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**AUSTRALIAN SPECIES OF SARGASSUM, SUBGENUS
PHYLLOTRICHIA**

By H. B. S. WOMERSLEY

AUSTRALIAN SPECIES OF *SARGASSUM*, SUBGENUS
PHYLLOTRICHIA

By H. B. S. WOMERSLEY*

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Summary

A revision of the Australian species of the subgenus *Phyllotrichia* of *Sargassum*, based on field knowledge of most species, abundant herbarium material, and a study of the type specimens in English, European, and Australian herbaria, results in the recognition of eight species. Specific variation, seasonal development, and the relationship of *Phyllotrichia* to the other subgenera of *Sargassum* are discussed.

INTRODUCTION

Phyllotrichia is largely a typically Australian section of *Sargassum*. Of the 10 species which may now be recognized, eight are Australian, with five found in the temperate waters of southern Australia, two around tropical Australia, and one so far known only from Lord Howe I. Two species are known from outside Australasia, one from the Canary Is. and one from Japan. These 10 species should probably be increased to 12 by the union of the subgenus *Schizophycus* with *Phyllotrichia* (see below).

Present-day knowledge of the species of *Sargassum* is still very largely dependent on J. G. Agardh's monograph (1889), which established five subgenera. Since then the only major works published are those of Grunow (1915, 1916), and Setchell (1931, 1933, 1935, 1936). Since Setchell summarized the taxonomic history of the genus and has given the best account of it of recent years, it is unnecessary to review the genus here.

Collections and ecological surveys on the southern Australian coast during the last 10 years have indicated the most unsatisfactory state of knowledge of *Sargassum*, and during 1952 the types† of Australian species in overseas herbaria were studied, notably those at Kew and the British Museum (Natural History) in England, at Lund in Sweden, and at Paris in France. This paper deals with only one section of *Sargassum*. It is proposed to deal with the subgenus *Arthrophyucus* and the southern Australian species of *Eusargassum* at a later date.

In view of the fundamental importance of J. G. Agardh's monograph, the specimens in the Agardh Herbarium in Lund are of great importance. It is rather disturbing, therefore, to find the specimens rather less impressive than his descriptions and figures. Frequently the representation

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† Photographs of the type specimens of the species of *Phyllotrichia* are deposited in the Algal Herbarium, University of Adelaide.

of a species is not good, and in *Arthrophyucus* the basal and upper parts of a plant associated on one sheet or in one folder are sometimes not united, thus giving rise to doubts whether they are the same species. In some instances also it is clear that J. G. Agardh did not have type material of previous authors, and his concepts are not always correct. Most subsequent authors have followed his concepts.

While J. G. Agardh's monograph of *Sargassum* is still the basis of our understanding of this difficult genus, and was in its time an outstanding account of the species and their relationships, it is clear that most of the species and groups need critical revision on the basis of wide field knowledge of developmental stages and ecological variations, together with a study of the type specimens.

Grunow's studies (1915, 1916) were published after his death and provide the only survey of the whole genus since that of J. G. Agardh. In general he followed J. G. Agardh's classification, and while he described relatively few new species, his varieties and forms are numerous. Fortunately perhaps, he described only a few varieties of the species of *Phyllotrichia*, and although his specimens have not been seen by the present author, it is abundantly clear that these varieties are mere developmental or ecological forms, quite unworthy of recognition. The same criticism probably applies to his work on the other subgenera of *Sargassum*.

Lucas (1935) described a new species from Lord Howe I., but in his account of the South Australian species (1936) he followed J. G. Agardh's classification and concepts, contributing nothing new.

The account of the seasonal development of the southern Australian species given below shows the necessity for collections of fully developed and fertile specimens.* Frequently it is necessary to study a species at all seasons of the year.

In the account of the species detailed locality data have not been given, owing to its large bulk and doubtful value. All specimens in Brisbane (Botanic Gardens Herbarium and University), Sydney (Botanic Gardens), Melbourne (National Herbarium and University), Tasmania (University and Launceston Museum), Adelaide (University), and Perth (University and State Herbarium) have been examined and annotation labels placed on the sheets. The distribution of each species is summarized below from all the above records and from reliable literature records.

PHYLLOTRICHIA AND ITS RELATION TO THE OTHER SUBGENERA

Phyllotrichia was defined by J. G. Agardh (1889) (see also Setchell 1931, p. 244) as having primary branches emerging from the stem or main axis as "foliar expansions", which are pinnatifid and usually flattened below, but may become cylindrical above where they bear vesicles and receptacles. The vesicles were regarded as being essentially without any terminal outgrowth (i.e. mutic).

* The same comment applies equally to species of *Arthrophyucus*.

J. G. Agardh's second subgenus, *Schizophycus*, has similar, though more subdivided, pinnate foliar expansions arising from the stems, but the vesicles were regarded as developing from the lower portion of a leaf or leaf segment, thus being crowned with a simple or branched prolongation.

The other subgenera (*Bactrophycus*, *Arthropycus*, and *Eusargasum*) differ from *Phyllotrichia* and *Schizophycus* in having only distinctly differentiated and essentially simple (very rarely branched) leaves.

Apart from the Australian species of *Phyllotrichia*, J. G. Agardh (1889, p. 55) recognized two other species, *S. piluliferum* (Turner) C. Agardh from Japan and *S. desfontainesii* (Turner) C. Agardh from the Canary Is. Though Setchell (1931, p. 244) queried whether these should be placed under *Phyllotrichia*, Turner's figures (1808, Plate 65; 1811, Plate 190, respectively) and Setchell's photograph (1933, Plate 4) of the type of *S. piluliferum* indicate that they probably come within this subgenus, since the branches bear pinnately branched laterals and the vesicles are mutic.

The two distinctions of Agardh (followed by Setchell) between *Phyllotrichia* and *Schizophycus* lie in the greater degree of branching and development of the laterals, and in the possession of a terminal leaflet on the vesicles in the latter. The range of form of the species of *Phyllotrichia* described below shows, however, that neither of these differences is satisfactory. The degree of branching of the laterals varies considerably in several species, such as *S. varians*, and is largely dependent on the age of the plant. Presence or absence of prolongations on the vesicles is a variable character in *S. varians* (where such prolongations are usually absent but may reach 2 cm long and 2 mm broad) and also in *S. verruculosum*, where the slender mucro may reach over 1 cm long and bear cryptostomata; in *S. decurrens* the vesicles are normally mutic but may have a slender mucro up to 1 cm long; in *S. heteromorphum*, *S. sonderi*, and *S. decipiens* there is normally a small, pointed mucro; while in *S. peronii* and *S. howeanum* the vesicles are probably always mutic.

J. G. Agardh's and Setchell's (1933, p. 34) belief that the vesicles in *Phyllotrichia* are always mutic is clearly wrong, and the distinction between *Phyllotrichia* and *Schizophycus* is rendered more doubtful by Setchell's (1933, pp. 34-6) account of the species of *Schizophycus*. In *S. patens* he recognized three varieties; var. *typicum* has "vesicles prolonged into an appendage which is still phyllode-like, in that it is usually divided"; var. *rodgersianum* has "the projection at the tip of the bladder reduced to almost a point (or mucro) or at least simple and undivided"; var. *schizophylla* is intermediate between these two.

It seems clear that these two subgenera cannot be maintained on vesicle or branching characters, and the species of *Schizophycus* can best be placed under *Phyllotrichia*. The vesicles in the different species form

a graded series from completely mutic ones to those with branched terminal prolongations (*S. patens* var. *typicum*).

Phyllotrichia (including *Schizophycus*) is then readily recognized by the branched character of the laterals on the main branches, i.e. the presence of "foliar pinnatifid expansions", as distinct from the individual, simple "leaves" of *Bactrophycus*, *Arthrophycus*, and *Eusargassum*. In a few species only of these latter groups are occasional branched leaves found. The only species of *Phyllotrichia* which may not be readily recognized is *S. decipiens*, which has crowded, slender, leaf-like appendages on all sides of the lower part of the main branches. These may be simple but are frequently branched once to several times, especially in mature plants.

Within *Phyllotrichia* J. G. Agardh distinguished five tribes. The differences between them are not well defined or important, and they will not be recognized here.

Besides the Australasian species, the following species may be included under *Phyllotrichia*:

- S. piluliferum* (Turner) C. Agardh, from Japan,
- S. desfontainesii* (Turner) C. Agardh, from the Canary Is.,
- S. pinnatifidum* Harvey, from Japan and Hong Kong,
- S. patens* C. Agardh, from Japan and Hong Kong,

and possibly

- S. tosatense* Yendo from Japan.

Setchell (1933) should be consulted for descriptions of the Japanese species.

SEASONAL DEVELOPMENT AND VARIATION OF THE SPECIES OF PHYLLOTRICHIA

Much of the duplication of species within *Phyllotrichia* has been due to a lack of understanding of the development of the species, which is perhaps to be expected when only herbarium specimens — and often only poor ones — are available.

The following general account applies to the southern Australian species, several of which have been studied in the field throughout the year. The development of the tropical species (*S. peronii* and *S. decurrens*) is probably very similar.

From the basal holdfast, which is usually conical and solid, arise one to a few stout stems, which may be compressed or terete, and vary from only about 1 cm in length up to 20 cm. From the stem apex arise usually two to several main branches which are well described as "pinnatifid foliar expansions", i.e. deeply divided, flattened, narrow to broad "phylloids" (e.g. Plate 3, Fig. 1), consisting of the main branch axis with laterals which may be simple or subdivided. The main branches are strongly distichous in some species (*S. peronii*, Plate 1, Fig. 2, and *S.*

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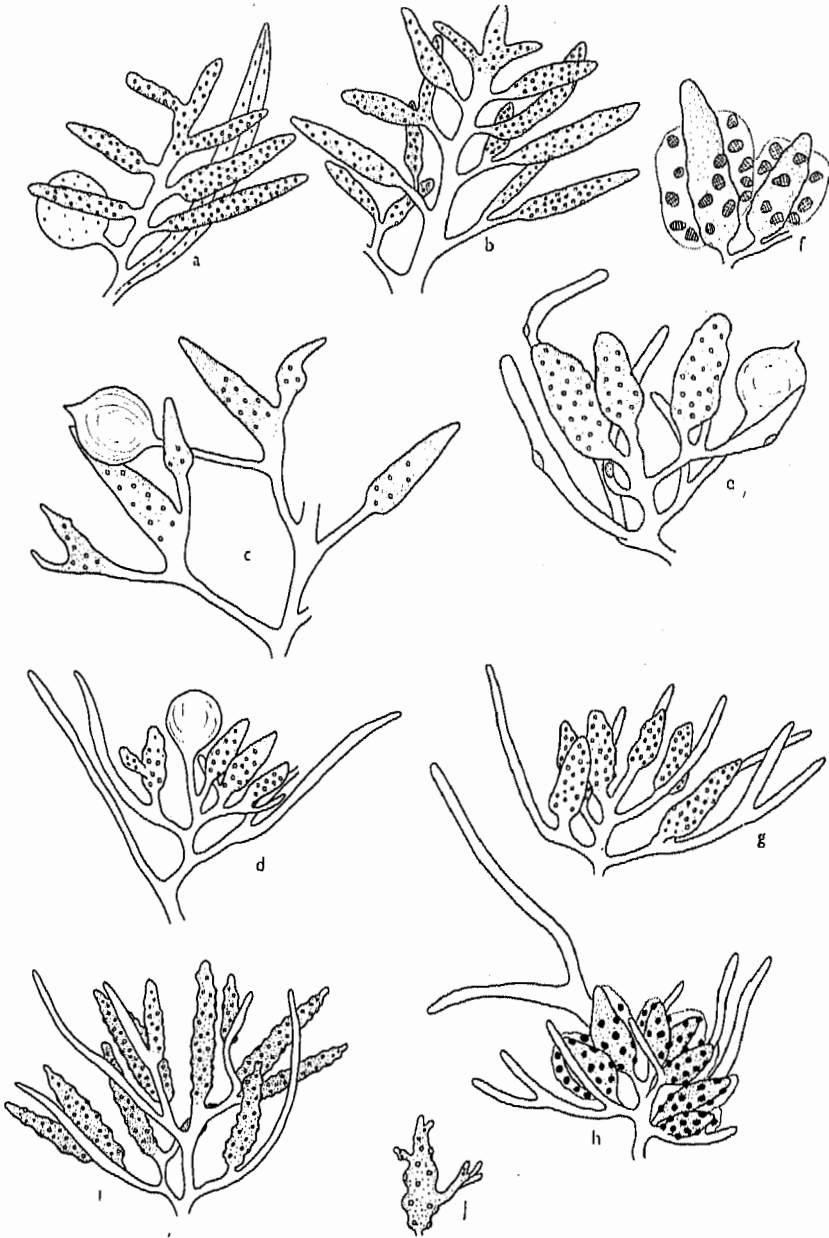


Fig. 1.—*a*, *S. peronii*: a group of young receptacles with a ramulus and vesicle. *b*, *S. peronii*: an older and more branched group of receptacles. *c*, *S. heteromorphum*: receptacles and vesicle. *d*, *S. sonderi*: receptacles and vesicle subtended by filiform ramuli. *e*, *S. decipiens*: receptacles of a male plant. *f*, *S. decipiens*: two receptacles of a female plant with developing zygotes held in the surrounding mucilage. *g*, *S. varians*: receptacles of a male plant. *h*, *S. varians*: receptacles of a female plant with developing zygotes. *i*, *S. verruculosum*: a group of mature receptacles. *j*, *S. verruculosum*: a single receptacle showing branching.

decurrens, Plate 2, Fig. 1), less so in others. In *S. decipiens* (Plate 4, Fig. 1) the axis of the main branches bears simple or branched narrow laterals ("leaves") on all sides.

The main branches are lost each year, and new ones arise from the apex of the stem. At certain times of the year (February to June in most species) only this basal part of the branches will be present. In winter (June onwards), however, growth of the ends of the main branches continues, forming much narrower (often terete and filiform) divisions than in the basal part. On these filiform upper ramuli the vesicles and receptacles develop, usually from July onwards. In early summer (November to January), depending on local rough weather, the fertile main branches are completely lost, leaving only scars on the stems.

In some species (*S. decipiens*, *S. sonderi*, *S. heteromorphum*) the vesicles are only formed on the upper ramuli, usually before receptacles are developed. In others (*S. peronii*, *S. decurrens*, *S. varians*, and *S. verruculosum*) they may be present on the basal parts, but are found in greater numbers when fertile fronds develop.

The receptacles are usually formed in racemose groups on, or subtended by, the upper ramuli (Fig. 1). They are formed by ramuli becoming swollen and developing conceptacles. At first they are short and bluntly pointed, but as they develop they elongate considerably. Whether the receptacles are petiolate or not depends largely on the state of development. Individual receptacles may branch furcately or, in some species, produce small outgrowths which may develop into small receptacles (e.g. *S. verruculosum*, Fig. 1j).

Variation within any particular species therefore depends largely on the season. Some rock pool forms, or plants growing in very rough habitats, appear to retain the juvenile form in which basal parts only occur (e.g. *S. heteromorphum*, Plate 2, Fig. 2, right-hand specimen; *S. sonderi*, Plate 3, Fig. 1).

The Australian species of *Phyllotrichia* are apparently normally dioecious. Differences in size between male and female receptacles may occur, but are usually only slight. The eggs are extruded in mucilage from the conceptacles before fertilization, and the zygotes (at least in *S. decipiens* and *S. varians*) develop to a many-celled stage held in the mucilage (Fig. 1f, h), without apparently reaching the rhizoid stage before liberation from the mucilage.

KEY TO AUSTRALIAN SPECIES OF THE SUBGENUS PHYLLOTRICHIA

1. Whole of mature main branches distichous, branch axes flat and winged, 5-10 mm broad, tapering evenly 2
- Mature main branches not completely distichous (though the basal part may be), branch axes terete or flattened but usually under 4 mm broad (lower segments of *S. heteromorphum* may be up to 1 cm broad) 3

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- 2(1). Laterals of main branches tapering fairly evenly from the axis to narrow acute apices, always branched *S. decurrens*
 Laterals of main branches more leaf-like, constricted at the base and mostly simple *S. peronii*
- 3(1). Main branch axes terete-angular, vesicles small (1-3 mm dia.), lower laterals not retrofract 4
 Main branch axes compressed below, lower laterals retrofract, vesicles large (4-10 mm dia.) 7
- 4(3). Lower parts of main branches very distinct from upper, lower segments 5-10 mm broad *S. heteromorphum*
 Lower parts of main branches grading into upper, lower segments narrow (up to 1-5 mm broad) 5
- 5(4). Lower laterals of main branches narrow, simple, or branched, not or only slightly differentiated 6
 Lower laterals of main branches distinct, often large and deeply pinnate (segments 2-5 mm broad) *S. sonderi*
- 6(5). Stem compressed, lower laterals only slightly broader than upper *S. decipiens*
 Stem terete, lower laterals not differentiated *S. howeanum*
- 7(3). Stem compressed, mature lower laterals markedly retrofract from the flattened axes of the main branches *S. varians*
 Stems terete, lower laterals retrofract and old branch axes usually flexuose *S. verruculosum*

Sargassum decurrens (R. Brown in Turner) C. Agardh, Sp. Algarum 1: 42 (1821); Syst. Algarum 308 (1824); J. Agardh, Sp. Gen. Ordines Algarum 1: 285 (1848); Acta Univ. Lund. 9: 53 (1872); K. Svenska VetenskAkad. Handl. 23 (3): 47, pl. 15, fig. 2 (1889); De Toni, Sylloge Algarum 3: 13 (1895); Grunow, Verh. zool.-bot. Ges. Wien 66: 334 (1915); Harvey, Phycol. Aust. 3: pl. 145 (1860); Sonder, Alg. trop. Aust. 7 (1871)

Plate 2, Fig. 1

- Fucus decurrens* R. Brown in Turner, Fuci Plant. Gen. Bot. 3: pl. 194 (1811).
Pterocaulon decurrens Kützing, Phycol. General. 360 (1843); Sp. Algarum 606 (1849); Tab. Phycol. 10: pl. 65 (1860).
Sargassum scabripes J. Agardh, Acta Univ. Lund. 9: 52 (1872); K. Svenska VetenskAkad. Handl. 23 (3): 48, pl. 2 (1889); De Toni, Sylloge Algarum 3: 14 (1895); Grunow, Verh. zool.-bot. Ges. Wien 66: 335 (1915); May, Contrib. N.S.W. Nat. Herb. 2: 50 (1953).

Holdfast discoid, producing 1 to several stems. Stems slightly compressed, verrucose with branch scars, to 12 cm long and 2-4 mm broad, bearing 1 to several main branches near the apex. Branches completely distichous; axes strongly winged, 5-12 mm broad with a prominent midrib, producing alternately from the edges simple, or more frequently divided, laterals, which are not, or only slightly, contracted at the base and taper evenly to narrow acute apices. Vesicles borne in the axils of the laterals or on the upper ramuli, petiolate, spherical, mutic, or rarely with a slender mucro up to 1 cm long, up to 6 mm in diameter. Receptacles racemose on the upper ramuli, simple or sometimes furcate, petiolate, linear lanceolate, smooth and terete, up to 6 mm long and 1/2-1 mm broad.

Type locality.—"North shores of New Holland".

Type.—British Museum (N.H.).

Distribution.—From Rottneest I., W.A., around northern Australia to Keppel Bay (Rockhampton), Qld.; with an isolated occurrence at Wallaroo, in Spencer's Gulf, S.A. Known also from New Caledonia.

The type, figured by Turner, is a young and fragmentary plant, and *S. decurrens* in the past has applied mainly to juvenile plants. J. Agardh's *S. scabripes* represents the older, more divided, and fertile plant. Occasionally old plants of *S. peronii* have basal laterals branched similarly to *S. decurrens* but not the tapering acute apices, and young plants of *S. peronii* have simple, distinctive laterals.

Sargassum peronii (Mertens) C. Agardh, Sp. Algarum 1: 43 (1821); Syst. Algarum 308 (1824); J. Agardh, Sp. Gen. Ordines Algarum 1: 284 (1848); Acta Univ. Lund. 9: 54 (1872); K. Svenska VetenskAkad. Handl. 23 (3): 47, pl. 15, fig. 1 (1889); De Toni, Sylloge Algarum 3: 12 (1895); Grunow, Verh. zool.-bot. Ges. Wien 65: 333 (1915); Sonder, Alg. trop. Aust. 7 (1871); Reinhold, Monogr. Siboga Exped. 59a: 153 (1913)

Fig. 1a, b; Plate 1, Figs. 1 and 2

Fucus peronii Mertens, Mém. Mus. Hist. Nat. Paris 5: 175, pl. 13 (1819); Turner, Fuci Plant. Gen. Bot. 4: pl. 247 (1819).

Sargassum boryi C. Agardh, Syst. Algarum 308 (1824); J. Agardh, Sp. Gen. Ordines Algarum 1: 285 (1848); Acta Univ. Lund. 9: 55 (1872); K. Svenska VetenskAkad. Handl. 23 (3): 47, pl. 3 (1889); De Toni, Sylloge Algarum 3: 13 (1895); Grunow, Verh. zool.-bot. Ges. Wien 65: 334 (1915).

Pterocaulon peronii Kützing, Phycol. General. 360 (1843); Sp. Algarum 606 (1849); Tab. Phycol. pl. 65 (1860).

Pterocaulon boryi Kützing, Phycol. General. 360 (1843); Sp. Algarum 606 (1849).

Stems slightly compressed, to 10 cm long and 1-3 mm broad, verrucose with old branch scars, bearing from the upper edges several distichous, pinnate main branches, to 40 cm long. Branch axes broadly winged, 5-12 mm wide below with a prominent midrib, tapering evenly above and bearing, when young, alternate simple laterals which are contracted at the base, 2-5 cm long and 2-8 mm broad. Laterals on older plants, both larger ones at the base and young ones above, occasionally branched, but invariably with some simple laterals present. Secondary branches arising in axils of main branch laterals (which are lost on older plants), alternate, pinnate, distichous, with simple or rarely divided laterals up to 2 cm long and 3-4 mm broad. Cryptostomata in a line on each side of smaller laterals, irregularly scattered on larger laterals, often dense. Vesicles numerous, borne regularly in axils of each lateral on the main and secondary branches, spherical, shortly petiolate, mutic, up to 4 mm diameter. Receptacles distichous, simple or furcate, terete and smooth, linear lanceolate, 3-8 mm long and $\frac{1}{2}$ -1 mm broad.

Type locality.—"Nov. Holl. Littus occident."

Type.—Paris Museum.

Distribution.—From Rockingham (just south of Fremantle), W.A., around northern Australia to Rockhampton, Qld.; Aru Is. and New Caledonia.

Turner's and Mertens's descriptions were both published in 1819, Turner's from a specimen (now in Kew Herbarium) sent him by Mertens.

The type of *S. peronii* is a young plant, with the main branch laterals still present, and without receptacles. In older plants these laterals are often lost, and secondary branches develop from the axils of the laterals, later forming receptacles. This is the plant described by C. Agardh as *S. boryi*. An excellent set of specimens collected by R. L. Specht in Arnhem Land (now in Adelaide University Herbarium) shows these growth stages clearly.

S. peronii differs from *S. decurrens* in possessing more definite laterals, which are contracted at the base and usually simple, though sometimes divided. Some simple laterals will always be found. The laterals of *S. decurrens* are always several times divided and taper from the base into narrow acute segments; simple laterals are rarely, if ever, found.

Grunow (1915, p. 334) described two varieties, var. *lanceolata* and var. *intermedia*, of *S. peronii*, and under *S. boryi* he described (1915, pp. 334, 335) var. *angustissima* and forma *neocaledonica*. These appear to be only developmental stages or ecological variations and not worth recognizing.

Sargassum heteromorphum J. Agardh, Acta Univ. Lund. 9: 60 (1872); K. Svenska VetenskAkad. Handl. 23 (3): 42, pl. 1 (1889); De Toni, Sylloge Algarum 3: 8 (1895); Grunow, Verh. zool.-bot. Ges. Wien 65: 332 (1915); Lucas, Seaweeds S. Aust. pt. 1: 63, fig. 40 (1936)

Fig. 1c; Plate 2, Fig. 2

S. halitrichum J. Agardh, K. Svenska VetenskAkad. Handl. 23 (3): 43, pl. 13 (1889); De Toni, Sylloge Algarum 3: 9 (1895); Grunow, Verh. zool.-bot. Ges. Wien 65: 332 (1915); Lucas, Seaweeds S. Aust. pt. 1: 63 (1936).

Stem short (about 1 cm long), terete, arising from a lacerate discoid holdfast, and giving rise to 1 to several subdistichous main branches which are pinnate to bipinnate below with the lobes rounded to subacute, depending largely on age; segments up to 1 cm wide, with numerous cryptostomata. Lower parts changing fairly suddenly (usually) or more gradually to the upper slender, terete or slightly flattened, pinnate ramuli, about $\frac{1}{2}$ mm broad. Upper ramuli bearing numerous petiolate vesicles, 1-2 (-3) mm diameter, with a prominent but acute and short apical mucro. Receptacles racemose, sessile or sometimes petiolate, terete, lanceolate, and often with a young receptacle near the base, 3-6 mm long when mature.

Type locality.—Georgetown, Tas. (Gunn).

Type.—Herbarium Agardh, Lund, No. 2626.