AN APPROACH TO THE TAXONOMY OF THE SEA-GRASS GENUS HALODULE ENDL. (POTAMOGETONACEAE)

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INTRODUCTION

Sea-grasses are phanerogams which are completely adapted to life in marine waters. They are recruited exclusively from two families, the *Potamogetonaceae* (7 genera with *ca.* 35 species) and the *Hydrocharitaceae* (3 genera with 12 species), and form together an interesting ecological group. Consequently, their taxonomy, morphology, flower biology, and geographic distribution have been much studied, especially by Ascherson (1868, 1889, 1906, 1907), Sauvageau (1890, 1891), Ostenfeld (1915, 1916, 1927), Setchell (1920, 1935), and Miki (1932, 1934). In spite of the work of these eminent investigators the taxonomy of several genera viz. *Halodule*, *Posidonia*, *Zostera*, and *Phyllospadix* is yet imperfectly known. One of the most serious gaps in our knowledge is no doubt the lack of ecological data; this greatly hampers the judgment of the biometric characters of the species with relation to their usefulness for taxonomical purpose. Less important is the fact that the generative parts of several species are partly or completely unknown.

The taxonomy of the genus *Halodule*, which had been known for a long time under the name *Diplanthera* [1]), has been studied in the scope of the revision of the *Potamogetonaceae* for the Flora Malesiana. The development of the taxonomy of this genus has been seriously obstructed not only by the difficulties in the interpretation of the slight morphological differences between the species but also by the fact that nearly all investigators based their identifications on the works of Ascherson (1889, 1906, 1907). According to this author the genus *Halodule* contains two species: *H. uninervis* (Forsk.) Aschers. and *H. wrightii* Aschers. Although he mentioned differences in generative and vegetative characters, the difference in geographic distribution he regarded as more important. Specimens from the Indo-Pacific were referred to as *H. uninervis* and those from the Caribbean were called *H. wrightii*. The geographic character was stressed in particular by Ostenfeld: "On the whole it is not possible to distinguish the two species when sterile, except using their quite different geographical distribution as criterion." (1902, p. 262). "Die zwei Arten der Gattung sind einander so ähnlich, dass es nicht sicher ist, ob sie als zwei Arten beibehalten werden können. Ganz wie beim Artenpaare *Halophila Baillonis* [2]) — *H. decipiens* sind die Verbreitungsareale eigentlich das beste Unterscheidungsmerkmal." (1927, p. 47). No wonder that the specimens in the herbaria all seem to be identified according to the traditional geographic scheme, even when the morphological characters of the plants de not agree with the species descriptions.

Miki (1932) was the first who described a new species in the genus (as *Diplanthera*)

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[1]) Mr. H. K. Airy Shaw (Kew) kindly informed me that the generic name *Diplanthera* Du Petit-Thouars has been antedated by *Diplanthera* Gleditsch, Syst. Pl. (1764) 154 and is thus illegitimate.

[2]) *Halophila baillonis* Auct. *non* Aschers., the correct name of which is *H. decipiens* var. *pubescens* Den Hartog, has been found also in the Indian and the Pacific Oceans (Den Hartog, 1957, 1959).

from Japan. Later I described some new species (also as *Diplanthera*) from the Pacific coast of Central America (Den Hartog, 1960). For the present revision of the genus I have examined all relevant material present in the herbaria of the British Museum (Natural History), London (BM), Royal Botanic Gardens, Kew (K), Laboratoire de Phanérogamie, Paris (P), Rijksherbarium, Leyden (L), Botanisch Museum, Utrecht (U), Arnold Arboretum, Cambridge (Mass.) (A), Gray Herbarium, Harvard University, Cambridge (Mass.) (GH), U. S. National Herbarium, Washington D. C. (US), Herbarium of the University of California, Berkeley (UC), Botanical Research Institute, Pretoria (PRE), Moss Herbarium, Johannesburg (J), Herbarium, University of Florence (FI), Botanisk Museum, Copenhagen (C), Singapore Botanic Gardens (SING), Department of Forests, Lae (LAE), and Herbarium Bogoriense, Bogor (BO).

The results of this study show that the diversity in the genus *Halodule* is considerable. As my work is completely based, however, on often scanty herbarium material with only a few ecological data, the delimitation of the species must be regarded as provisional, because the influence of the modifying environmental factors on the appearance of the species is still insufficiently known.

TAXONOMIC CRITERIA

1. The generative parts

Flowers and fruits of many sea-grasses have been rarely observed or never found at all. This has caused taxonomists to look for vegetative characters by which sterile material can be identified. In some cases the morphology of the flowers is so similar that the generative characters can not be used for distinguishing species. In the marine Hydrocharitaceous genus *Halophila*, for example, the flowers show a striking similarity, although the 9 species may be easily identified by their vegetative parts. These show even such a strong diversity that this genus had to be divided into 4 sections (Den Hartog, 1957).

In the genus *Halodule* flowers and fruits have seldom been found. In herbarium material I have seen only a few flowers and fruits. Investigators who have studied specimens of this genus *in situ* also remarked on the rare occurrence of flowers (Taylor, 1928; Phillips, 1960 b). As a result of the rarity of the generative parts their range of variation within the species is unknown. The value of characters derived from the flowers and the fruits, therefore, seems doubtful.

As an example the case of the two species of the related genus *Syringodium* may be mentioned. These have conspicuous cymose inflorescences and for this reason specimens with flowers or fruits are relatively more often found in herbaria than the other *Cymodoceaceae*. According to Ascherson (1869 b, 1907) the flowers of *S. filiforme* Kütz. (*sub nomine Cymodocea manatorum* Aschers.) should be double the size of those of *S. isoetifolium* (Aschers.) Dandy (*sub nomine Cymodocea isoetifolia* Aschers.). Later Ostenfeld (1916) investigated both species and did not find any difference in the female flowers; in both species the variation in size had the same maxima and minima. The fact that Ascherson's type of *Cymodocea manatorum* has large flowers and his type of *C. isoetifolia* small flowers must be considered merely accidental. In the male flowers Ostenfeld found only such a very slight difference that he could not use it for taxonomic purpose. The differences found in the size and the shape of the fruits were also only slight.

Although the likelihood of errors is considerable some authors, nevertheless, made reference to characters of the flowers. According to Ascherson (1882, 1889, 1907) the anthers of *H. uninervis* are 3 mm and those of *H. wrightii* 6 mm long. I do not know from which plants Ascherson obtained these measurements. He had at any rate seen the material of Du Petit Thouars and Steinheil, as in the description of the male flowers of *H. wrightii* (Ascherson, 1869 b) he stated that the male flowers are considerably larger than those of *Diplanthera tridentata* Steinheil, which was regarded by him as a synonym of *H. uninervis*. As the same author (1875, 1906) recorded the remarkable fact that the male plants of *H. uninervis* are much more delicate and slender than the female ones, it is certain that the male plants he referred to were *H. tridentata* (Steinheil) F. v. M. and the female plants *H. uninervis*. From the statement that in *H. wrightii* just the reverse is the case, male plants being coarser than the female ones, it seems likely that he had at his disposal male plants of *H. beaudettei* and female plants of *H. wrightii*. Sauvageau (1890, 1891) found no differences in size in male, female, and non-flowering plants of *H. tridentata* (narrow form of *H. uninervis*, according to him), collected by Balansa in New Caledonia.

Miki (1932) used characters of the female flower in recording the differences between *H. uninervis (sub nomine D. uninervis)* and *H. pinifolia (sub nomine D. pinifolia)*. He stated that in the first species the style would be short and terminally inserted on the carpel, while in the other species the style is long and laterally inserted. However, in a later paper he mentioned just the reverse (Miki, 1934).

Other data on floral characters of *Halodule* species are scarce in literature. In his original diagnosis of the genus *Diplanthera* Du Petit Thouars (1806) gave a good description of the male flowers of a specimen from Madagascar, but the description of the vegetative parts was highly inadequate. Steinheil (1838) gave beautiful drawings of the male flower of this specimen *sub nomine Diplanthera tridentata*. Camus (1942) described the flowers of *H. uninervis* from Indo-China but did not mention whether they were from typical plants or slender plants (= *H. tridentata*). Moreover, his drawings disagree in several respects with remarks made in the text. Feldmann (1936) recorded male flowers of a species referred to as *Diplanthera wrightii* from Guadeloupe, but as no data about the plants are given it is quite uncertain whether his material belongs to *H. wrightii* or to *H. beaudettei*.

2. The vegetative parts

In sea-grasses the characters of the vegetative parts are usually more important for recognizing the species than those of the generative parts of the plants. Sauvageau (1890, 1891), who studied the morphology of the leaves of many sea-grasses and other aquatic plants, found many characters suitable for distinguishing species and other characters which were of generic value. As, however, the modifying effect of the environment on waterplants is a well-known fact, taxonomists have to treat the vegetative characters with the greatest care and be always on their guard against unexpected tricks of nature. The habit of the same species may be rather different in sheltered and exposed localities, in currents and in standing waters, in shallow and in deep waters, on muddy and on sandy bottoms. The modifying environmental factors have usually a similar effect on species with the same life form, occurring in the same habitat. For the taxonomist it may be a great help, indeed, to find two species of the same genus together, as it enables him to eliminate the environmental modifications. In particular, this is true for the sea-grasses with their uniform life form and consequently their small number of distinguishing characters. Therefore, it has to be stressed here, that for a final solution of the specific delimitation of the sea-grasses, ecological studies must be regarded as absolutely indispensable.

In literature on the genus *Halodule* reference has been made to the following characters: shape of the leaf-tip, width of the leaf, and the development of intercellular spaces between the cells above and below the median vascular bundle of fullgrown leaves.

a. The leaf-tip

The character of the leaf-tip was studied by Sauvageau (1890, 1891). His descriptions of the leaf-tips of *H. uninervis* and *H. wrightii* are very clear and detailed. The same is true for the descriptions given by Feldmann (1938).

The leaf-tip of *H. uninervis* consists of three teeth (fig. 2—3). Two slender, linear marginal teeth continue the prolongation of the leaf-margin. In the wide hollow between these teeth the shorter median tooth arises. This tooth has a blunt top, is often ragged, and its cells are delicate and transparent, being more or less devoid of protoplasm. In young leaves, still enclosed in the sheath of an older leaf, this tooth is at least as long as the marginal teeth and has then an entire, obtuse tip. When the leaves grow the apical cells of the median tooth disintegrate and fall off, while the base persists giving rise to the blunt, rounded elevation between the marginal teeth.

The leaf-tip of *H. wrightii* is quite different (fig. 6—7) and consists of two more or less triangular marginal teeth. Their outer sides form a prolongation of the leaf-margin; the inner sides reach the midrib. In young plants the midrib projects into the triangular incision between the marginal teeth. This projection of the midrib is easily broken off, and is mostly absent in fullgrown plants.

Ascherson (1869 a, 1889, 1907) considered the shape of the leaf-tip a useful character for separating *H. uninervis* and *H. wrightii*. In his key to the species (1907) he recorded for *H. uninervis*: "Lamina foliorum inter dentes apicales parum rotundati-producta" and for *H. wrightii*: "Lamina plerumque semilunatim bicuspidata". Although he does not say so by 'plerumque' he means probably that in *H. wrightii* other possibilities also exist, for instance, the occurrence of the projecting midrib between the marginal teeth. More probably, however, it may be considered a covert reference to the fact that he had seen plants with a well-developed median tooth between normal *H. wrightii*. In the original description of *H. wrightii* Ascherson (1869 a) made the following remark: ". . . . höchst wahrscheinlich wegen der viel längeren, relativ und auch absolut schmäleren Blätter (¼—1 mm, bei *H. australis* bis 2 mm), welche an den feinblättrigen Exemplaren lang- und fein zweispitzig mit abgerundeter Bucht enden[1]), als Art zu trennen". Thus the specimens with wider leaves do not agree with his description of *H. wrightii*. The material of *Wright 3720* from Cuba, identified by Ascherson as his *Halodule wrightii*, consists in fact of two species: *H. wrightii* and *H. beaudettei*. His insufficient and indiscriminate description of *H. wrightii* certainly has contributed to the fact that a well-defined species like *H. beaudettei* escaped attention.

A further contribution to the confusion within the genus *Halodule* was given by Ascherson (1906) in his work about the geographic distribution of the sea-grasses: "Die schmalen Blätter, ..., haben an der Spitze zwei oder drei stark hervortretende Zähne, von denen der mittlere gewöhnlich bei 19 (= *H. wrightii*), manchmal auch bei 20 (= *H. uninervis*), frühzeitig abgestossen wird (Ostenfeld), sind aber sonst ganzrandig." In this statement he did not stress the clear difference in structure between the median tooth of the leaf-tip of *H. uninervis* and the projection of the midrib at the leaf-tip of *H. wrightii*.

Ostenfeld (1902) considered the shape of the leaf-tip an insufficient character for distinguishing between the two species, as he thought the young leaves were tridentate and the older ones bidentate. In his publication on the Australian sea-grasses (Ostenfeld, 1916) he gave, nevertheless, a good description of the leaf-tip of *H. uninervis*. Bernatowicz (1952) also had not much confidence in the shape of the leaf-tip as a distinguishing character. He recorded from Florida a plant, referred to as *Diplanthera wrightii*, having

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[1]) Spacing mine.

bidentate as well as tridentate leaf-tips. The third tooth in the tridentate leaves will have been no doubt the projection of the midrib. It is a pity that this author did not give further details. In Florida Phillips (1960 a) found bidentate as well as tridentate specimens of *Halodule*. Without doubt he had both *H. wrightii* and *H. beaudettei*, but the latter species was not recognized by him as an independent taxon. So he came to the conclusion that *H. wrightii* and *H. uninervis* perhaps belong to one species.

Miki (1932) used the shape of the leaf-tip for separating *H. uninervis* with its tridentate leaf-tip from *H. pinifolia* with many serratures at the top (fig. 10).

According to my experience the shape of the leaf-tip is a very useful character. The old species *H. wrightii* and *H. uninervis*, as well as the more recently described *H. pinifolia*, can be easily distinguished by means of this character. Recently I made use of it in the definitions of some new species from the Pacific coast of Central America (Den Hartog, 1960). The new species described in this paper has also a very characteristic leaf-tip. However, the character should be handled carefully, as the tips of the young leaves are often somewhat different from those of the older leaves. In this work, therefore, use has been made only of fullgrown leaves for the description of the tip. Moreover, the possibility can not be excluded that the species may sometimes show dimorphism of the leaves. Although I have not met with such plants in the genus *Halodule*, leaf dimorphism occurs in the related sea-grass *Amphibolis antarctica* (Labill.) Sonder & Ascherson. The tips of the earlier leaves in this species are obtusely rounded, but the later leaves have a bidentate tip. Both leaf-types are linked by transitional forms.

b. The width of the leaf

The width of the leaf of *Halodule* has rarely been used for taxonomic purposes. Miquel (1855) recorded that his *H. australis* was much more delicate than *Diplanthera tridentata* Steinheil. Ascherson (1882, 1907) referred to the difference in width in the leaves of *H. uninervis*: some specimens had leaves as delicate as those of *Ruppia*, while others were coarser, more like those of *Zostera nana*. In fact Ascherson here confused two species. The coarse specimens belong indeed to *H. uninervis*, but the fine ones were no doubt *H. tridentata*. The same is true when Ascherson stated that the male plants of *H. uninervis* were fine and the female plants much coarser; in this case too the male plants were *H. tridentata* and the female ones *H. uninervis*. Sauvageau (1890, 1891) also referred the delicate plants from New Caledonia (belonging to *H. tridentata*) and the robust plants from the Red Sea (belonging to *H. uninervis*) to one species. Miki (1932) recorded a clear difference in the width of the leaves between *H. uninervis* and *H. pinifolia*. The first species has leaf-blades 2—2.7 mm wide, those of the latter are only 1—1.2 mm wide.

In fact the width of the leaf is a character which can be used for distinguishing *H. uninervis* from the other species of the genus. According to my measurements the width of the leaf of *H. uninervis* is 1¼—3½ mm; in the other species the leaves are 1¼ mm wide or narrower.

c. Intercellular spaces in the leaf

According to Sauvageau (1890, 1891) an important difference between *H. uninervis* and *H. wrightii* is that between the cells situated above and below the median vascular bundle in fullgrown leaves of *H. uninervis* intercellular spaces exist, while in the leaves of *H. wrightii* these spaces become well-defined lacunae. Feldmann (1938) also referred to these intercellular spaces.

Phillips (1960 a) investigated this character for *H. wrightii* and found it to be untenable. In general, plants found in the eulittoral belt, being exposed during every low-tide period, had only intercellular spaces as indicated by Sauvageau for *H. uninervis*; in material from low-water-mark, exposed only during spring tides, lacunae were slightly evident, and in the sublittoral specimens large lacunae were found, as indicated by Sauvageau for *H. wrightii*. There is thus a change of this character under influence of environmental conditions. As Phillips (1960 a), however confused *H. wrightii* and *H. beaudettei* it is interesting to note that the plants with 3 projections at the leaf-tip had no lacunae at all or only very small ones. However, he did not mention such plants from the sublittoral region. In material of *H. beaudettei* collected in the sublittoral at 3—5 m depth from the Pacific coast of Central America, the parenchyma between the midrib and the epidermis had many intercellular spaces but no lacunae could be observed (Den Hartog, 1960). In this species the intercellular spaces seem to be smaller than in *H. wrightii*, and rarely become lacunous. Nevertheless, the variability of this character makes it unsuitable for taxonomic purposes.

3. The rank of the recognized taxa

Although the diversity within the genus *Halodule* is considerable the differential characters between the taxa are only slight and few in number. Therefore, the question may be raised as to whether all these taxa have specific rank or not. As the grade of variation within the generative characters and the modifying effect of the environment on the vegetative characters, however, are yet insufficiently known, it is very arbitrary to evaluate the one taxon as a species and the other only as a subspecies or a variety. Moreover, the different taxa have their own distribution patterns. For these reasons I have decided to consider provisionally all taxa to be of specific rank.

PHYTOGEOGRAPHICAL AND EVOLUTIONARY CONSIDERATIONS

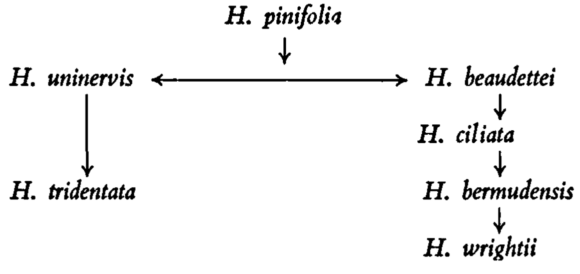
The genus *Halodule* has a pantropical distribution and only extends beyond the tropics into some subtropical waters influenced by warm sea currents. The old idea that the genus consists of only 2 vicarious species, *H. uninervis* and *H. wrightii*, which show slight morphological differences but have a widely separated area of distribution, has been maintained till the present time (Ascherson, 1869, 1875, 1882, 1889, 1906, 1907; Ostenfeld, 1902, 1915, 1927; Setchell, 1935; Feldmann, 1936, 1938; Phillips, 1960 b). According to this idea *H. uninervis* is confined in its distribution to the Indo-Pacific, and *H. wrightii* to the Caribbean. A similar distribution was noted for some other sea-grass species: *Syringodium isoetifolium* and *Thalassia hemprichii* (Ehrenb.) Aschers. are confined to the Indo-Pacific, while their closest relatives *Syringodium filiforme* and *Thalassia testudinum* Banks *ex* König occur only in the Caribbean. Ostenfeld (1915) supposed, that these twin-species descended from ancestors which were widely distributed in the tropical seas, and that their present differentiation into an Indo-Pacific and a Caribbean species was due to a change in the geographical situation of oceans and landmasses. He attached for this reason much importance to the formation of the Isthmus of Panama in the Tertiary Period, as this split up the original areas of the ancestors allowing them to start an independent development in the Caribbean area and in the Indo-Pacific. The close resemblance of each Caribbean species to an Indo-Pacific one seems to agree very well with this supposition.

As a consequence of my studies it seems more sensible to consider *H. uninervis* and *H. beaudettei* to be a species pair, as these species are certainly very closely allied, while the affinity of *H. uninervis* to *H. wrightii* seems less close. I am quite prepared to accept that *Halodule uninervis* and *H. beaudettei* have been derived from each other or from a common ancestor on the base of their striking similarity. However, these species must date from before the Miocene, when the uplift of the Isthmus of Panama took place, as *H. beaudettei* occurs on both sides of this land-bridge. At present the two species are widely separated by the wide oceanic region between Polynesia and America, which is known by marine biogeographers as the East Pacific barrier (Ekman, 1934, 1953). In my opinion it must be considered impossible for sea-grasses to cross this barrier. They are bound to the shallow coastal areas by their dependence on light for their photosynthesis. Further they are not equipped with special means for long-distance dispersal and, what is more, uprooted plants transported by currents soon die. According to Ekman (1953) there has not been a land-bridge or series of islands between Polynesia and America since the Tertiary Period. Van Steenis (1962 b) thinks that a tropical transpacific land-bridge must have existed in the Mesozoic Period, as otherwise the distribution of pantropical angiosperm families seems inexplicable. The biological evidence for such a land-bridge is quite considerable; the geological evidence is scantier. The sea-grasses must have been widely distributed in the coastal waters of this tropical land connection. At the time that it began to disintegrate, which is thought to have happened from the middle Cretaceous onwards, the genera *Halodule*, *Syringodium*, *Thalassia*, and *Halophila* must have been already well-developed. The close resemblance of the twin-species, therefore, must not be regarded as an indication of their recent origin, but rather it must be seen as a reflection of the evolutionary conservatism of phanerogams in the marine environment.

The most primitive species of the genus *Halodule* with respect to generative as well as to vegetative characters is certainly *H. pinifolia*. In this species the anthers are sometimes supported by a minute scale, which may be regarded as a reduced perianth (Miki, 1934). Its leaf-tips are rounded and the lateral teeth, so characteristic in other members of the genus, are not or hardly developed. The species is found in the West Pacific only and must be of great age.

From *H. pinifolia* the *uninervis-beaudettei*-group may have been derived. *H. uninervis* is widely distributed in the Indo-West Pacific, but it should be observed that it is an extremely rare species in the northern part of the Indian Ocean. *H. tridentata* which occurs in Madagascar and along the northern coasts of the Indian Ocean via Malesia to New Caledonia, is certainly a derivative of *H. uninervis*.

In the tropical American waters *H. beaudettei* has been the origin of a series of taxa, which culminated in the development of *H. wrightii* as is shown in the following scheme:



H. wrightii has a very remarkable distribution (fig. 8); it occurs in the West Indies as well as along the African west coast, but it has also a wide distribution in the western part of the Indian Ocean, extending from Mozambique and Madagascar northward to Kenya and the Persian Gulf. Such an area of distribution seems to be highly unusual for a species dependent on the sea for its dispersal. Van Steenis (1962 a) records that the

West African and East African mangrove swamps do not have a single species in common. Among the sea-grasses *H. wrightii* is the only species known from both the East and the West African coasts.

Among the algae a few taxa exist which seem to have a similar Atlantic-East African distribution. The phycological data must be considered, however, with the greatest care. Although the geographic distribution in general outline is known of the larger or otherwise conspicuous algae, new records repeatedly cause us to alter our original ideas and so transfer species or genera from one biogeographic group to the other. Svedelius (1924) has recorded two examples of algal taxa with an Atlantic-East African distribution, viz. *Chamaedoris peniculum* (Sol.) Kuntze (an old representative of the *Siphonocladiaceae*) and the genus *Cladocephalus* (a well-defined genus of the family *Codiaceae*). The first example can not be maintained any longer, as *C. peniculum* has been split into an Atlantic and an East African species, and moreover two other species of the genus have become known, one of them from Japan (Børgesen, 1940). I am unable to say in what measure the knowledge of the genus *Cladocephalus* has increased, since Svedelius (1924) recorded two West Indian species and a third one from Mauritius. Prof. Dr. J. Feldmann (Paris) has kindly given me information about another example, *Cystoseira myrica* (Gmel.) J. Ag. (a representative of the *Sargassaceae*), which is commonly distributed in the West Indies, the Red Sea and along the east coast of Africa. *Cystoseira* is a well-known Mediterranean-Atlantic genus, and is represented in the Pacific by only one very distinct species and in the Indian Ocean only by the already mentioned *C. myrica.*

Nevertheless, the possibility should not be excluded that the Atlantic and the East African forms of *Halodule wrightii* will appear to be not conspecific. Although I have not found any morphological character in which they differ, it is generally so that the East African form has slightly wider leaves than the Atlantic form, but both show the same maximum and minimum measurements. A study of living plants and cytological data are indispensable for a final solution of this problem.

HALODULE

Endl. Gen. Pl. Suppl. 1 (1841) 1368; Aschers. Linnaea 35 (1868) 163, 187—189; Benth. & Hook. *f.* Gen. Pl, 3 (1883) 1019 ("*Halodula*"); Aschers. in E. & P. Pfl. Fam. 2, 1 (1889) 212; Sauvageau, Journ. Bot. 4 (1890) 321—327; Ann. Sc. Nat. VII, 13 (1891) 245—252. — *Diplanthera* Du Petit Thouars, Gen. Nov. Madag. 2 (1806) 3; Steinheil, Ann. Sc. Nat. II, 9 (1838) 98; Aschers. Pfl. Reich Heft 31 (1907) 151; Miki, Bot. Mag. Tokyo 48 (1934) 134, 135.

Dioecious. Rhizome creeping, herbaceous, monopodially branched, with 2 vascular bundles in the cortical layer, and at each node one or more unbranched roots and a short erect stem bearing 1—4 leaves. Internodes ½—6 cm long. Scales 2, scarious, ovate or elliptic, with a varying number of longitudinal dark stripes and dots (tannin cells). *Leaves* distichous. Sheaths 1—6 cm long, compressed, amplexicaulous, scarious, at the top biauriculate and ligulate, with many short longitudinal dark stripes and dots (tannin cells), longer persistent than the leaf-blades, leaving circular scars which give the stem an annular appearance. Leaf-blades linear, often narrowed at the base. Nerves 3; midrib conspicuous, widened at the apex and there often even furcate; intramarginal veins inconspicuous, both ending in a mostly well-developed lateral tooth. Parallel with the nerves more or less short longitudinal dark stripes and dots (tannin cells). Leaf-tips very variable in outline. *Flowers* solitary and terminal, enclosed in a leaf similar to the others, while a bud in the axil of the penultimate leaf develops into the prolongation of the main axis giving rise to a sympodium. *Male flowers* pedunculate, consisting of 2 unequally inserted, extrorsely lengthwise dehiscent, 4-celled anthers with their lower parts joined dorsally. Pollen confervoid. *Female flowers* subsessile, consisting of 2 free carpels with 1 long style each. *Fruits* with stony pericarp, round-ovate, more or less compressed, not dehiscent, containing 1 pendulous seed.

KEY TO THE SPECIES

1. Leaf-tips with well-developed lateral teeth.
  2. Leaf-tips tridentate.
    3. Median tooth obtusely rounded.
      4. Leaves 1¼—3¼ mm wide, without secondary teeth. . . . . **1. H. uninervis**
      4. Leaves ½—1 mm wide; with many secondary teeth and ciliae at the median tooth. **6. H. ciliata**
    3. Median tooth acute.
      5. Leaves filiform, ¼—½ mm wide, median tooth as long as the lateral teeth . **2. H. tridentata**
      5. Leaves linear, ⅜—1¼ mm wide, median tooth 1—10 times as long as the lateral teeth. **3. H. beaudettei**
  2. Leaf-tips bicuspidate.
    6. Leaves ⅛—⅘ mm wide; no secondary projections on the lateral teeth; innerside of the lateral teeth concave . . . . **4. H. wrightii**
    6. Leaves ⅜—1¼ mm wide, often with secondary projections on the lateral teeth; innerside of the lateral teeth convex . . . . **5. H. bermudensis**
1. Leaf-tips rounded, more or less serrulate; lateral teeth faintly developed or absent. Leaves ⅗—1⅕ mm wide. **7. H. pinifolia**

1. **Halodule uninervis** (Forsk.) Aschers. in Boiss. Fl. Orient. 5 (1882) 24; in E. & P. Pfl. Fam. 2, 1 (1889) 213; Sauvageau, Journ. Bot. 4 (1890) 321—326, f 1A, 2—4; Ann. Sc. Nat. VII, 13 (1891) 246—251, f. 51A, 52—54; K. Sch. & Laut. Fl. Deutsch. Schutzgebiete (1901) 162; Ostenfeld, Bot. Tidsskr. 24 (1902) 262, *pro parte*; Safford, Contr. U.S. Nat. Herb. 9 (1905) 290. — *Zostera uninervis* Forsk. Fl. Aeg.-Arab. (1775) CXX, 157 — *Zostera tridentata* Ehrenb. & Hempr. *ex* Solms in Schweinf. Beitr. Fl. Aethiop. (1867) 196. — *Halodule australis* (*non* Miq.) Aschers. Linnaea 35 (1868) 163, 187—189, *pro parte*; in Neumayer, Anl. Wiss. Beob. Reisen ed. 1, 1 (1875) 364, *pro parte*. — *Cymodocea australis* (*non* Trimen) Bennett in This.-Dyer, Fl. Trop. Afr. 8 (1902) 229, *pro majore parte*. — *Diplanthera uninervis* Aschers. in E. & P., Pfl. Fam. Nachtr. 1 (1897) 37; F. N. Williams, Bull. Herb. Boiss. II, 4 (1904) 221; Aschers. in Neumayer, Anl. Wiss. Beob. Reisen ed. 3, 2 (1906) 401; Pfl.Reich Heft 31 (1907) 152; Merrill, Philip. Journ. Sc. 10 (1915) Bot. 3; Ostenfeld, Dansk Bot. Ark. 2,6 (1916) 30; Backer, Handb. Fl. Java 1 (1925) 51; Merrill, Enum. Philip. Fl. Pl. 1 (1925) 24; Ostenfeld, Pflanzenareale 1,4 (1927) 47, map 34; Miki, Bot. Mag. Tokyo 46 (1932) 783, f. 8; Van Steenis, Trop. Natuur 22 (1933) 44, f. e; Kanehira, Enum. Micron. Pl. (1935) 246; Camus, Flor. Gén. Indo-Chine 6,9 (1942) 1215, f. 116 no 1—5, *pro parte*; Jumelle in Humbert, Fl. Madagascar, fam. 21 (1950) 16, *pro parte*; Dawson, Pacif. Sc. 8 (1954) 376, f. 2a — f; Dickson, Wild Flowers Kuwait and Bahrein (1955) 38; Yuncker, Bishop Mus. Bull. 220 (1959) 51; Pham-Hoang Ho, Contribution à l'étude du peuplement du littoral rocheux du Sud-Vietnam (1961) 101 (*"forme à larges feuilles"*) **Fig. 1—3.**

Rhizome creeping with 1—6 roots and a short erect stem at each node. Internodes ½—4 cm long. Scales elliptic, 6—7 mm long. Sheaths 2—3½ cm long. Leaf-blades 10—15 cm long and 1¼—3¼ mm wide, narrowed near the base, sometimes falcate. Midrib conspicuous, widening but rarely furcate near the apex. Leaf-tip with 2 linear lateral teeth and an obtusely rounded median tooth in which the midrib ends, as long as or

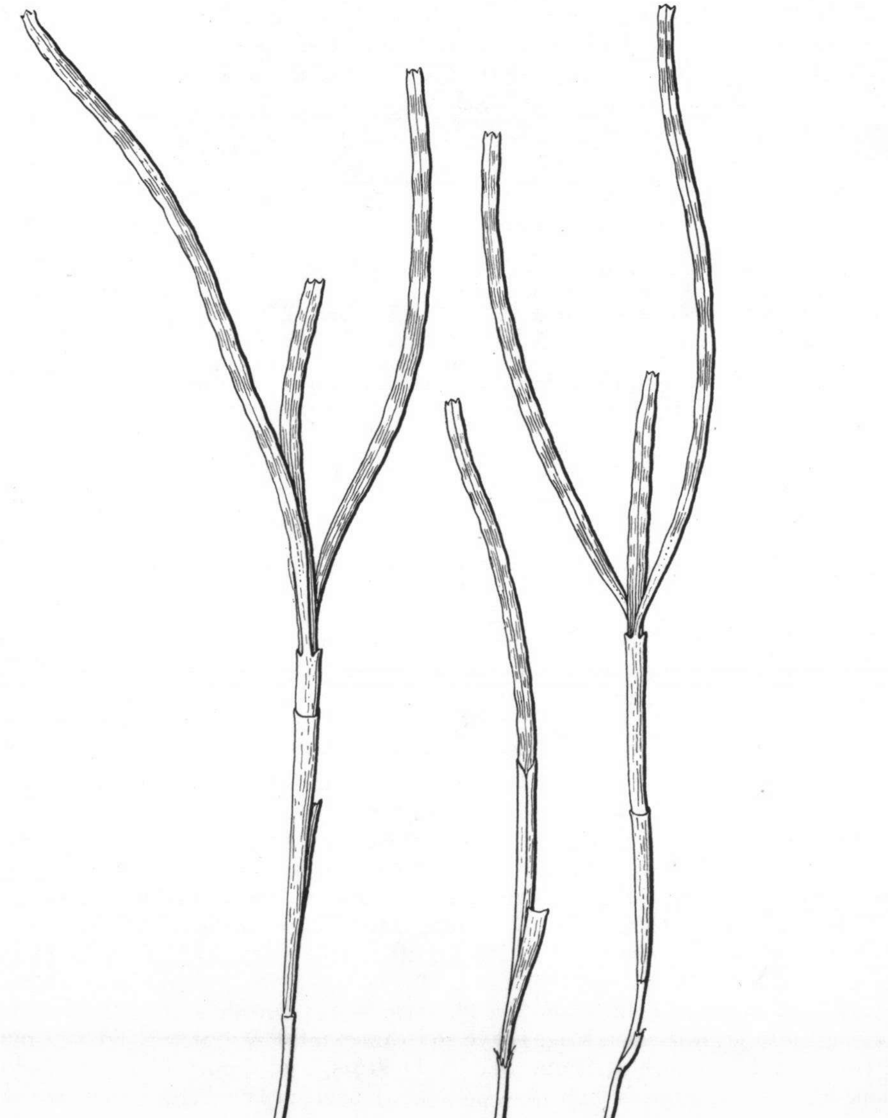


Fig. 1. *Halodule uninervis* (Forsk.) Aschers. (Sorong, *Beccari 11818A* = *P.P. 139*).

shorter than the lateral teeth, rarely slightly longer. Male flower pedunculate; anthers 3 mm. Female flower: ovary ovate, ½ mm, style 3—4 mm long, terminal (according to Miki, 1932, f. 8). Fruit roundish-ovate, scarcely appressed, 2½ by 2 mm, with an 1 mm long apically inserted rostrum.

Distribution: *H. uninervis* is widely distributed along the coasts of the Indian Ocean and the western Pacific. Along the east coast of Africa it extends from the Red Sea as far south as Delagoa Bay, and it occurs also on Madagascar and the Seychelles. Along the southern coast of Asia it is extremely rare and only found in the Persian Gulf and on Ceylon. The eastern part of the area reaches from the Gulf of Siam and Japan via Malesia to Australia and the Tonga Achipelago.

EGYPT. Jern-sah near Gimsah, 22-8-1868 (K); "Aegypte" *ex Herb. Persoon* (L).
ERITREA. Massaua, southern side, 3-1-1891, *Schweinfurth 5* (K).
FRENCH SOMALILAND. Danakiel coast, January 1873, together with *Halophila ovalis, Hildebrandt 701* (L).
KENYA. Diani Beach, 20 miles south of Mombasa, January 1961, *A. K. Miller* 355 (BM).
ZANZIBAR. Zanzibar, in the port, December 1906, *ex Herb. d'Alleizette* (L).

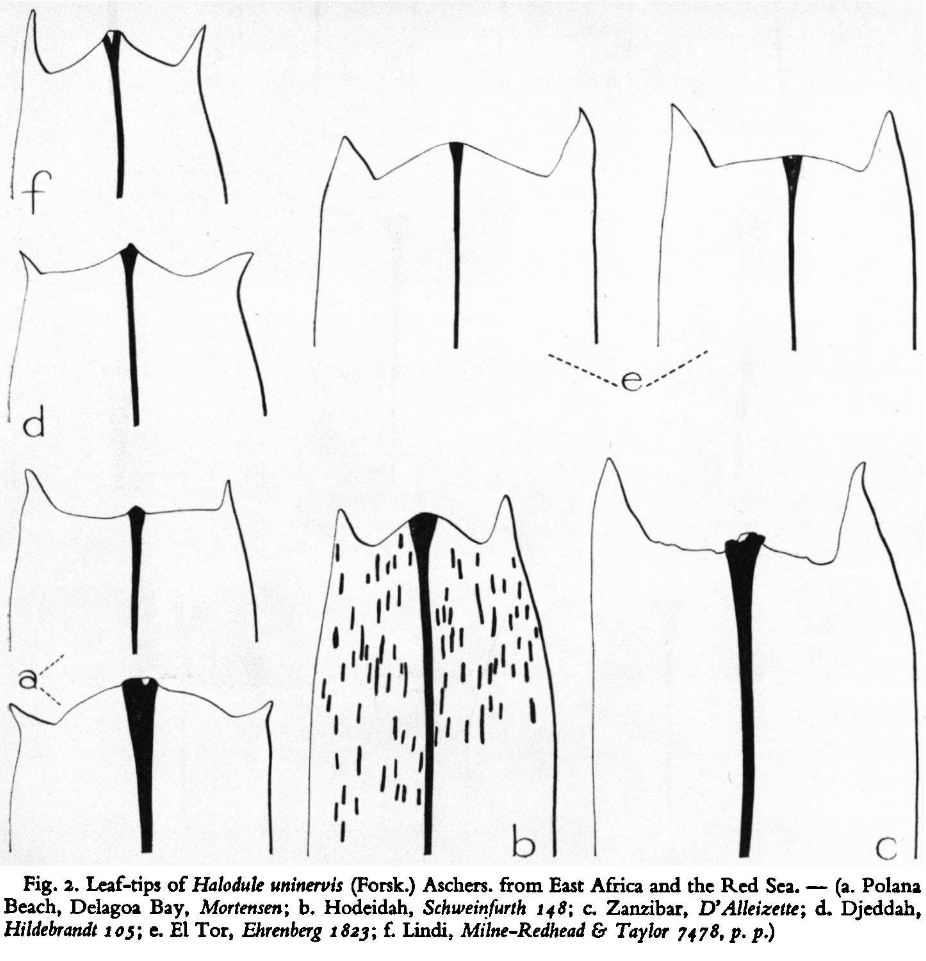


Fig. 2. Leaf-tips of *Halodule uninervis* (Forsk.) Aschers. from East Africa and the Red Sea. — (a. Polana Beach, Delagoa Bay, *Mortensen*; b. Hodeidah, *Schweinfurth 148*; c. Zanzibar, *D'Alleizette*; d. Djeddah, *Hildebrandt 105*; e. El Tor, *Ehrenberg 1823*; f. Lindi, *Milne-Redhead & Taylor 7478, p. p.*)

TANGANYIKA. Tanga District, Sawa, sandy mud close to the shore and also on coral reefs, together with *H. wrightii*, 20-7-1956, *Helen Faulkner 3* (BM, only *H. uninervis*; K, only *H. wrightii*). — Lindi District, about 6½ km north of Lindi, in about 15 cm of water at low tide rooting in about 5 cm sand over long flat rock, together with *H. wrightii*, 9-12-1955, *E. Milne-Redhead & P. Taylor 7478* (K, BM).

MOZAMBIQUE. Polana Beach, Delagoa Bay, together with *H. wrightii*, 3-9-1929, *Th. Mortensen* (C, K, BM). — Inhaca Island, Saco, mangrove swamp, 19-7-1956, *Y. M. Chamberlain 29* (BM); idem, mud-flats south-east of Saco-Peninsula opposite Ponte Torres, together with *H. wrightii*, 17-7-1957, *A. O. D. Mogg 27219* (K); Inhaca Island, together with *H. wrightii*, 30-8-1959, *R. Watmough 300, 302* (K, BM); Inhaca Island, Ponte Torres, Saco Bay, 29-10-1962, *Mauve & Verdoorn 36* (PRE); idem, opposite biological station, plentiful, 31-10-1962, *Mauve & Verdoorn 65* (PRE); idem, intertidal mud-flat between Melville village and Ilha de Portugueses, 27-12-1956, *A. O. D. Mogg 27177* (PRE).

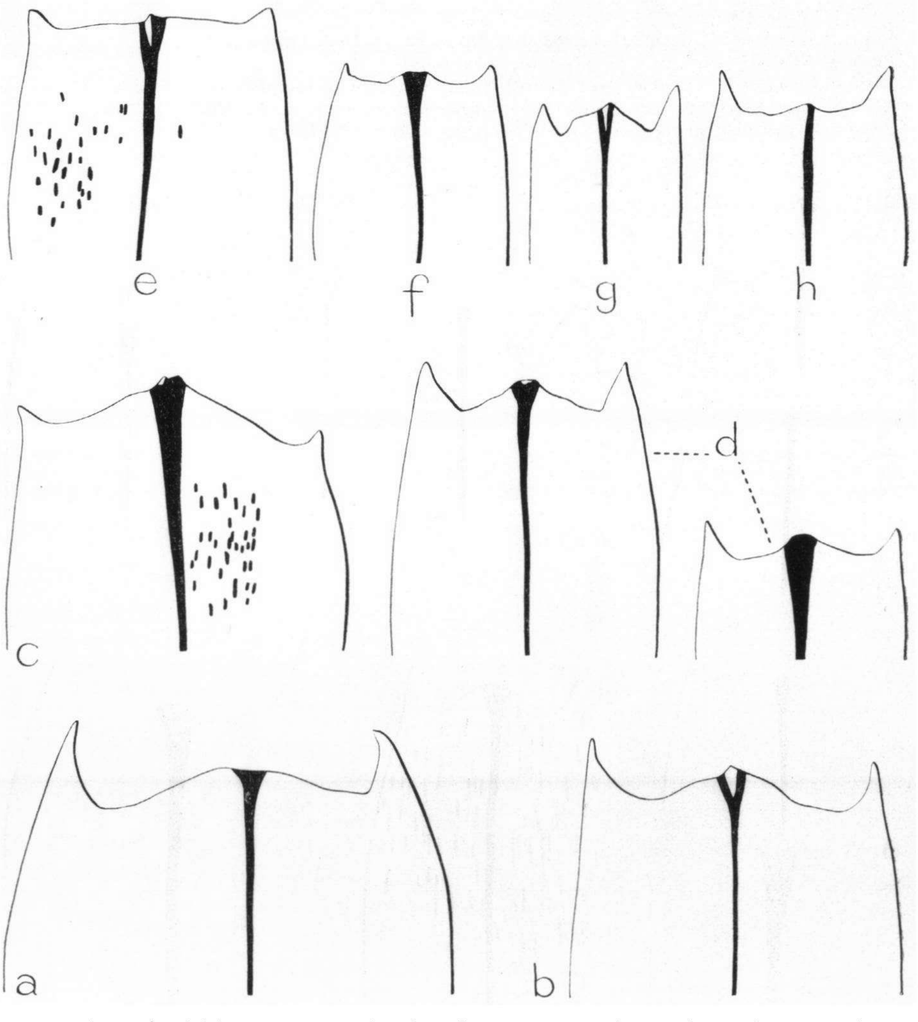


Fig. 3. Leaf-tips of *Halodule uninervis* (Forsk.) Aschers. from East Asia, Malesia, and Australia. — (a. Palawan, *Merrill 1264, p.p.*; b. Palawan, Taytay, *Merrill 9223*; c. Aru Islands, *Beccari 11819*; d. Carnarvon, *Ostenfeld 261*; e. Guam, *Mc Gregor 448*; f. Aru Islands, *Beccari 11820*; g. Koh Saket and Koh Kong, *Schmidt 350*; h. Singapore, *Burkill 547*).

Seychelles. Grande Anse Raslin, October 1952, *E. S. Brown* (BM).

Madagascar. Baie de Morombe, *Perrier de la Bâthie 13819* (P).

Saudi Arabia. Djeddah, on Madrepores in 1 m depth, April 1872, *Hildebrandt 105* (L. GH); Bay of Djeddah, floating in the water, 20-2-1954. *P. van Royen 2850* (L); El Tor, as "*Zostera tridentata*", 1823, *Ehrenberg* (L, K, C).

Jemen. Hodeidah, 23-12-1889, *Schweinfurth 148* (L, GH).

Kuwait. Ras-al-Ajusa, in sea on mud-banks exposed at very low tides, with *Halophila ovalis*, *Mrs. V. Dickson 566A* (K); Reefs at Meena-al-Ahmadi, May 1951, *F. G. Kellelt* (BM).

Bahrein Islands. Washed up in quantity on shore of Umm Nasan Island, 26-3-1950, *R. Good 399* (K); Bahrein, at 3—4 m depth, 29-3-1937, *M. Koie*, distributed by Rechinger as "*Plants of Iran 1734*" (C).

Ceylon. Without locality, *Willis* (K); Galle, *Børgesen 6014*, 1928 (US).

Thailand. Koh Saket and Koh Kong, January 1900, *J. Schmidt 350* (C); Rami Satut, growing in sand just exposed at low tides, with *Halophila minor*, 13-1-1928, *Kerr* (BM).

Vietnam. Phuquôc, just below the *Sargassum*-belt, January 1961, *Pham-Hoang Ho 2048* (L).

Malay Peninsula. Singapore, Pulau Senang, littoral in sandy pools of coral reef, 1-4-1956, together with *H. tridentata*, *Syringodium isoetifolium*, and *Halophila ovalis*, *Burkill 547* (SING, L, BO, A).

Japan. Ryu Kyu Islands, Okinawa, east side of the island, 10—20 miles north of Kadena, together with *Cymodocea rotundata*, 9/11-4-1953, *Dawson 11666* (UC).

Philippines. Palawan, May 1913, together with *Cymodocea rotundata*, *Merrill 1264* (BO, S, P); idem, Taytay, April 1913, together with *Syringodium isoetifolium*, *Merrill 9223* (P). — Mindoro, Puerto Galera, Censenada Bay, May 1924, *Pascasio 499 (15470)* (UC); idem, Censenada Bay, tidal flat, 3-6-1924, *Pascasio 496* (UC); idem, Censenada Bay, coral sand. *Pascasio 492 (15472)* (UC); idem, Medio Island, north side, coral sand behind coral reef, together with *Halophila ovalis*, May 1924, *Pascasio 381 (15486)* (UC); idem, Balateros Maliit, May 1924, *Pascasio 370 (15475)* (UC), *376 (15481)* (UC); idem, Balateros Maliit, tidal flat, coral sand behind coral reef, together with plenty of *H. pinifolia*, May 1924, *Pascasio 371 (15476)* (UC); idem, Balete Bay, May 1924, *Pascasio 385 (15491)* (UC).

Indonesia. Moluccas, Ternate, together with *Enhalus acoroides* and *Halophila ovalis*, *Teysmann* (BO); Aru Islands, P. Wokam, *Beccari 11819A* (L, FI); Aru Islands, 1873, *Beccari 11820* (L). — New Guinea, Sorong, 1872, together with fruiting *Cymodocea rotundata*, *Beccari 11818A (P.P. 139)* (L, FI); Radjah Ampat Islands, Batanta Island, Andoei village on the northern bank, 2-10-1954, together with *Syringodium isoetifolium*, *P. van Royen 3307* (L); Port Moresby, Ela beach, 17-6-1960, *Thorne 12564*, *pro parte* (LAE).

West Australia. Carnarvon, 31-10-1914, cast ashore, *Ostenfeld 216* (C).

Marianne Islands. Guam, October 1911, *Mc Gregor 448* (C, K, US); idem, 21-1-1939, without further data (K, BO, UC, US).

New Caledonia. Noumea, from beach at Anse Vata on day following typhoon, 16-3-1948, together with abundant *Syringodium isoetifolium* and *Halophila ovalis*, *T. J. Buchholz 1778* (K, UC, US); idem, Ile aux Canards, May 1949, *Mrs. R. Catala* (UC); idem, Ilot Maître, 29-7-1950, *M. J. Baumann-Bodenheim 5077* (GH).

Tonga Islands. Tongatapu, along the beach at Nuku'alofa, 15-4-1953, exposed at low tide, together with *H. pinifolia* and *Halophila ovalis*, *Yuncker 15288* (BM).

Ecology: *H. uninervis* is a characteristic species of shallow water. It occurs in the lower part of the eulittoral belt as well as in the upper part of the sublittoral. It has been found on sand-flats and mud-banks, in sandy pools on coral reefs and in creeklets in the mangrove swamps. *H. uninervis* is often associated with *Cymodocea rotundata*, *Syringodium isoetifolium*, and *Halophila ovalis*, and aong the coast of East Africa also with *Halodule wrightii*.

Note: As *H. uninervis* and *H. tridentata* were confused formerly, it is not always clear to which species the flower descriptions in literature refer to. Many data in the work of Ascherson, in particular, seem unreliable in this respect. The description by Camus (1942) gives no indication whether it had been made from typical *H. uninervis* or the "forme grêle" (= *H. tridentata*). The peduncle of his plant was 1.2—1.6 mm, and the anther 2½—3 mm; these data, however, do not agree with his figure.

2. Halodule tridentata (Steinheil) F. v. M. Census Austr. Pl. (1882) 121. — *Diplanthera tridentata* Steinheil, Ann. Sc. Nat. II, 9 (1838) 98, pl. 4B; F. v. M. Sec. Census Austr. Pl. (1889) 204. — *Diplanthera madagascariensis* Steud. Nomencl. Bot. 1 (1840) 515, *nomen.* — *Ruppia sp.* Zollinger, Syst. Verzeichnis (1854) 74. — *Halodule australis* Miq. Fl. Ind. Bat. 3 (1855) 227; Aschers. Linnaea 35 (1868) 163, 187—189, *pro parte*; Sitz. Ber. Ges. Naturf. Fr. Berlin 1867 (1868) 3; in Neumayer, Anl. Wiss. Beob. Reisen ed. 1, 1 (1875) 364, *pro parte.* — *Cymodocea australis* Trimen, Syst. Cat. Ceyl. Pl. (1885) 99; J. Bot. 23 (1885) 174; Hook. *f.* Fl. Br. India 6 (1894) 570; Trimen, Handb. Fl. Ceylon 4 (1898) 377; Bennett, Fl. Trop. Afr. 8 (1902) 229, *pro minore parte.* — **Fig. 4.**

Rhizome creeping, with 2 roots and a short erect stem at each node, very thin. Internodes 1—3 cm long. Scales ovate. Sheaths 1—1½ cm long. Leaf-blades filiform, 6—8 cm long and ¼—½ mm wide, not narrowed at the base. Midrib conspicuous, bifurcate or widened at the apex. Leaf-tip tridentate, the median tooth as long as or even slightly longer than the linear lateral teeth. Male flower on a 6—7 mm long peduncle; anthers 2—3 mm, the upper anther inserted less than ¼ mm higher than the lower one, according to Steinheil (1838), but in male flowers from New Caledonia this distance was ½ mm *(Balansa 1529)*. Female flower recorded by Sauvageau (1890, 1891) in New Caledonian material, but not seen by me. Fruit unknown.

Distribution: *H. tridentata* is described from Madagascar. It occurs also in Mauritius, but its main distribution is no doubt in the northern part of the Indian Ocean; it has been found in the Red Sea, the Persian Gulf, India, the Gulf of Siam, and Malesia, extending eastwards to New Caledonia.

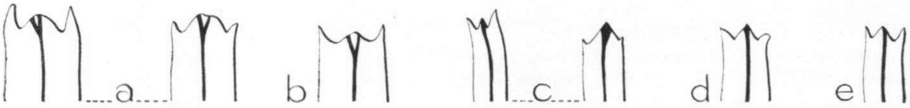


Fig. 4. Leaf-tips of *Halodule tridentata* (Steinheil) F. v. M. — (a. Bima, *Zollinger 3431*; b. Cannoniers Point, Mauritius, *Mortensen*; c. Kaibóbo-Oernitoe on Ceram, *P. J. Eyma 2975*; d. Tanjong Behala Kuda, Singapore, *Sinclair 38895*; e. Port Dickson, *Van Steenis 18492*).

MOZAMBIQUE. Inhaca Island, Ponte Torres, Saco Bay in shallow pool at low tide, 30-10-1962, *Mauve & Verdoorn 73* (PRE).

MAURITIUS. Flat Island, 17-10-1929, *Th. Mortensen* (C, K); Cannoniers Point, 21-9-1929, *Th. Mortensen* (C, K).

MADAGASCAR. Without locality, *Du Petit Thouars*, with ♂ flower (*Type*, P).

EGYPT. Abu Zencima, Red Sea, 13-4-1937, *Rehabetai* (K).

BAHREIN ISLANDS. Coral reef Jufaer, 2-3-1950, *R. Good 330* (K).

INDIA. Tuticorin, Tumevally, 2-10-1916 (K); Tuticorin, 25-2-1928, *Børgesen 281 pro parte*; idem, Hare Island, 29-2-1928, *Børgesen* (GH).

JAPAN. Ryukyu Islands, Okinawa, north side of Kachin Peninsula, on sandy sea bottom at low tide, 4-7-1951, *E. H. Walker, S. Tawada & T. Amano 6013a* (US); Okinawa, on exposed shore of mud and coral fragments of broad bay on the east side of the island, opposite Cadena, 9/11-4-1953. *E. Y. Dawson 11618* (UC).

PHILIPPINES. Palawan: May 1913, together with *Halophila ovalis* and *Halodule pinifolia*, *Merrill 1263* (GH). — Mindoro: Puerto Galera, Balete Bay, May 1924, together with *Cymodocea serrulata*, *Pascasio 388 (15490)* (UC); idem, Balete Bay, tidal flat, coral mud, together with *Halophila ovalis*, *Pascasio 390 (15488)* (UC); idem, Censenada Bay, tidal flat, May 1924, *Pascasio 498* (UC).

MALAY PENINSULA. Perak: Pangkor Island, Pasir Bogak, 10-7-1955, sheltered water to 3 fathoms depth, sandy coral substratum, washed up or brought up by fishing nets, *H. M. Burkill 309* (bad material, probably this species) (SING). — Negri Sembilan: Port Dickson, 13-1-1954, submerged on sand-covered reef in front of the beach, *Van Steenis 18492* (L). — Johore: Pulau Tinggi, 19-6-1915, growing near low tide level on sandy coral beach, some plants show cecidiae caused by the fungus *Plasmodiophora diplantherae*, *Burkill 899* (SING). — Singapore, without locality, 1892, *Ridley* (SING); Singapore, Pulau Senang, 1-4-1956, littoral in sandy pools on coral reef, together with *H. uninervis*, and a few *Syringodium isoetifolium* and *Halophila ovalis*, *Burkill 547* (SING), BO, A, L); Singapore, Labrador, 21-3-1928, *R. E. Holttum* (SING); idem, Tanjong Behala Kuda, Pulau Pawai, together with *Halophila minor*, 14-3-1950, *Sinclair 38895* (L, BO, SING); Singapore, *Eduard*, as "*Zostera nana* Roth", photo from material *ex* Mus. Bot. Berolensis (UC).

Indonesia. Java: Bondowoso, Pani poeteh, common on coral reef, June 1931, *Clason-Laarman F71* (BO). — Lesser Sunda Islands: Bima near Kambing, 18-10-1847, *"repens in arena submersa"*, *Zollinger 3431*, as *"Ruppia sp."* (P). — Moluccas: western part of Ceram at Kaibóbo-Oernitoe, common on sandy soil at 1 m depth, 17-2-1938, *P. J. Eyma 2975* (L, BO).

New Caledonia. Alcmène, 1868—70, *Balansa 1529*, with ♂ flowers (K); Balade, on muddy bottom, 8-1-1961, *H. S. McKee 8009*, as *"Ruppia maritima"* (US).

Ecology: *H. tridentata* occurs in small patches on sandy coasts, in the upper part of the sublittoral; exceptionally it extends above the mean low water level and rarely descends below a depth of 4 m. Furthermore, it has been found on coral reefs. The species prefers some shelter. It may be accompanied by *Halophila minor* or *H. ovalis*.

3. Halodule beaudettei (Den Hartog) Den Hartog, *nov. comb.* — *Diplanthera beaudettei* Den Hartog, Pacif. Natur. 1, 15 (1960) 4—5, f. 2a—c. — *Diplanthera dawsonii* Den Hartog, Pacif. Natur. 1, 15 (1960) 6, f. 2d—e. — **Fig. 5.**

Rhizome creeping, with 2—4 roots and a short erect stem at each node. Internodes ½—4 cm long. Scales elliptic, 5—10 mm long. Sheaths 1½—6 cm long. Leaf-blades 5—20 cm long and ⅜—1¼ mm wide, narrowed near the base. Midrib conspicuous, widening and often furcate near the tip. Leaf-tip with a very prominent, acute median tooth which is 1—10 times as long as the narrow, linear lateral teeth. Flowers unknown.

Distribution: *H. beaudettei* is widely distributed in the Caribbean and also in the Gulf of Mexico. Along the Atlantic coast of North America the species extends northwards to North Carolina. The species also occurs along the Pacific coast of Panama and Nicaraqua.

United States of America. North Carolina, Onslow County, New River at Marines, 11-11-1935, *N. Hotchkiss & C. Cottam 4780* (K, GH, UC, US). — Florida, Monroe County, Big Pine Key, 5-3-1936, sandy ocean bottom in shallow water, *E. P. Killip 31733* (K, P, U, UC); idem, 3-2-1952, *E. P. Killip 41880* (GH); idem, 1/17-2-1937, *E. P. Killip 32018* (GH), *32019* (UC); Monroe County, Joe Kemp's Key, sand dunes, 27-11-1916, *J. K. Small 8003* (GH, US); Cape Sable (Northwest Cape), 28-11-1916, *J. K. Small 8044* (GH); Franklin County, Lanark station, very abundant on tidal flats, 18-7-1956, *R. Kral 2824* (GH); Pinellas County, Tampa Bay, St Petersburg, shallow water at extremely low tide, 24/28-12-1951, *R F. Thorne 10304* (UC); idem, Boca Ciega Bay off Gulf port, shallow water, 24/28-12-1951, *R. F. Thorne 10306* (UC, US); Brevard County, Allenhurst, shallow water of Mosquito Bay, 5-5-1930, *N. Hotchkiss & L. E. Eksvall 3865* (US); Taylor County, Jug Island, in large patches on very muddy bottom, 16-8-1957, *R. K. Godfrey 55951a* (GH); West Florida, Zauark, 12-4-1925, *A. M. Heury* (UC); Cedar Keys, with *Syringodium filiforme*, August 1936, *E. B. Gist 117*. — Texas, Cameron County, Lagune Madre, west of Port Isabel, 6-3-1936, *N. Hotchkiss 4876* (UC, US); Aransas County, St Joseph Island in Aransas Bay, 25-1-1936, *N. Hotchkiss 4856* (GH).

Cuba. Without locality, *C. Wright 3720, pro parte* (K, GH). — Province of Matanzas, Varadero, sea level, together with *H. wrightii*, 27/29-12-1937, *E. P. Killip 32404* (US). — Province of Oriente, near Cabo Cruz, in shallow water, July 1935, *Bro. Léon 16312* (US); idem, Belig between Nianero and Cabo Cruz, 20-7-1935, *Bro. Léon* (GH).

Hispaniola. Haiti, Ile de la Tortue, Tete de l'Ile, 11-6-1925, on shallow sea-bottom, *E. L. Ekman* (K, US).

Jamaica. Portland Ridge near Clarendon, northeast side, in sea off Mahoe Gardens, 15-4-1956, *Stearn 762* (BM, A); South Caicos, east bay, together with *Syringodium filiforme*, 22-6-1954, *G. R. Proctor 8910* (GH).

Bahama Islands. Bimini Island group, submerged in Bimini Bay, together with *Syringodium filiforme*, May 1948, *R. A. & E. S. Howard 10035* (GH, US).

Virgin Islands. St Thomas, "Saen ved Tutu", as "*Zostera nana* Roth", *Krebs* (C); idem, *ex herb. Hornemann*, as *"Zostera nana"* (C); idem, Mosquito Bay, 25-1-1914, *Ostenfeld 182* (C). — St Croix, coast of Krause Lagoon, 14-2-1906, *Børgesen* (K, C).

St. Martin. Simsons Bay, 11-11-1906, *Boldingh 2264* (narrow form, revised by Stoffers as *"Cymodocea manatorum"* and distriuuted as *Plant. Ind. occid. Boldingh anno 1906, no 3260 B*) (U).

Panama. Pacific coast, north side of Isla Jicarón, 25-3-1959, *Dawson 21104* (*Type* in Herb. Beaudette Foundation; UC, L); North side of Punta Naranja, 23-3-1959, *Dawson 21419* (Herb. Beaudette Foundation; L).

NICARAGUA. Corinto, on a sand bottom subjected to strong tidal currents at a depth of 3 m along the east side of the outer harbour, 3-4-1959, *E. Y. Dawson 21429* (Herb. Beaudette Foundation, UC, L).
GUATEMALA. Dept. Izabel, Bay of Santo Tomás, between Escobas and Santo Tomás, 13-4-1940, *J. A. Steyermark* (US).

Ecology: In the upper part of the sublittoral the species forms extensive submarine meadows on silty bottoms and sometimes occurs together with *H. wrightii* and other sea-grasses.

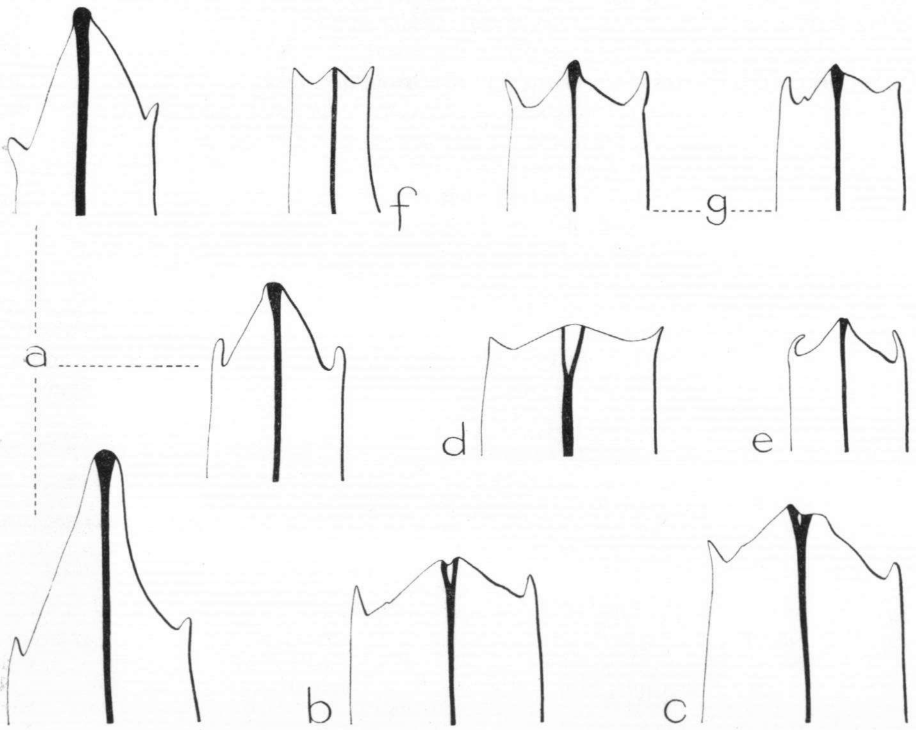


Fig. 5. Leaf-tips of *Halodule beaudettei* (Den Hartog) Den Hartog. — (a. Isla Jicarón, Panama, *Dawson 21104*; b. Big Pine Key, Florida, *E. P. Killip 31733*; c. Cuba, *Wright 3720, pro parte*; d. Ile de la Tortue, Haiti, *Ekman*; e. St Thomas, *Hornemann*; f. St Martin, *Boldingh 3260B*; g. St Thomas, *Krebs*).

Note: *H. beaudettei* may be regarded as the American twin species of *H. uninervis*, as they are very closely related, and differ only by the width of their leaves and in the shape of the median tooth of their leaf-tips. Sometimes, however, specimens with leaf-tips very similar to those of narrow *H. uninervis* may be found and then can not be distinguished from it by this character. Nevertheless, the two species as a whole are quite distinct.

4. **Halodule wrightii** Aschers. Sitzber. Ges. Naturf. Fr. Berlin 1868 (1869) 19, 24; in Neumayer, Anl. Wiss. Beob. Reisen ed. 1, 1 (1875) 364; Bth. & Hook. *f.* Gen. Pl. 3 (1883) 1019; Aschers. in E. & P. Pfl. Fam. 2, 1 (1889) 213; Sauvageau, Journ. Bot. 4 (1890) 326—327, f. 1B, 5; Ann. Sc. Nat. VII, 13 (1891) 251—252, f. 51B, 55; Stehlé,

Bull. Soc. Bot. Fr. 84 (1937) 422—423. — *Diplanthera wrightii* Aschers. in E. & P. Pfl. Fam., Nachtr. (1897) 37; in Neumayer, Anl. Wiss. Beob. Reisen, ed. 3, 2 (1906) 400; in Pfl.Reich Heft 31 (1907) 153; Ostenfeld, Pflanzenareale 1,4 (1927) 47, map 34; Feldmann, Bull. Soc. Bot. Fr. 83 (1936) 606; Bull. Soc. Hist. Nat. Afr. Nord 29 (1938) 107—112, f. 1; Bernatowicz, Bull. Mar. Sci. Gulf & Caribbean 2 (1952) 338; Humm, *op. cit.* 6 (1956) 306; Phillips, *op. cit.* 10 (1960) 346—353, f. 1b, 2, 4—8; Florida State Board of Conservation Prof. Pap. 2 (1960) 47—53. — *Zostera nana* (*non* Roth) Bennett, Fl. Trop. Afr. 8' (1902) 225. — **Fig. 6—8.**

Rhizome creeping, with 2—5 roots and a short erect stem at each node. Internodes ¾—3½ cm long. Scales elliptic, 4—9 mm long. Sheaths 1½—4 cm long. Leaf-blades 5—18 cm long and ⅓—⅘ mm wide, narrowed near the base. Midrib conspicuous, sometimes ending in a very small tooth which easily breaks off, mostly not projecting. Intramarginal veins inconspicuous, both ending in a narrow, triangular lateral tooth, giving the leaf-tip a bicuspidate appearance. The inner sides of the lateral teeth are more or less concave. Male flower pedunculate; anthers slender, 4 mm long; the upper anther is inserted *ca.* 1 mm higher than the lower one (Ascherson, 1869 b; in Ascherson's later publications — 1889, 1907 — the lenght of the anthers is given as being 6 mm). Female flower: ovary elliptic, compressed, 1½—2 mm, with an 11—12 mm long subterminal style (description according to *Moss 20793*). Fruit ovate, slightly compressed, 1½—2 mm, with a very short rostrum.

Typification: Ascherson (1869 a) based his species *H. wrightii* on material from Cuba collected by C. Wright in 1865, which had the number 84. This material was burnt in Berlin during the Second World War. It is not certain whether these plants were part of the material distributed as '*Plantae Cubensis Wrightiana*' *n. 3720*. From the original description it is quite clear that Ascherson had a heterogeneous material at his disposal, and that the character of the bicuspidate leaf-tip is only valid for the finer plants. A description of the coarser plants was not given at all. The material distributed as *Wright 3720* is also not homogeneous but consists of two species. In the Kew Herbarium a sheet is present on which both species are mounted and on which the name '*Halodule wrightii*' was written by Ascherson himself. The fine specimens on the right side of the sheet agree very well with Ascherson's description and I want to indicate them as the neotype of *H. wrightii*. The coarser specimens on the left side of the sheet belong to *H. beaudettei*.

Distribution: *H. wrightii* is widely distributed in the Caribbean. It has been recorded also from the Bermuda Islands (Bernatowicz, 1952). It is highly remarkable that not a single record is available from the continental coast of South America. The species has been recorded from the west coast of Africa from Angola by Ascherson (1869, 1907) and from Mauretania and Senegal by Feldmann (1938). Moreover, the species is not uncommon along the African east coast, where it extends from Madagascar, Mauritius, and Mozambique to Kenya, and further into the Persian Gulf. It may be mentioned here that the area of the species in the Indian Ocean in general outline coincides with the area of *Halophila stipulacea* (Forsk.) Aschers. Almost all records of *Halodule wrightii* from the coast of the U.S.A. refer to *H. beaudettei*; I have not seen a single specimen of *H. wrightii* from the U.S.A., but it is apparent from the descriptions of Phillips (1960 a, b) that this species occurs in Florida. (Fig. 8.).

CUBA. *Pl. Cub. wrightiana 3720, pro parte* (K, C, GH, US). — Province of Oriente, Guantanamo Bay, 17/30-3-1909, *N. L. Britton 2129* (US). — Province of Matanzas, Varadero, 27/29-12-1937, together with *H. beaudettei*, *E. P. Killip 32404* (US).

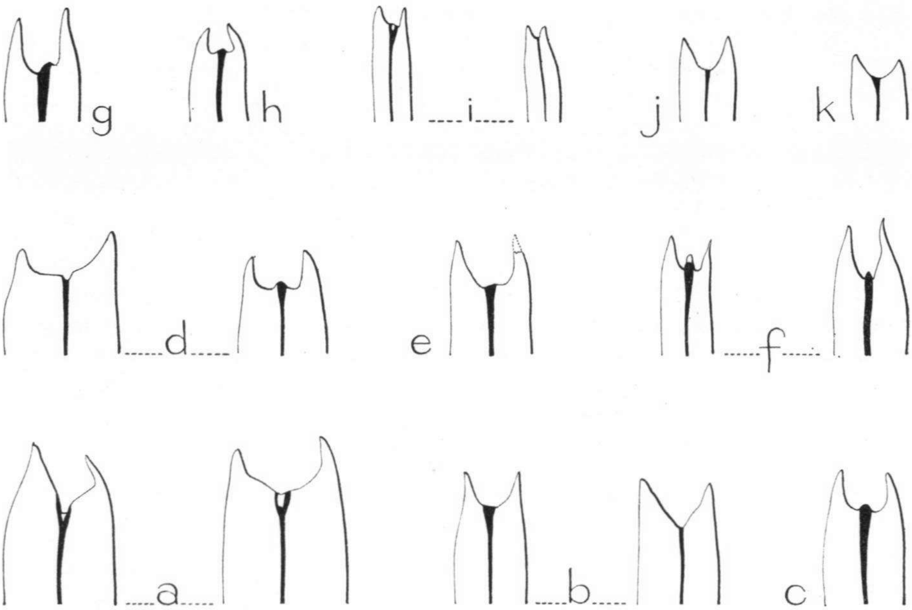


Fig. 6. Leaf-tips of *Halodule wrightii Aschers.* from the Atlantic Ocean. — (a. Guánica, *P. Sintensis*; b. San Juan, Condade Bay, *Ostenfeld 2*; c. Colon, *Howe*; d. Guánica, *P. Sintensis 3357*; e. St. Croix, Krause Lagoon, *Børgesen 5876*; f. Cuba, *Wright 3720, p.p.*; g. St Croix, Christiansted Lagoon, *Ostenfeld 289*; h. idem, *Børgesen*; i. Salinas de Cabo-Rojo, *P. Sintensis 837*; j. Loanda, *Welwitsch 246*; k. Punta Tuglesa. Hispaniola, *Fuertes 798*).

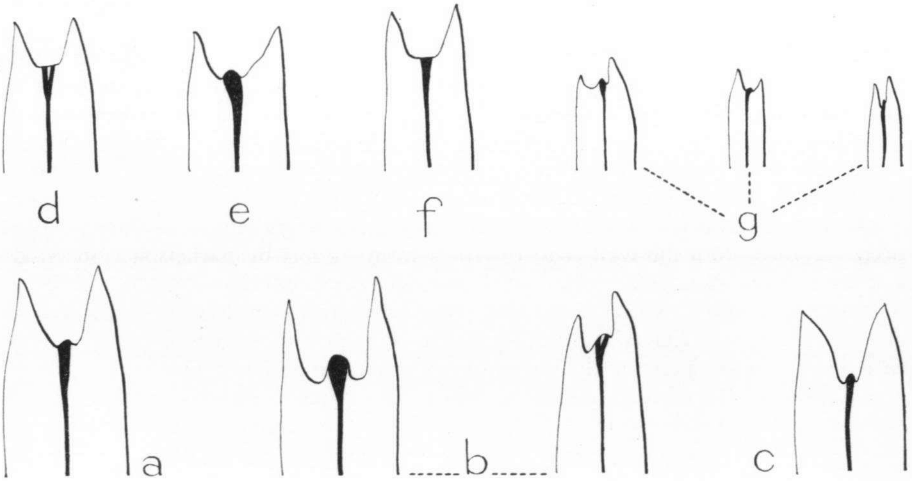


Fig. 7. Leaf-tips of *Halodule wrightii* Aschers. from the Indian Ocean. — (a. Tanganyika, Bomandani, *Drummond & Hemsley 3690*; b. Mombasa, *Wild 4835*; c. Nyali beach, Mombasa, *Verdcourt 1066*; d. Lindi, *Milne-Redhead & Taylor 7478 p.p.*; e. Madagascar, *D'Alleizette*, July 1906; f. Norontsánga, *Hildebrandt 3213*; g. Polana Beach, Delagoa Bay, *Mortensen*).

HISPANIOLA. Dominican Republic, Prov. Barahona, near Punta Tuglesa, May 1911, mixed with *Syringodium filiforme*, *Fuertes 798* (K, L, C, U, GH, US).

PORTO RICO. Salinas de Cabo-Rojo, 6-2-1885, *P. Sintensis 837* (L, K, US); Guánica, 22-1-1886, *P. Sintensis* (C, K); idem, 23-1-1886, *P. Sintensis 3357* (GH, US), 23-1-1906, *J. Curtiss* (L); San Juan, Condale Bay, 20-12-1913, *Ostenfeld 2* (U, C); Island of Culubrita, 11-3-1906, *M. A. Howe 283* (US); Morillos de Cabo-Rojo, 28-2-1915, *N. L. Britton, J. F. Cowell & S. Brown 4736* (GH, US).

VIRGIN ISLANDS. St Croix: Krause Lagoon, 4-2-1906, *Børgesen 5876* (C, U, US); Frederiksted, 1905/06, *Børgesen 5877* (C, GH); Christiansted Lagoon, 18-1-1906, *Børgesen* (C, U, Us); idem, 9-12-1914, *Ostenfeld 289* (C). — St Thomas, Mosquito Bay, 25-1-1914, *Ostenfeld* (US).

BAHAMA ISLANDS. Mariquana: Abraham Bay and vicinity, 6/8-12-1907, *P. Wilson 7539* (K, GH).

ST VINCENT TERRITORY. The Grenadines, Union Island: Chattam Bay 26/31—3 and 8/20-4-1950, *R. A. Howard 10999* (BM, GH).

PANAMA. Caribbean coast, Colon, near low-water-mark in the sea, 4-1-1910, *M. A. Howe* (C).

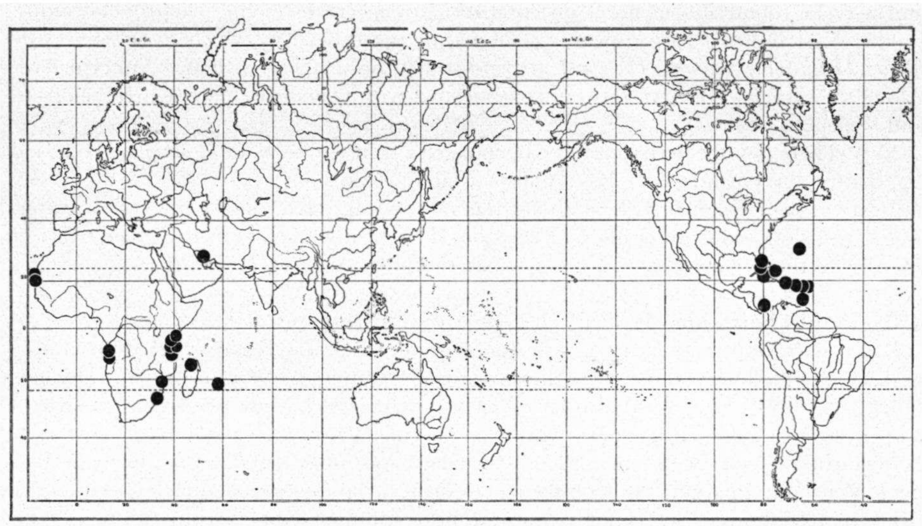


Fig. 8. The geographical distribution of *Halodule wrightii* Aschers.

ANGOLA. Loanda, *Welwitsch 246*, as "*Zostera nana*" (C, K); Ambriz, *Welwitsch 246B*, as "*Zostera nana*" (K).

KENYA. Kikambala, coast province, in sand towards low-water-mark, 1-1-1956, *D. Napper 443* (K); Kilifi district, Vipingo (20 miles north of Mombasa), growing with *Cymodocea rotundata* on sand in 2 ft water at high tide, 16-12-1953, *Verdcourt 1066* (K); Nyali beach near hotel, 6 miles north of Mombasa, around low-water-mark, growing in coral sand, 18-4-1950, *R. W. Rayner 289* (BM, K); Mombasa, washed up on shore, opposite the old harbour, in a few inches of sea water under *Sonneratia*, as "*Zostera? nana*", *H. Wild 4835* (K).

ZANZIBAR. Mangapwani, growing in shallow coral pools but covered with 6—10 ft of water at high tide; very common all around the coast, together with *Cymodocea rotundata*, 24-1-1929, *Greenway 1130* (K); without locality, June 1960, *A. K. Miller 368* (BM).

TANGANYIKA. Tanga District: Sawa, sandy mud close to the shore and also on coral reefs, together with *H. uninervis*, 20-7-1956, *Helen Faulkner 3* (K, only *H. wrightii*; BM, only *H. uninervis*); coast near Bomandani, 7 miles south of Moa, in sand in pools on coral reef on the seaward side of a mangrove swamp, 10-8-1953, *R. B. Drummond & J. H. Hemsley 3690* (K). — Lindi District: about 6½ km north of Lindi, in about 1½ dm of water at low tide, together with *H. uninervis*, 9-12-1955, *E. Milne-Redhead & P. Taylor 7478* (BM, K).

MOZAMBIQUE. Polana Beach, Delagoa Bay, together with *H. uninervis*, 3-9-1929, *Th. Mortensen* (C, K, BM); Inhaca Island, west coast, Delagoa Bay, rooting in firm sand in the intertidal belt, often growing with *Halophila ovalis*, 17-1-1952, *Moss 20793*, ♂ and ♀ plants (K); idem, Saco, 19-7-1956, *Y. M. Chamberlain 26* (BM); idem, intertidal mud-flats opposite the Marine Laboratory, 8-9-1957, *A. O. D. Mogg 27730* (K); idem, S. E. Saco Bay, mud-flats, 17-7-1957, *A. O. D. Mogg 27217* (K); idem, S. E. Saco peninsula opposite

Ponte Torres, together with *H. uninervis*, 17-7-1957, *A. O. D. Mogg 27219* (K); idem, on sandy flats, half-exposed by receding tide, together with *H. uninervis*, 30-8-1959, *R. Watmough 300* (BM); Inhaca Island, July 1935, ♀ flowers and fruits, *M. Moss* (J); idem, Oct/Nov 1962, together with *Zostera capensis*, *A. O. D. Mogg 30099* (PRE); idem, opposite the biological laboratory on sandy beach, 1-11-1962, *Mauve & Verdoorn 105* (PRE); Bazaruto Island, together with *Halophila ovalis*, ♂ flowers, *A. O. D. Mogg 28670* (PRE).

MADAGASCAR. Norontsánga, July 1879, *J. M. Hildebrandt 3213* (L, GH, K); idem, July 1906, *D'Alleizette* (L).

MAURITIUS. Ilot Brocus, in brackish and salt-water lagoon, 28-11-1947, *R E. Vaughan* (BM).

PERSIA. Bushire, *Køie*, distributed by Rechinger in "*Plants of Iran, 1731*" as *Diplanthera uninervis* Aschers. (K, C, BM).

Ecology: *H. wrightii* is widely distributed in the lower part of the eulittoral belt and in the upper part of the sublittoral. The species occurs on sandy as well as on muddy bottoms, and may be found also in pools on coral reefs, or in creeks in the mangrove swamps. In the West Indies it forms extensive submarine meadows , in which *Syringodium filiforme*, *Thalassia testudinum*, *H. beaudettei*, and sometimes *Ruppia sp.* may be interspersed. Along the east coast of Africa it is often associated with *Cymodocea rotundata*, *H. uninervis*, and *Halophila ovalis*.

Note: There is in the herbarium of Copenhagen a fruit said to be of *H. wrightii*, collected by Britton in Guantanamo Bay, Cuba (March, 1909) but regrettably without any vegetative plant fragments. It is round, laterally compressed, and 2 mm in diameter. The 2 mm long rostrum is inserted laterally. This fruit differs from the other fruits of *H. wrightii* that I have seen and it is possible that it is a fruit of *H. beaudettei*.

5. **Halodule bermudensis** Den Hartog, *nov.sp.* — **Fig. 9.**

Rhizoma repens, radicibus 1—2, in quoque nodo caule erecto brevi praeditum. Internodia ¾—1½ cm longa. Cataphylla elliptica, acuta, 7 mm longa. Vaginae 1—2 cm longae. Folia 2,5—5 cm longa, ⅔—1 mm lata, basi angustata. Folia vetustiora laminis destructis ad petiolos pro parte tantum persistentibus reducta, caules modo cataphyllorum tegentia. Foliorum costa conspicua, apice parum dilatata, haud super laminae marginem protrudens. Venae intramarginales inconspicuae, in dentes conspicuos abeuntes, facie interiore dentium lateralium ± convexa saepiusque processibus praedita. Flores ignoti.

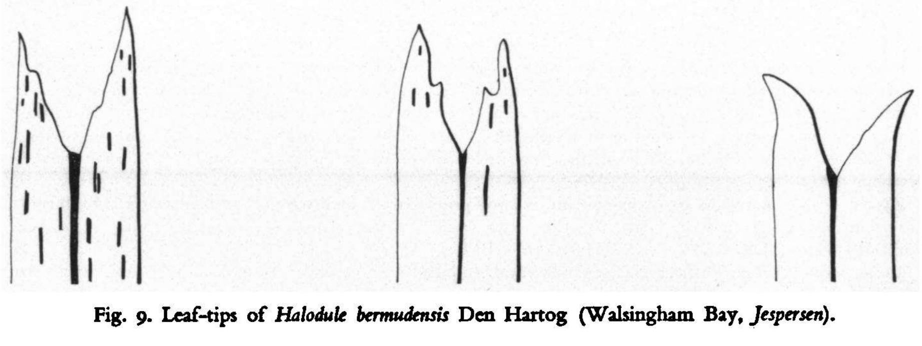


Fig. 9. Leaf-tips of *Halodule bermudensis* Den Hartog (Walsingham Bay, *Jespersen*).

Rhizome creeping, with 1—2 roots and a short erect stem at each node. Internodes ¾—1½ cm long. Scales elliptic, acute, 7 mm long. Sheaths 1—2 cm long. Leaf-blades 2½—5 (20—25) cm long and ⅔—1¼ mm wide, narrowed near the base. Old leaves which have lost their laminae and are reduced to partially persistent sheaths, cover the old stems with their scarious remains. Midrib conspicuous, only slightly widened at its tip and not projecting. Intramarginal veins inconspicuous, both ending in a strongly developed tooth. The innersides of these lateral teeth are more or less convex and often provided with some secondary processes. Flowers unknown.

BERMUDA ISLANDS. Walsingham Bay, *P. Jespersen*, 26-5-1922, Dana Expedition (*Type*; C, GH, U); Shore of Gibbit Island, in sand below low-water-mark, 2-9-1913, *F. S. Collins 330* (GH).

Note: Bernatowicz (1952, p. 338—340) states in his paper on the sea-grasses of the Bermuda Islands: "In some areas, for example Richardsons Cove and Mullet Bay, St. Georges I., dwarfed and blackened growths of this species *(H. wrightii)* occurred at the shore where they were partially exposed at each low tide. The moribund appearance of these stunted plants suggests they were mere stragglers which were able to get started but unable to flourish in very shallow water. Regrettably, it was never possible to connect them with any stands of healthy, typical plants and it may be that there exists here a subspecies or variety, which occupies its own niche. None of the dwarfed material obtained was in condition suitable for herbarium preparations." (sic!). It is unfortunate that he did not give the characters of this second form, as it is possible that it was *H. bermudensis*.

6. Halodule ciliata (Den Hartog) Den Hartog, *nov. comb.* — *Diplanthera ciliata* Den Hartog, Pacif. Natur. 1, 15 (1960) 4, f. 1.

Rhizome creeping, with 1—3 roots and a short erect stem at each node. Internodes 1—3½ cm long. Sheaths 1—1½ cm long. Leaf-blades 5—6 cm long and ½—1 mm wide, narrowed near the base. Midrib conspicuous, often ending in a small irregular tooth; intramarginal veins inconspicuous, both ending in a lateral tooth considerably longer than the median tooth, but often broken off. Leaf-tip variable, the median part being rather prominent to completely reduced, dentate to ciliate. Flowers unknown.

PANAMA. Taboga in the Gulf of Panama, *Mortensen*, 6-2-1916 (*Type*; C, U, GH, US).

7. Halodule pinifolia (Miki) Den Hartog, *nov. comb.* — *Diplanthera pinifolia* Miki, Bot. Mag. Tokyo 46 (1932) 787, f. 9; ditto 48 (1934) 132, 135. — **Fig. 10.**

Rhizome creeping, with 2—3 roots and a short erect stem at each node. Internodes 1—3 cm long. Scales ovate, 2½—3 mm long. Sheaths 1—4 cm long. Leaf-blades 5—20 cm long and ⅗—1⅕ mm wide. Midrib conspicuous, widening and sometimes furcate at the apex. Intramarginal veins inconspicuous, both ending in a very small tooth. Leaf-tip obtusely rounded, set with more or less numerous irregular, small serratures. Male flower on a 10 mm long peduncle. Lower anther 2½ mm, upper anther 3 mm, sometimes with scales on the lateral and basal portions (abortive perianth, according to Miki, 1934). Female flower sessile; ovary ovate, 1 mm; style 13 mm, lateral. Fruit ovate, 2—2½ mm long with an 1 mm long laterally inserted beak. (Description of the generative parts according to Miki, 1932, f. 9).

Type: Miki did not designate a holotype, but recorded material from three localities (Ryu Kyu Archipelago: Sumuide in Hanijimura, Miki, 19-7-1930, and Yakena in Yonagusuku, Miki, 22-7-1930; Formosa: Takao, Miki, 16-12-1925). As I had not the opportunity to study these plants I will refrain from choosing a lectotype.

Distribution: Western Pacific and its marginal seas: Formosa, Ryu Kyu Archipelago, Philippines, Lesser Sunda Islands, Moluccas, New Guinea, Queensland, Fiji and Tonga Islands.

JAPAN. Ryu Kyu Islands: Okinawa, Itoman in shallow water, common, together with *Halophila ovalis*, 10-6-1955, *S. Hatusima 18134* (US).

VIETNAM. Nha Trang, 22-8-1949, *Feldmann 14978* (UC); idem, in drift along Cua Be, 1 km south of Cau Da, 25-1-1953, *E. Y. Dawson 11095* (UC); idem, on sand flats of Cau Be near Truong Dong, 30-1-1953, *E. Y. Dawson 11166* (UC).

PHILIPPINES. Palawan: July 1912, *E. Fénix 15559*, together with *Cymodocea rotundata* (C); idem, May 1913, *Merrill 1263*, together with *Halophila ovalis* (L, P, BO), together with *Halodule tridentata* (GH); Cavilli Island in the Sulu Sea, on coral sand, submerged at low tide or in tidal pools on the reef, September 1910, *Merrill 7179* (C, K, US). — Sulu Group, Pearl Bank, June 1923, *R. Kienholz* (UC). — Mindoro: Puerto Galera, Medio Island, eastside, tidal flat, coral, together with *Halophila ovalis*, May 1924, *Pascasio 379 (15483)* (UC); idem, Balateros Maliit, tidal flat, coral sand behind the reef, together with a few *H. uninervis*, *Pascasio 371 (15476)* (UC).

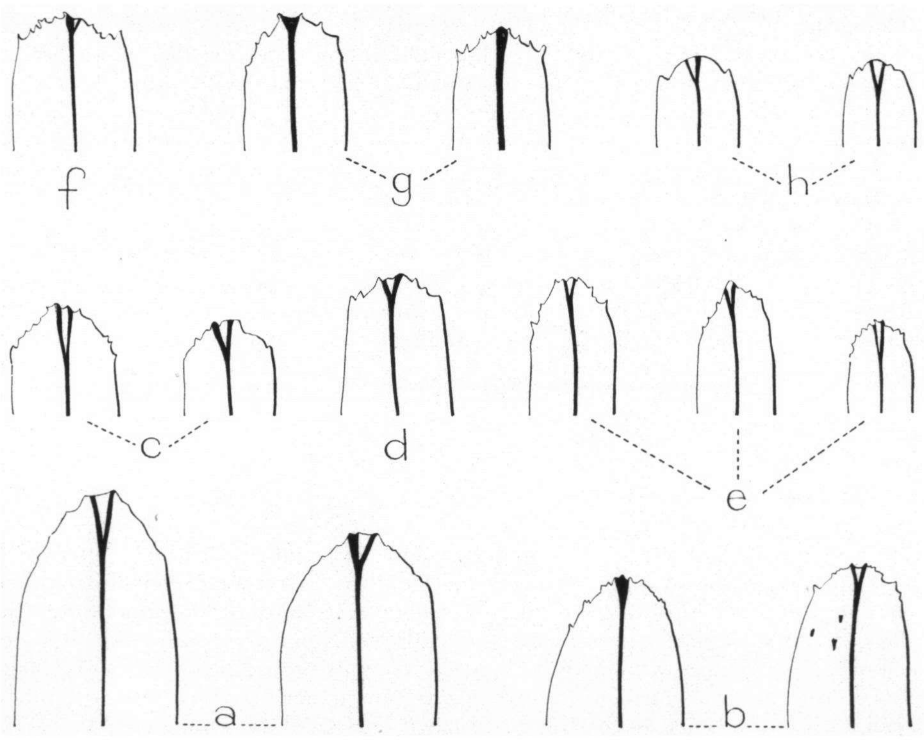


Fig. 10. Leaf-tips of *Halodule pinifolia* (Miki) Den Hartog. — (a. Palawan, *Fénix 15559*; b. Loré, Timor, *Van Steenis 18192*; c. Cavilli Island in the Sulu Sea, *Merrill 7179*; d. Tongatapu, *Moseley*; e. Rockingham Bay, Queensland, *F. v. Müller*; f. Nuku'alofa, Tongatapu, *Yuncker 15288, p.p.*; g. Palawan, *Merrill 1263*; h. Kai Islands, Jamtil, *Jensen 247*).

INDONESIA. Lesser Sunda Islands, Bali: 1-4-1936, *Van Steenis* (BO). — Timor: Koepang, on coral reef, 17-6-1941, *L. v. d. Pijl 824* (BO); South coast near Loré, coastal forest, in shallows and pools on a coral reef, 20-12-1953, *Van Steenis 18192* (L, BO, BM). — Moluccas: Kai Islands, Jamtil, 9-5-1922, *H. Jensen 247*, in the surf at *ca.* 1 m depth, on the stem cecidiae caused by the fungus *Plasmodiophora diplantherae* (C, BO, A, GH, US). — New Guinea: Sorong, 1872, *Beccari 11821 (P.P. 132)* (L, FI); Port Moresby, Ela beach, with *H. uninervis*, 17-6-1961, *Thorne 12564* (LAE).

QUEENSLAND. Rockingham Bay, 1883, *F. von Müller* (C.)

FIJI ISLANDS. Suva, Viti Levu, 22/28-5-1926, *W, A. Setchell & H. E. Parks 17739* (GH, UC).

TONGA ISLANDS. Island of Tongatapu, July 1874, *Moseley*, Challenger Expedition, together with *Halo-*

phila ovalis (K); idem, along beach at Nuku'alofa, 15-4-1953, *T. G. Yuncker 15288*, together with *H. uninervis* (U), without *H. uninervis* (GH); idem, Nuku'alofa, in mud, reef flat exposed at low tides, 9-8-1926, *W. A. Setchell & H. E. Parks 15170* (UC).

Ecology: In the upper part of the sublittoral and the lower part of the eulittoral belt, on coral sand; also in tide pools on the reefs, in quiet places as well as in the surf.

Notes: There exists some uncertainty with respect to the insertion of the style. Miki (1932) recorded in his diagnosis of *H. pinifolia* a long laterally inserted style and illustrated it. Yet in the same paper he wrote that the species is distinguished by its long terminal style. Then in his later work (Miki, 1934) he again stated that the style is attached on the apex of the ovary.

The species is well-characterized by its rather obtuse, irregularly serrulate leaf-tip. The lateral teeth which are very conspicuous in all other species of the genus are only faintly developed in *H. pinifolia*. In the material from Timor, the obtusely rounded leaf-tip and the very inconspicuous lateral teeth are sufficient characters to refer these specimens to *H. pinifolia*, although the serratures are nearly suppressed. In the material from Palawan (*Fénix 15559*) the lateral teeth are completely suppressed.

The internodes of the stem between the leaf-scars are sometimes slightly swollen as is the case in the material from Cavilli Island (*Merrill 7179*), but these swellings are inconspicuous in comparison with those caused by the parasitic fungus *Plasmodiophora diplantherae* (Ferdinandsen & Winge) Ivimey Cook.

Miki (1932) refers to the record of *Zostera nana* from Takao, Formosa, by Matsumura and Hayata (1906) as being *H. pinifolia*, without any comment.

EXCLUDED SPECIES

Diplanthera sp. Griffith, Icon. Pl. Asiat. 3 (1851) t. 161, C. fig. 2 = *Halophila ovalis* (R. Br) Hook. *f.*

Diplanthera indica Steud. Nomencl. Bot. ed. 2, 1 (1840) 515 (Wall. Cat. *n.* 7465) = *Halophila ovalis* (R. Br.) Hook. *f.*

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