THE MORPHOLOGY, TAXONOMY, AND NOMENCLATURE OF CYSTOPHYLLUM TRINODE (FORSSKÅL) J. AGARDH AND CYSTOSEIRA MYRICA (S. G. GMELIN) C. AGARDH (FUCALES: CYSTOSEIRACEAE) ¹

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CYSTOPHYLLUM TRINODE

In the early part of 1962 Dr. R. F. Scagel and the senior author collected at several localities in East Africa (from Malindi, Kenya, southward as far as Moçambique Island, Mozambique) a member of the Fucales which the present authors determined as a species of Cystophyllum (fig. 1). On the basis of material in the herbarium of the University of California and from previous descriptions it seemed that the East African plants could be referred either to C. trinode (Forsskål) J. Agardh, the lectotype of the genus (vide DeToni, 1891, p. 175), or to C. muricatum (C. Agardh) J. Agardh. This uncertainty caused us to make a careful examination of the fairly ample material of these two taxa available to us. ²

We could find no character whereby an eastern species, Cystophyllum muricatum, which extends westward to the Persian Gulf and Mauritius (Børgesen, 1939, 1948), can be separated from a Red Sea and East African species, C. trinode.

In the past these two taxa have been separated largely on vesicle morphology, Cysto-phyllum trinode being considered to have vesicles that tend to be spherical and close

1) The senior author is indebted to the National Science Foundation for supporting this work in several ways: The research was done with the aid of grants (G-24302 and GB-1656) from the Foundation and the material was collected under the auspices of the United States Program in Biology for the International Indian Ocean Expedition, which Program received its funds from the National Science Foundation. As a participant in the United States Program, he had two opportunities in 1962 of collecting marine algae in East African waters. During March and April he was a participant in the Israel South Red Sea Expedition and from September to December Dr. R. F. Scagel of the University of British Columbia and he had their own expedition to East Africa. He should like to express his appreciation to the Israel South Red Sea Expedition and especially to its leader, Professor H. Steinitz, of the Hebrew University of Jerusalem, for inviting him to join the Expedition. The material of Cystoseira trinodis from Bali was collected in 1957 with the aid of a grant to the senior author from the Associates in Tropical Biogeography of the University of California. Dr. R. B. Searles of Duke University kindly loaned us for examination the material of C. trinodis that he collected at several localities in the Great Barrier Reef and Torres Strait. We ar indebted to Dr. M. Nizamuddin of the University of Karachi for bringing to our attention the papers by Guern, which we had overlooked.

This material included specimens from several localities in the Red Sea (Tor is the type locality of Cystophyllum trinode), a number of localities in East Africa (ranging from Malindi, Kenya, to Lourenço Marques), the Island of Karek (= Khark, Kharg) in the Persian Gulf, Western Australia, South Australia, Great Barrier Reef, New Caledonia, Torres Strait (between Queensland and New Guinea), Arnhem Land in the Northern Territory of Australia, and Bali Island in Indonesia (the Strait of Sunda in Indonesia is the type locality of C. muricatum). The Island of Karek is the type locality of Cystoseira virgata Endlicher et Diesing (1845). The Herbarium of the University of California owns an isotype of this species. It is conspecific with Cystophyllum trinode. The plant from the coast of Somalia described by Grunow (in Hauck, 1889, p. 190) as Cystophyllum? hildebrandtii is perhaps also conspecific with C. trinode, but we have

seen no material of that taxon.

together and that decrease in size from the base to the apex of each series, whereas C. muricatum was considered to have vesicles that tend to be somewhat oblong and separated by a greater distance than in C. trinode and that do not decrease as much in size from the base to the apex of each series.

We have found that these characters vary in a single plant, and in the Red Sea, East Africa, Australia, and Bali, plants occur that are intermediate between the two species in vesicle characters.

We have also found that the plants cannot be separated on the basis of habit or degree of murication; some specimens are densely muricate, some less so, and others are almost devoid of murications. They also cannot be separated on receptacle morphology or conceptacle anatomy. Hence, we have concluded that this complex represents only one species, Cystophyllum trinode (Forsskål) J. Agardh.

Having concluded that Cystophyllum muricatum and C. trinode represent a single species, the important question remaining was: to which genus does this species belong?

The genus Sirophysalis was erected by Kützing (1843b) for the reception of Cystoseira muricata C. Agardh (1820), which name is based on Fucus muricatus Turner [1809, non Gmelin, 1768 = Eucheuma muricatum (Gmelin) Weber-van Bosse, 1928, p. 413], and in 1849 Kützing had also placed Fucus trinodis Forsskål (1775), among other species, in this genus. J. Agardh in 1848 erected the genus Cystophyllum for nine species, some of which previously had been placed in Sargassum or in Cystoseira by C. Agardh (1820, 1824). Cystoseira muricata C. Agardh and Fucus trinodis Forsskål were two of the nine species. DeToni (1891) by implication lectotypified Cystophyllum with Fucus trinodis, a typification which has been accepted by Silva (1952) and Fensholt (1953). Cystophyllum is illegitimate because J. Agardh disregarded the two genera erected by Kützing for members of this complex 1, namely, Sirophysalis, referred to above, and Myagropsis, in which Kützing (1843a) had placed two species, M. camalina, a new species, and M. turneri (= Fucus myagroides Turner, 1809, p. 28, pl. 83), both of which J. Agardh (1848) assigned to Cystophyllum sisymbrioides (Turner) J. Agardh (= Fucus sisymbrioides Turner, 1809, p. 150, pl. 129).

In view of the illegitimacy of Cystophyllum, the question of whether C. trinode should be referred to Sirophysalis, or to Myagropsis, or to Cystoseira C. Agardh (a genus regarded as closely related to Cystophyllum and in which C. Agardh had, in fact, placed Fucus trinodis) thus had to be resolved.

Fensholt (1955) has resurrected Myagropsis for two of the species previously placed in Cystophyllum. One of them, M. myagroides (Turner) Fensholt, the type of the genus, includes both of the species that Kützing (1843a) had placed in Myagropsis, namely, M. turneri Kützing (a name created by Kützing for Fucus myagroides Turner) and M. camalina Kützing, and also Cystophyllum sisymbrioides (Turner) J. Agardh²; the other species is M. yendoi Fensholt (= Cystophyllum turneri Yendo, 1907, p. 40, pl. 3, figs. 7—11; see also Kützing, 1860, pl. 92, fig. II; non Myagropsis turneri Kützing, 1843a, p. 57 = M. myagroides).

In an attempt to resolve the question posed, it is necessary to consider first the differences between Myagropsis and Cystoseira. In segregating Myagropsis from Cystoseira, Fensholt

¹⁾ Kützing's (1843a, p. 55) genus Spongocarpus included Fucus sisymbrioides Turner, which J. Agardh placed in Cystophyllum, but Spongocarpus has been lectotypified by Setchell (1931, p. 240) with S. horneri (Turner) Kützing, a species which is usually referred to Sargassum C. Agardh (1820), nomen conservandum.

²⁾ As pointed out above, J. Agardh (1848, p. 234) had previously regarded these three taxa as representing a single species, which he called Cystophyllum sisymbrioides.

utilized features that had been brought to light by the work of Dodel-Port (1885) and Nienburg (1910, 1913) on C. barbata; by Inoh (1932) on C. crassipes and C. hakodatensis; by Dawson (1941) on C. foeniculacea; by Gardner (1910) on C. osmundacea; by Okabe (1929), Inoh (1930, 1932) and Tahara (1940) on M. myagroides and M. yendoi; and by her own work on C. osmundacea and C. geminata. The observations of Sauvageau (1912) on C. foeniculacea and C. canariensis and especially those of Guern (1959, 1963) on 13 species of this genus are also relevant.

Fensholt regarded the following characters as important in distinguishing Myagropsis from Cystoseira. (1) The manner of conceptacle development: in Myagropsis the tonguecell remains undivided (Tahara, 1940, fig. 7), whereas in Cystoseira it undergoes division to form a several-celled (6-8) filament (Nienburg, 1913, fig. 1; Fensholt, 1955, figs. 6 and 10). (2) The manner of oogonium discharge from the conceptacle: in Myagropsis the oogonia mature and are discharged simultaneously (Tahara, 1913, p. 6, pl. 3, fig. 1; Shimotomai, 1928, p. 577), whereas in Cytoseira they mature and are discharged successively (Dawson, 1941, p. 317; Fensholt, 1955, pp. 311 and 313). (3) The position of the seven non-functional nuclei in the mature oogonium: in Myagropsis they are retained and degenerate within the egg cytoplasm (Tahara, 1913, pl. 3, fig. 4; Inoh, 1930, fig. 13), whereas in Cytoseira they are extruded from the egg into the region between the egg and the endochite (Gardner, 1910, fig. 18; Sauvageau, 1912, figs. 1 and 2; Guern, 1963, figs. 2, 3, 8). (4) The size and number of oogonia per conceptacle and whether they are embedded in the conceptacular wall or not: in Myagropsis the oogonia are large, measuring 300–400 \times 200–350 μ , only 2 to 4 are produced per conceptacle, and they are embedded (Fensholt, 1955, p. 317), whereas in Cystoseira the oogonia are small, measuring 70-78 μ in diameter (in two of the species studied by Guern the oogonia are much larger, measuring $180 \times 130 \mu$), 20 to 30 are produced per conceptacle (2—12 in C. foeniculacea according to Dawson, 1941, p. 317, but she did not give their size), and they are not embedded (Dawson, 1941, fig. 1A; Fensholt, 1955, figs. 28 and 38). (5) The number of primary rhizoids produced by the embryo: in Myagropsis the embryo forms 32 primary rhizoids (Okabe, 1929; Inoh, 1930), whereas in Cystoseira it forms 4 or 8 primary rhizoids, depending upon the species (Dodel-Port, 1885; Inoh, 1932; Guern, 1959, 1963).

Although the development of the conceptacle, oogonum, and embryo in the lectotype of Cystoseira, C. concatenata (Linnaeus) C. Agardh (vide De la Pylaia, 1829, p. 66) is unfortunately not yet known 1, the evidence assembled by Fensholt (and which has been extended and summarized above) from work on other species of this genus and on species of Myagropsis indicates that it is desirable to recognize Myagropsis as a genus distinct from Cystoseira.

Whether the lectotype of Cystophyllum, C. trinode, and the type of Sirophysalis, S. muricata, belonged to Myagropsis or to Cystoseira or to neither of them remained unknown pending a study of these two species. In the meantime they have continued to be assigned to the illegitimate generic name Cystophyllum.

Nizamuddin (1962) recently studied Cystophyllum muricatum. He observed the following: (1) The tongue-cell of the conceptacle divides to form a filament of three cells (i.e., comparable to the condition in Cystoseira). (2) The oogonia mature and are discharged simultaneously (i.e., as in Myagropsis). (3) The non-functional nuclei are

¹⁾ Examination of material of Cystoseira concatenata in the herbarium of the University of California has shown that the oogonia are not embedded (in which respect the species agrees with other species of Cystoseira), they measure about $98 \times 77 \mu$, and about 14 are formed per conceptacle.

extruded from the egg (i.e., as in Cystoseira) 1. (4) The oogonia measure 120—200 \times 100—150 μ (i.e., they are intermediate in size between those of Cystoseira and those of Myagropsis), but Nizamuddin did not say how many are formed per conceptacle; however, he did state that they are embedded in the wall of the conceptacle (i.e., as in Myagropsis), a feature also observed by us in East African material (fig. 2) 2. (5) The embryo forms four primary rhizoids (i.e., as in Cystoseira).

Of the characters used by Fensholt for the separation of Myagropsis from Cystoseira, the more important ones probably are those relating to (1) the behavior of the tongue cell of the conceptacle - whether it divides or not, (2) the position of the seven non-functional nuclei of the oogonium, (3) the manner of insertion of the oogonium - whether it is embedded in the wall of the conceptacle or not, and (4) the number of primary rhizoids produced by the embryo. The number of oogonia formed in Cystoseira ranges from 2 to 30, and Dawson (1941, p. 319) obtained indirect evidence suggesting that in C. foeniculacea some of the oogonia are discharged simultaneously as in Myagropsis. The features relating to number, size, and manner of discharge of oogonia are, therefore, probably of little, if any, significance as criteria for the separation of taxa at the level of genus.

With respect to the important characters, it is evident from the work of Nizamuddin that Cystophyllum muricatum agrees with species of Cystoseira in (1) the number of primary rhizoids formed by the embryo, (2) the formation of a tongue filament by the tongue cell of the conceptacle, and (3) the extrusion of the non-functional nuclei from the cytoplasm of the egg. It agrees with species of Myagropsis in having large and embedded oogonia.

Nizamuddin retains Cystophyllum as an autonomous genus. He states (p. 241) that it '.... greatly differs from the allied species of Cystophyllum in which reproductive structures have been studied', that is, C. sisymbrioides and C. turneri [= Myagropsis myagroides (Turner) Fensholt and M. yendoi Fensholt, respectively]. Nonetheless he rejects the bases for separation of Myagropsis and Cystoseira employed by Fensholt, and remarks (p. 242): 'The development of conceptacles, size of oogonia, oogonial discharge and the presence of non-functional or supernumerary nuclei [a statement referring presumably to their position in the oogonium] should not be considered as diagnostic features.... From a consideration of Cystophyllum muricatum the vesicle character appears to be a diagnostic criterion at the generic level.'

Nizamuddin does not say how he would separate Cystophyllum from Cystoseira on vesicle characters. For this information it is necessary to turn to Kjellman (1893), O. C. Schmidt (1938), and Womersley (1964). In his paper on Cystophora, Womersley (1964) gives a key to the genera of Cystoseiraceae. The relevant part reads as follows:

¹⁾ In his text (pp. 239 and 241) and in the legend to figure 12, Nizamuddin states that the non-functional nuclei are situated at the periphery of the oogonium. That they are extruded from the egg is shown in his figure 12.

^{*)} In East African plants 4—6 oogonia are formed per conceptacle; they measure 155—175 × 125—130 μ in the undischarged condition and 180 × 140 μ in the discharged condition. The conceptacles of East African plants were found to be bisexual (fig. 2), an observation that is at variance with published statements, according to which the species is dioecious. Out plants appear to be strongly proterogynous, but a few antheridia are initiated at about the time that the oogonia reach maturity.

However, Womersley qualifies his separation on this basis by a footnote (p. 65) in which he says: 'No attempt is made here to provide more satisfactory criteria for the separation of these genera, if indeed they should be separated. The difference in vesicle position is not satisfactory as is evident from a perusal of herbarium material of numerous species, and the separation of Fensholt (1955) needs extension to other species. On Fensholt's basis the Australian Cystophyllum muricatum... falls closer to Cystoseira than to Myagropsis....'

We concur with Womersley that a separation of *Cystoseira* and *Cystophyllum* on vesicle position is not possible. In fact, Gardner already in 1917 (p. 390) pointed out that these two genera cannot be separated on this basis.

In assessing the relationship that Cystoseira, Cystophyllum, Myagropsis, and Sirophysalis may bear to one another, we are hampered by a lack of knowledge about the lectotype of Cystoseira, C. concatenata, with respect to most of the characters employed by Fensholt. Until the appearance of the paper by Nizamuddin, we also had been uninformed in regard to the situation in the type of Sirophysalis, S. muricata (= Cystophyllum muricatum). Our own work on the lectotype of Cystophyllum, C. trinode, even if incomplete in many respects, has confirmed, insofar as it went, the observations of Nizamuddin on Cystophyllum muricatum. Furthermore, as pointed out above, our observations on plants from the Red Sea, East Africa, Bali, and the Australian region have convinced us that Cystophyllum trinode and C. muricatum represent a single species, for which the epithet trinode must be used. The illegitimate Cystophyllum J. Agardh thus becomes a synonym of Sirophysalis. However, with the exception of the embedded nature of the oogonia (in which respect Sirophysalis agrees with Myagropsis), there appear to be no important characters whereby this genus can be separated from Cystoseira sensu Fensholt. Pending a detailed study of the lectotype of Cystoseira, we consider it advantageous to accept the bases for separation of Myagropsis from Cystoseira employed by Fensholt. We propose, therefore, to merge both Cystophyllum and Sirophysalis in Cystoseira. The synonymy of Cystoseira and of C. trinodis follow.

Cystoseira C. Agardh (nom. cons.)

C. Agardh, 1820, p. 50. — Phytocoma Donati, 1753, p. 25, as Fitocoma. — Gongolaria Boehmer, in Ludwig, 1760, p. 503. — Baccifer Roussel, 1806, p. 94. — Abrotanifolia Stackhouse, 1809, pp. 56 and 81. — Ericaria Stackhouse, 1809, pp. 56 and 80. — Carpodesmia Greville, 1830, p. xxxiv. — Sirophysalis Kützing, 1843b, p. 368. — Halerica Kützing, 1843b, p. 354. — Treptacantha Kützing, 1843b, p. 353. — Phyllacantha Kützing, 1843b, p. 355. — Stephanocystis Trevisan, 1843, p. 332. — Cystophyllum J. Agardh, 1848, p. 228. — Polycladia Montagne in Kützing, 1849, p. 769; see also Montagne and Millardet, 1862, p. 13, pl. 27, fig. 2 (2nd, 1863, ed. seen, p. 160, pl. 27, fig. 2).

Cystoseira trinodis (Forsskål) C. Agardh, 1820, p. 67. — Fucus trinodis Forsskål, 1775, pp. cxxv and 192. — Cystophyllum trinode (Forsskål) J. Agardh, 1848, p. 230. — Sirophysalis trinodis (Forsskål) Kützing, 1849, p. 603. — Fucus onustus var. trinodis (Forsskål) Mertens, 1819, p. 183.

Blossevillea arabica Kützing, 1849, p. 630.

Cystoseira trinodis var. confluens C. Agardh, 1824, p. 286. — Sirophysalis trinodis var. confluens (C. Agardh) Kützing, 1849, p. 603.

Sirophysalis trinodis var. enodis Kützing, 1860, p. 22, pl. 59, fig. I.

Sirophysalis muricata (C. Agardh) Kützing, 1843b, p. 368. — Cystoseira muricata C. Agardh, 1820, p. 66. — Fucus muricatus Turner, 1809, p. 108, pl. 112 [non Gmelin, 1768,

p. 111, pl. 6, fig. 4 = Eucheuma muricatum (Gmelin) Weber-van Bosse, 1928, p. 413]. — Cystophyllum muricatum (C. Agardh) J. Agardh, 1848, p. 231.

Cystoseira virgata Endlicher et Diesing, 1845, p. 268. — Sirophysalis virgata (Endlicher et Diesing) Kiitzing, 1849, p. 603. — Cystophyllum virgatum (Endlicher et Diesing) Rabenhorst in Hohenacker, 1852, no. 73. — Cystophyllum muricatum var. virgatum (Endlicher et Diesing) J. Agardh, 1848, p. 231.

CYSTOSEIRA MYRICA

Cystoseira myrica was described by S. G. Gmelin (1768) as Fucus myrica. The species was placed in Cystoseira by C. Agardh when he erected the genus in 1820.

The source of Gmelin's material is unknown. He gave Kamchatka and, with a query, the Mediterranean Sea as localities. The species does not occur in Kamchatka and is also not known from the Mediterranean Sea. It is known from the Red Sea, the Persian Gulf, East Africa as far south as Inhaca Island in Mozambique, Madagascar, Mauritius, and Réunion Island, and from Florida and the Bahama Islands in the Caribbean region (as var. occidentalis J. Agardh, 1896, p. 40) 1.

The senior author's interest in this species dates back to 1938 when Dr. Mary A. Pocock and he collected it in the northeastern part of South Africa. At first he suspected the South African plant (fig. 3) of being a representative of the red algal genus *Rhodomela*, some species of which it superficially resembles. In fact, Montagne (in Kützing, 1849, p. 769; see also Kützing, 1868, p. 24, pl. 67, figs. a and b; and Montagne and Millard, 1862, p. 13, pl. 27, fig. 2 [2nd, 1863, ed. seen, p. 160, pl. 27, fig. 2]) had described it as a monotypic genus of red algae (*Polycladia commersonii*) on the basis of material from Réunion Island. Later the South African plant was suspected of being a species of *Cystoseira*, possibly *C. myrica*, but a disturbing feature was the absence of vesicles in all the specimens.

The same species was subsequently collected by Isaac in southern Mozambique at Xai-Xai (Isaac, 1957) and Inhaca Island (Isaac and Chamberlain, 1958). He sent material of it to Professor Feldmann, who determined it as *Cystoseira myrica* and who also furnished the record for Madagascar, whence the species had not previously been reported. The species had previously been reported from Kenya by Lind (1956), from Zanzibar by Sonder (1879) and from Tanganyika (Dar es Salaam) by Schröder (1912), and in 1957 Gerloff also reported it from Dar es Salaam.

In the early part of 1962 the senior author collected this species (fig. 4) in the Red Sea and later that year Dr. Scagel and he collected it at a number of localities in East Africa, from Djibouti, French Somaliland, southward as far as Trafalgar Port O' Call (where it was cast ashore) in southern Natal, South Africa. This material provided the present authors with an excellent opportunity to study the changes in morphology that the species undergoes as it approaches the southern limit of its distribution.

In the Red Sea and northern East Africa, Cystoseira myrica attains a height of about 50 cm., is provided with many vesicles, and has well-spaced spine-like appendages on the axes. As it ranges southward, the stature of the plant decreases, but in other respects it remains unmodified. At Moçambique Island, some plants are provided with vesicles and some lack vesicles. In southern Mozambique (e.g., Vilanculos and Xai-Xai) all the plants lack vesicles, a feature which, according to Isaac and Chamberlain (1958), is also true of the plants from Mauritius, Réunion, and Madagascar. Finally, at Inhaca Island

¹⁾ In general appearance the plants from the Caribbean are somewhat different from those in East Africa, and it may be questioned that they are representative of the same species.

and in South Africa (fig. 3) the plants do not exceed 7 cm., are without vesicles, and exhibit extreme stunting, as is evident from the densely arranged spine-like appendages and irregularity of branching pattern, as contrasted with the pinnate pattern of the ultimate orders of branches in plants of northern latitudes.

As regards the geographic distribution of this species, it will be recalled that it occurs in the Caribbean (as represented by var. occidentalis), as well as in the western Indian Ocean and the Red Sea. Its distributional pattern differs from that of many other species of algae that range from the Caribbean to East Africa in that it is not known to be present in the Pacific and the eastern Indian Ocean. It would be of interest if it were discovered in these regions and we should like to suggest that phycologists be on the lookout for it. The synonymy of the species follows:

Cystoseira myrica (S. G. Gmelin) C. Agardh, 1820, p. 53. — Fucus myrica S. G. Gmelin, 1768, p. 88, pl. 3, fig. 1. — Phyllacantha myrica (S. G. Gmelin) Kützing, 1849, p. 598. Fucus seticulosus Forsskål, 1775, pp. cxxv and 190.

Fucus antennulatus Delile, 1813a, p. 80; 1813b, p. 291, pl. 55, fig. 1.

Polycladia commersonii Montagne in Kützing, 1849, p. 769 [see also Kützing, 1868, p. 24, pl. 67, figs. a and b; and Montagne and Millardet, 1862, p. 13, pl. 27, fig. 2 (2nd, 1863, ed. seen, p. 160, pl. 27, fig. 2)].

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Fig. 1. Cystoseira trinodis, habit of plant (Praia Chokas, north of Lumbo, Mozambique, 15/17-xi-1962, Papenfuss & Scagel PR-XXVIII-30).

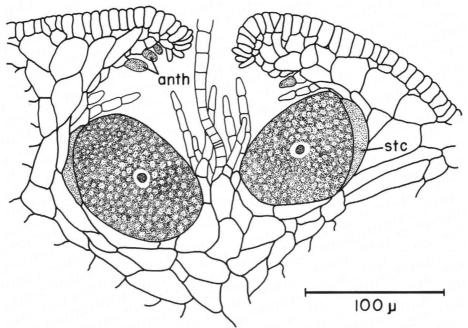


Fig. 2. Cystoseira trinodis, section through conceptacle, showing oogonia embedded in conceptacular wall and young antheridia (anth); stc, stalk-cell. (From material, PR-VIII-141, collected by Papenfuss and Scagel on 11/13-x-1962 at Oyster Bay, Dar es Salaam, Tanganyika).

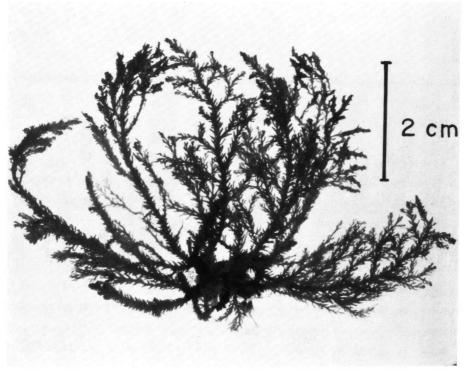


Fig. 3. Cystoseira myrica, habit of plant from Perriers Rocks, St. Lucia Bay, South Africa (Pocock & Papenfuss 1036, 22-vii-1938).

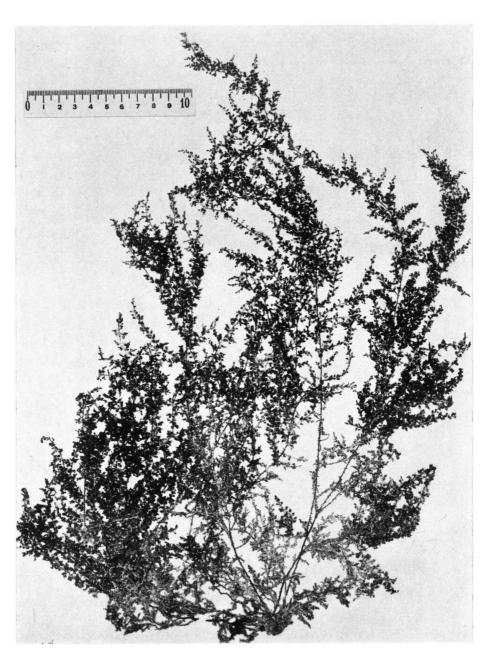


Fig. 4. Cystoseira myrica, habit of plant from Dahlak Kebir Island, Dahlak Archipelago, Red Sea (Israel South Red Sea Expedition E62/20096, 20-iii-1962).