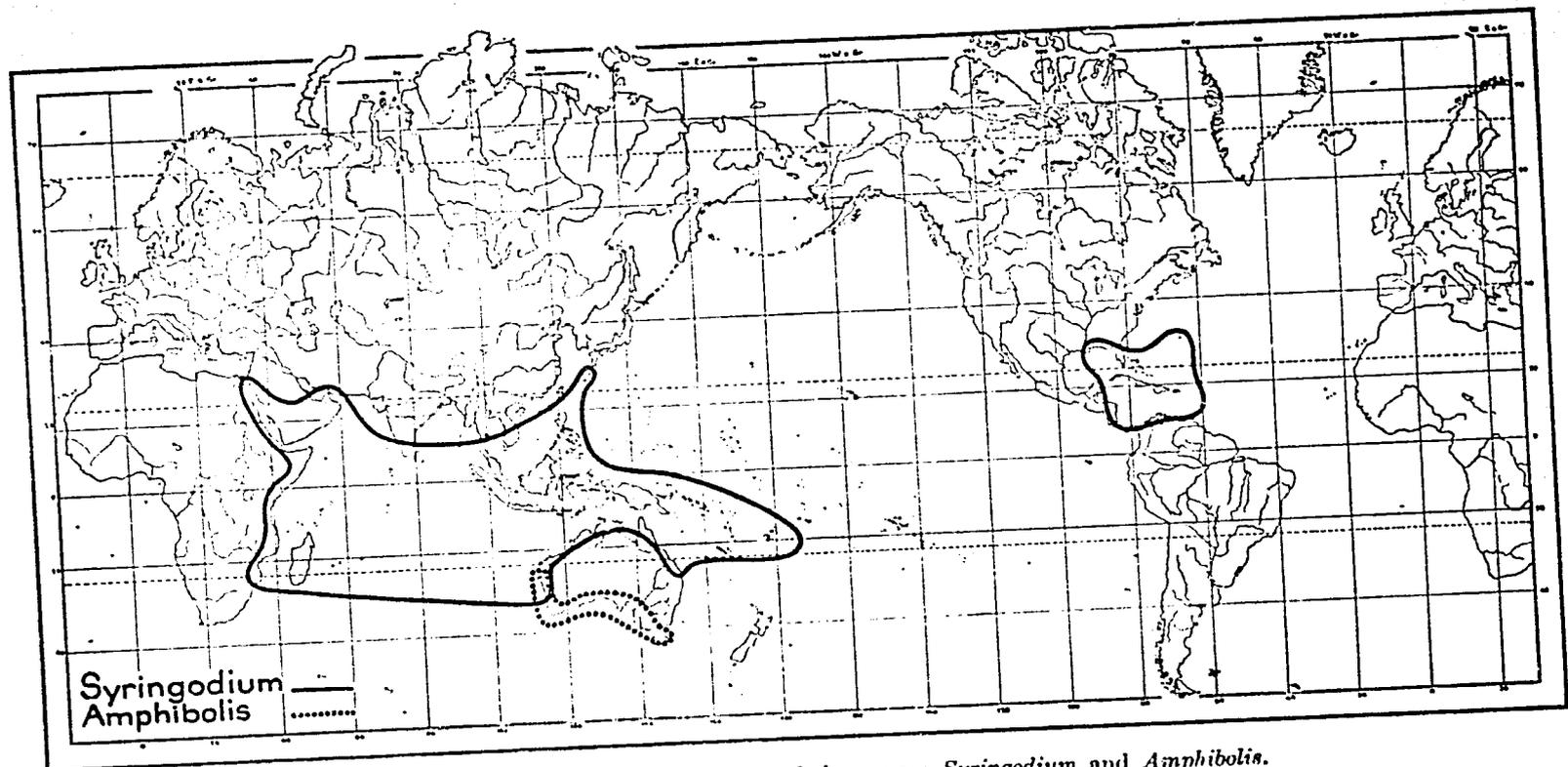


Fig. 6. The geographical distribution of the genera *Syringodium* and *Amphibolis*.

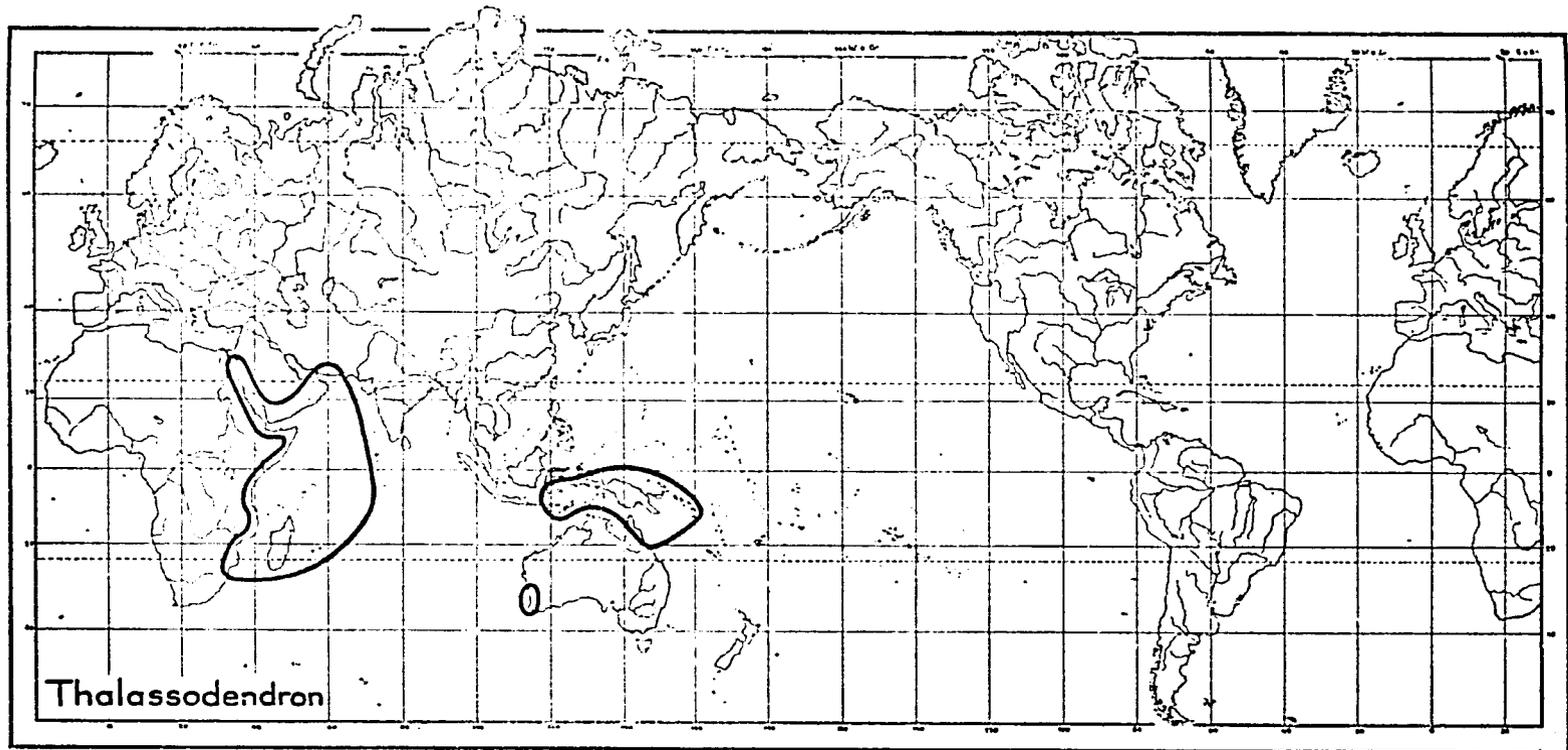


Fig. 7. The geographical distribution of the genus *Thalassodendron*.

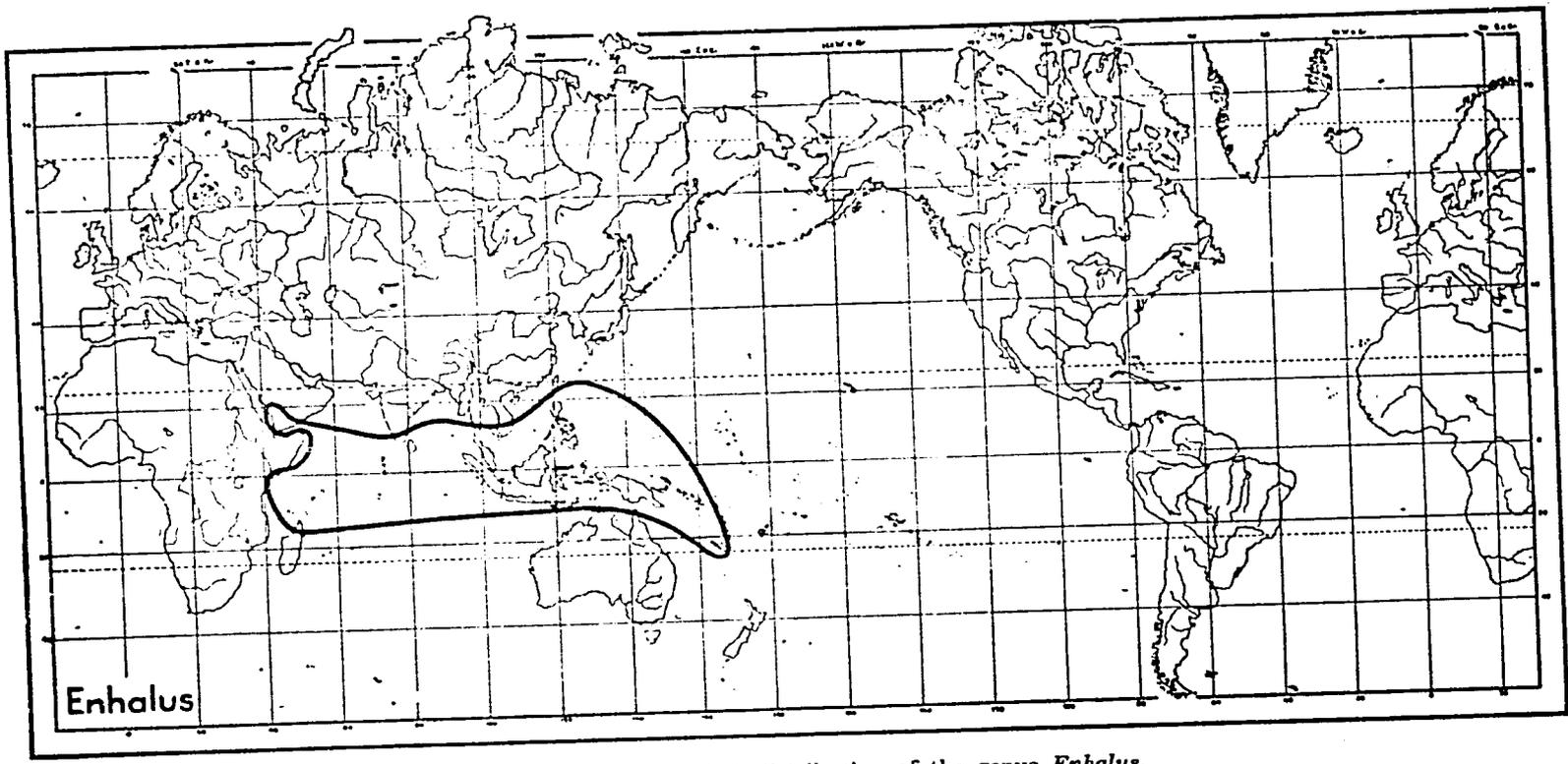


Fig. 8. The geographical distribution of the genus *Enhalus*.

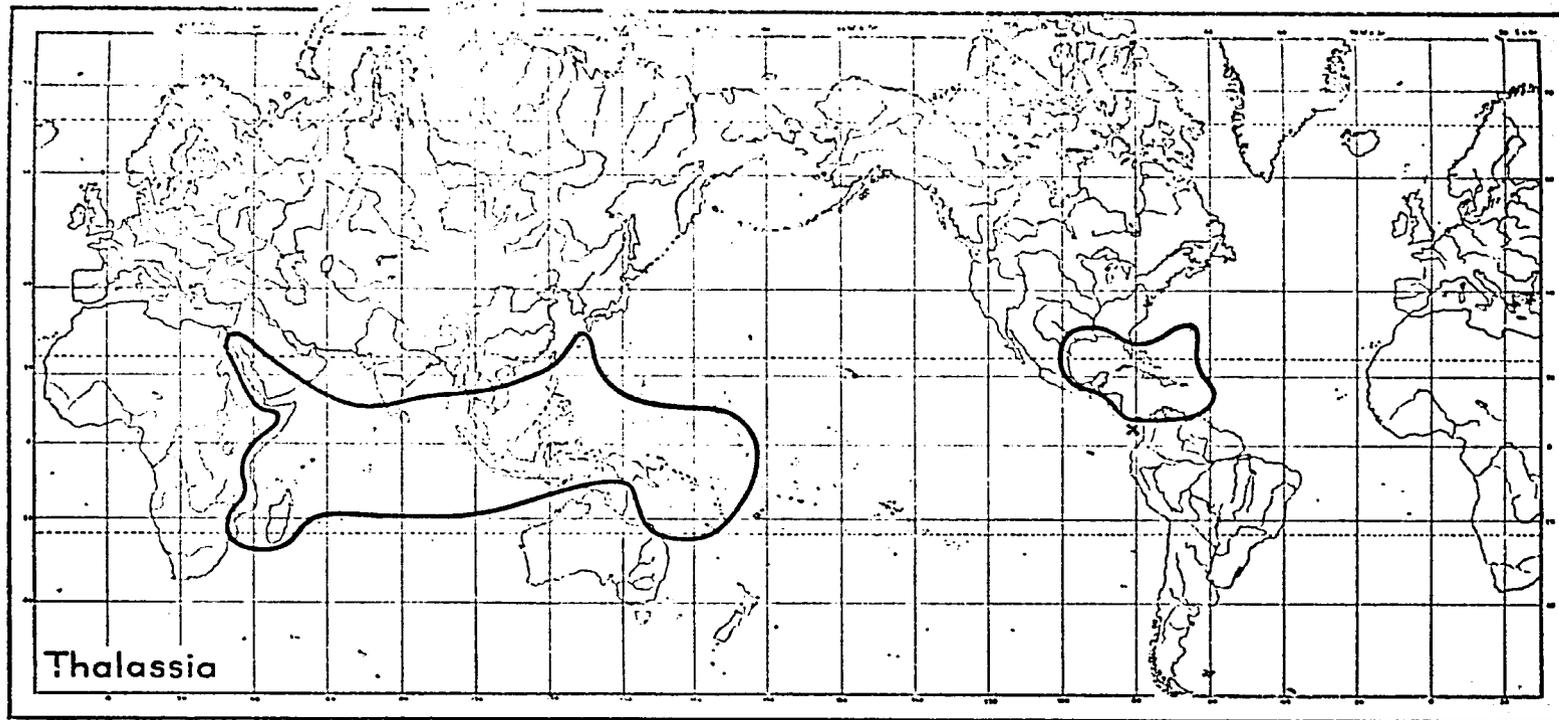


Fig. 9. The geographical distribution of the genus *Thalassia*. The cross indicates an unconfirmed record of *T. testudinum* in the Gulf of Panama (Setchell, 1935a, p. 563).

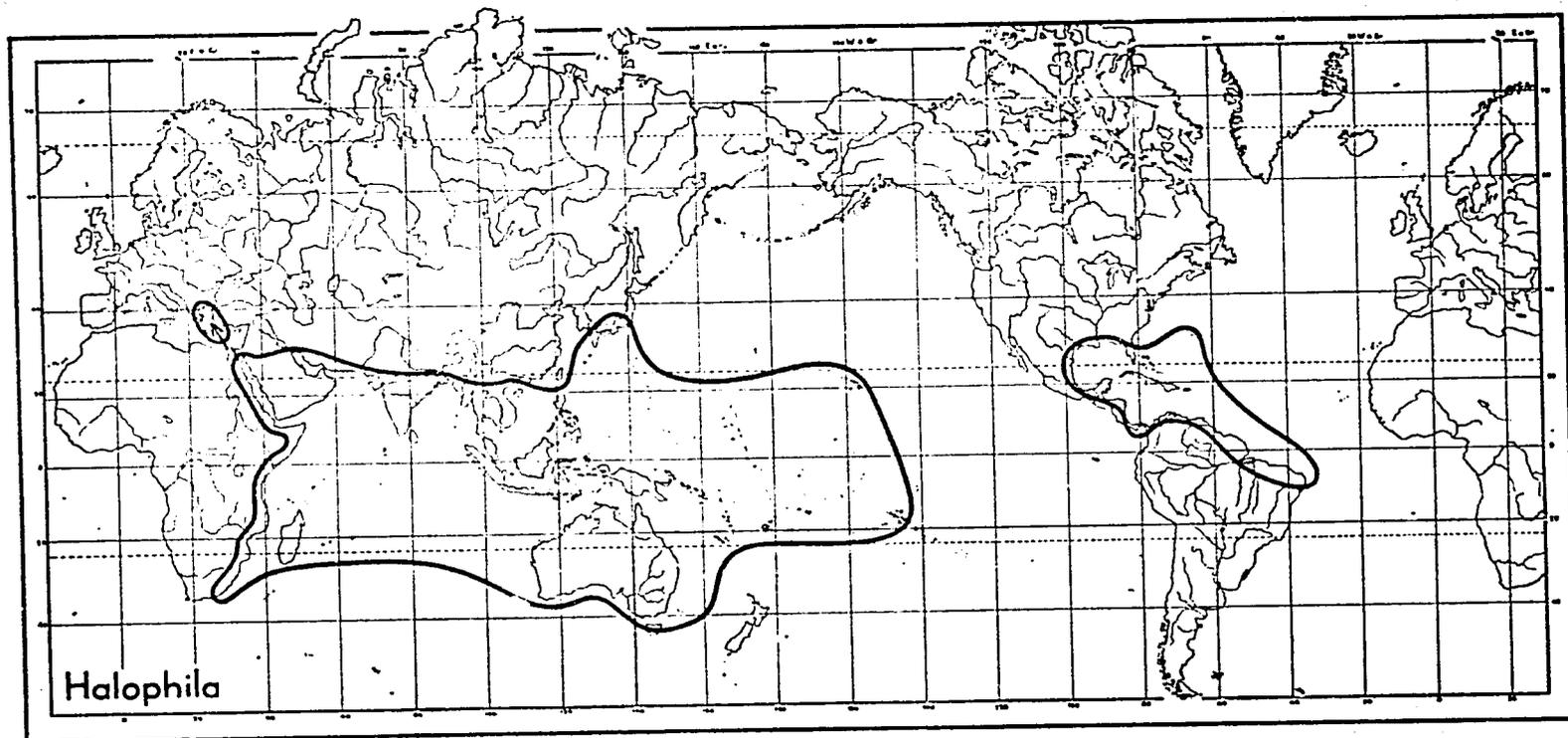


Fig. 10. The geographical distribution of the genus *Halophila*.

ical epochs is taken into account. It is known that a belt of seas, the Tethys, surrounded the earth, with some temporary and local interruptions, from at least the end of the Palaeozoicum to the Tertiary epoch. This Tethys had a rich, relatively homogeneous shelf fauna (EKMAN, 1934, 1953). During the Cretaceous, and probably already earlier, a deep-sea, thousands of kilometres wide and without islands, was formed. This deep-sea was called the East-Pacific Barrier by EKMAN (1934), as it appeared to be insurmountable for the shelf fauna which accordingly became divided into a West-Pacific and a Caribbean group. Nor could it be crossed by sea-grasses, as these have in general no suitable means for long-distance dispersal¹⁾. If the 4 recent, pantropical genera have migrated from the West Pacific in eastern direction to the Caribbean they must have been in existence at least since the Middle Cretaceous, as after that time it would not have been possible for them to cross the East-Pacific Barrier. The only known fossils of sea-grasses from the Cretaceous, however, are primitive types like *Archeozostera* and *Thalassocharis*, much less adapted to life in the water than the 4 genera concerned. If they had reached the Caribbean from the East via the "old Mediterranean" and the Mid-Atlantic they would have had more time. According to Ekman the shelf fauna of this part of the Tethys was still very rich and homogeneous during the early Tertiary. It was not before the Miocene that a very strong impoverishment of the Atlantic shelf fauna took place due to a decrease in temperature. Moreover, during the Miocene the Suez and the Panama Isthmuses became definitively closed. The point of view that the westward route was taken by the sea-grasses finds support in the recent area of distribution of *Halodule wrightii*, which occurs in the Indian Ocean, along the Atlantic coast of Africa and in the West Indies but which has so far not been found in the Pacific (DEN HARTOG, 1964, fig. 8). Another example of such an area of distribution is shown by the Phaeophyceean alga *Cystoseira myrica* (Gmel.) J. Ag., which is widely distributed in the West Indies, the Red Sea and along the eastern coast of Africa. Ekman also gives some zoological examples of such distributions.

There are, however, some problems with regard to this westward route which are difficult to solve. There are, for example, 3 genera which are widely distributed in the Indo-West Pacific, but which are absent from the Caribbean, viz. *Enhalus*, *Cymodocea* and *Thalassodendron*. The rather specialized *Enhalus* is probably one of the last evolved genera and for this reason may never have reached the Caribbean. However, this is certainly not true for the other two genera. *Cymodocea* occurred already during the Eocene in Europe, and nowadays it occurs even in the subtropical seas. Therefore, the absence of this genus from the Caribbean area

¹⁾ Paradoxically, the species of the few genera with buoyant fruits (*Posidonia*, *Thalassodendron* and *Enhalus*) are rather restricted in their distribution.

cannot be ascribed to the temperature decrease in the Miocene. Although the archaic *Thalassodendron* has developed one warm-temperate species, its absence from the Caribbean may perhaps be a result of the already mentioned decrease in temperature during the Miocene. The recent Indo-Pacific area of this genus shows a disrupted relict character; in the past this genus must have had a much wider distribution.

A pattern of distribution similar to that of the tropical sea-grasses is also shown by the mangroves. According to VAN STEENIS (1962b) there is a rich centre in the Indo-West Pacific and a poorer centre in tropical America, although the latter centre has two genera peculiar to it, viz. *Laguncularia* and *Conocarpus*. Among the mangroves there appear to be no species which occur along the coast of West Africa as well as along the coast of East Africa. However, he recorded one species, viz. *Rhizophora mangle* L. which occurs not only in tropical America and West Africa, but also in New Caledonia and the eastern part of Melanesia (see also DING HOE & VAN STEENIS in Pacific Plant Areas 1, 1963, p. 256, map 5). The occurrence of this species in the SW. Pacific may perhaps be due to dispersal by a westward current (cf. Kontiki).

Mention must be made of the so-called twin species among the sea-grasses, i.e. pairs of species which show only slight morphological differences but have widely separated areas of distribution. The 3 pairs of twin species are listed below:

Indo-West Pacific	Caribbean
<i>Halodule uninervis</i>	<i>Halodule beaudettei</i>
<i>Syringodium isoetifolium</i>	<i>Syringodium filiforme</i>
<i>Thalassia hemprichii</i>	<i>Thalassia testudinum</i>

OSTENFELD (1915) and SETCHELL (1935a) supposed that these twin species had originated from ancestors which had a very wide distribution in tropical seas; they ascribed the present differentiation into an Indo-West Pacific species and a Caribbean species to changes in the geographical situation of oceans and land-masses. For this reason they stressed the importance of the definitive closure of the Panama Isthmus during the Miocene, as this would have divided the original area of the ancestors. However, the differentiation of these species must date from before the Miocene, as e.g. *Halodule beaudettei* and *Halophila baillonis* (of the endemic section *Americanae*) occur on both sides of the Panama Isthmus.

The area of distribution of *Halodule wrightii*, which is split into an Atlantic and an Indian Ocean part, shows that this species must have been in existence before the Suez Isthmus was closed. Other evidence for the great age of the recent species is shown by the pantropical distribution of *Halophila decipiens*. Furthermore, this view is supported by the fact that the fossil remains of *Cymodocea* from the European Eocene

can be identified with still existing species. Therefore, the close resemblance which exists between the twin species, and also between many other sea-grasses, should not be regarded as an indication of their recent origin. It should be seen rather as a result of the very slow rate of evolutionary progress of the Angiosperms in the relatively uniform marine environment. SCULTHORPE (1967), who still has "every reason to believe that *Halodule*, *Syringodium* and *Thalassia* and other hydrophilous marine monocotyledons evolved from brackish- or fresh-water ancestors", supposed that the sea-grasses terminate evolutionary lines which reach back a very long time, "even perhaps to pre-Cretaceous time". Judging from the scanty fossil evidence (*Thalassiocharis*, *Archeozostera*) it seems more likely that the monocotyledons did not invade the marine environment before the Cretaceous. Many of the recent marine species evolved during the early Tertiary, but others did so perhaps already during the late Cretaceous.

Among the 5 genera which are more or less characteristic for the extratropical seas there are two, *Zostera* (fig. 1) and *Posidonia* (fig. 3), which have a bipolar distribution, i.e. their area extends partly north of the tropical zone and partly south of it. The discontinuity in the distribution of these taxa is without doubt a secondary feature which may have come about in various ways. Several theories have been put forward in order to explain the distribution of bipolar taxa. Of these the migration theory, according to which temperate and even "arctic" species and genera cross the tropical zone by means of "equatorial submergence" (EKMAN, 1953) cannot possibly be applied to benthic plants, as these are dependent on light for photosynthesis and thus are exclusively confined to shallow coastal seas. There are also various relict theories and these are more acceptable as an explanation of the geographical distribution of the bipolar sea-grass genera. *Posidonia* and *Zostera* subgen. *Zosterella* must originally have had a very large, coherent area of distribution, comprising the temperate as well as the tropical seas. In the course of time they have been pushed out of the tropical waters by more stenothermic genera but were able to maintain themselves in the extratropical parts of their area. Judging from the wide disjunction between the Mediterranean and the Australian part of its area of distribution, it seems likely that *Posidonia* had already disappeared from the tropical seas at a rather early stage in the history of marine Angiosperms. That the Mediterranean species on the one hand and the Australian species on the other show rather essential morphological differences, which may even justify placing them in separate sections or subgenera, is also an indication of the great age of the gap in the area of distribution, especially when the extreme evolutionary conservatism of the marine Angiosperms is taken into account.

Zostera subgen. *Zosterella* has not completely disappeared from the tropics as 4 of the 8 species of the subgenus still have smaller or larger populations in the tropical waters, viz. the East Atlantic *Zostera noltii*, the East Asiatic *Z. japonica*, the East Australian *Z. capricorni* and the East

African *Z. capensis*. The area of the latter still lies for the greater part within the tropics and its northernmost populations cross the equator.

The geographical distribution of *Z. noltii* is the most interesting, as it is the only species of the subgenus occurring beyond the Indo-Pacific area. It must have occurred in the Mediterranean before the closure of the Suez Isthmus in the Miocene. Moreover, it occurs in the Caspian and the Aral Sea, which nowadays have no communication with the Mediterranean. The species would have reached the Caspian during the Miocene, or at the end of the Pleistocene. During the Middle Miocene the Paratethys, a large marginal sea of the Tethys, came into existence. This sea, which extended from Hungary to Turkestan, lost its connection with the Tethys during the Upper Miocene and became the brackish Sarmatic Sea. The history of the Sarmatic Sea was rather spectacular with respect to its extensions, its regressions and its splitting into the Black Sea and the Caspian Sea (see ZENKEVITCH, 1963). At the end of the Pleistocene the Black Sea became connected with the Mediterranean via the Bosphorus, soon after this in the same period the connection between the Black Sea and the Caspian Sea was definitively broken. The time between the opening of the Bosphorus and the closure of the Pontic-Caspian connection was long enough, however, to allow a number of Mediterranean immigrants to reach the Caspian. The Aral Sea lost its contact with the Caspian during the late Pleistocene. The almost complete absence of "Mediterranean" elements makes it likely that the Late-Pleistocene invaders from the Mediterranean never reached the Aral Sea. This implies that the few "Mediterranean" species, including *Zostera noltii*, which occur in the Aral Sea, are in fact relicts of the Miocene Sarmatic Sea.

The distribution of *Zostera capricorni* also shows some interesting features: it occurs along the coasts of Queensland and New South Wales, is absent from Victoria and Tasmania, but has been found on the South Australian Kangaroo Island. The isolated occurrence on the latter island indicates that during the Oligocene and Miocene, when the Australian climate was much warmer, it must have had a continuous area in southeastern Australia. The species occurs also on North Island, New Zealand and on Lord Howe Island. According to KNOX (1963) New Zealand has been an isolated land-mass since the Upper Cretaceous. Without fossil evidence, however, it cannot be established whether the occurrence of *Z. capricorni* in New Zealand is original or whether it is a result of a later settlement after crossing the Tasman Sea under influence of the Western Wind Drift. Lord Howe Island could have served as a "stepping stone". It is true, however, that New Zealand also has an endemic species, *Z. novaezelandica*. As there is reason to assume that the development of new species in marine Angiosperms is an extremely slow process, it may be regarded as certain that *Zostera* sect. *Zosterella* was already present in New Zealand in the early Tertiary.

In the northern Pacific the genus *Zostera* underwent a further differen-

tiation and evolved the subgenus *Zostera* (fig. 1). This subgenus is represented by several species in the northern Pacific, while only one of them, *Z. marina*, occurs also in the northern Atlantic. This species reached the Atlantic rather late. According to EKMAN (1953), there were communications between the northern Pacific and the northern Atlantic during the Pliocene and the Pleistocene, and it is likely that *Z. marina* made use of them. The isolated occurrence of the species in the Hudson Bay may be considered a relict station (PORSILD, 1932), and further it is noteworthy that it has been obtained from the Pleistocene of Montreal (PENHALLOW, 1900). The late appearance of *Z. marina* in the Atlantic, is also supported by its absence from the Caspian Sea, which was connected temporarily with the Black Sea at the end of the Pleistocene. In the Black Sea the species is nowadays common.

The genus *Phyllospadix* (fig. 2) is completely confined to the northern Pacific, where it has given rise to a number of closely related vicarious species.

Two genera are restricted to the temperate zone of the southern hemisphere, viz. *Heterozostera* (fig. 1) and *Amphibolis* (fig. 6). Morphologically *Heterozostera* is certainly the most primitive recent genus of the subfamily *Zosteroideae*, because its rhizome is sympodial and its erect stems are stiff, strongly vascularized and lignified. It is widely distributed in Australia south of the 30th parallel and has also been found in one locality along the coast of Chile. It is absent, however, from New Zealand. The distribution of this genus indicates a previous connection between Australia and South America during the Cretaceous, as has been supposed by VAN STEENIS (1962a). *Amphibolis*, which is restricted to the western and southern coasts of Australia, is the only completely extratropical genus of the subfamily *Cymodoceoidae*. It is in every respect more primitive than the recent tropical genera (*Thalassodendron* excepted), and for this reason the genus must be very old and date from the early Tertiary or even from an earlier epoch. From the reviews given by EKMAN (1953) and KNOX (1963) it is known that the South Australian marine fauna has had its independent character already since the Cretaceous, and there is no reason to suppose that this should not also apply to the marine flora.

This exposition of the geography of the marine Angiosperms is for the greater part based on the evidence of the present distribution of the taxa as there are only a very few palaeontological records. However, the general pattern of distribution shown by the sea-grasses is also shown by many groups of marine animals restricted to the continental shelf, e.g. groups of Mollusca and Echinodermata, of which the fossil record is much more complete. Therefore, I think that the geography of the sea-grasses has had more or less the same history.