A TAXONOMIC REVISION OF THE EUROPEAN SPHACELARIACEAE
(*Sphacelariales*, *Phaeophyceae*)

BY

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To my parents
To Hilda, Simone, and Barbara
To my promotores
Prof. Dr. C. van den Hoek and
Prof. Dr. C. Kalkman

CONTENTS

SUMMARY

The present study deals with the taxonomy of a family of the brown algal order *Sphacelariales* in Europe. The taxonomy of this order is much influenced by the works of Sauvageau as published between 1900 and 1914. A short survey of the work on *Spacelariales* by him and his phycological predecessors is given in the introduction.

The order *Sphacelariales* is described and its nomenclatural history is given. Other paragraphs deal with distribution, morphology and the used descriptive terminology, ecology, variability and culture studies, reproduction and life-history, systematic position and classification. In the notes on morphology the history of the descriptive terminology is incorporated, as well as discussions on the correct use of this terminology. Most technical terms are also included in the glossary, located near the end of this book. In the sections on 'Form range and cultures' and on 'Reproduction and life-history' the methods used for unialgal cultures and methods for chromosome counts are discussed. Also a review of life-histories in *Sphacelariales* is incorporated, as well as a discussion on the criteria used for the distinction of taxa and the delimination of the order. A key to the families concludes the treatment of the order.

The family *Sphacelariaceae*, which is the largest and most cosmopolitan family of the order, is treated in a similar way. The two genera in this family, the monotypic genus *Sphacella* and the complex genus *Sphacelaria*, which contains four subgenera, seven sections and 16 species in Europe, are also treated in comparable paragraphs. Keys to the taxa and to ecological growth-forms (ecads) are given.

In the paragraph on relationship of genera, subgenera, sections and species, several approaches for the construction of a classification are mentioned. The phyletic-cladistic approach, based upon methods developed by Hennig (1950), is discussed in detail. One conclusion is that the genus *Choristocarpus* cannot be considered to belong to a monophyletic group together with the *Sphacelariaceae*. Further it can be concluded that the *Sphacelariaceae* all belong to one group with a monophyletic origin. The monotypic genera *Battersia*, *Disphacella* and *Chaetopteris* have to be included into the genus *Sphacelaria*. *Sphacella*, however, is maintained as a monotypic genus. For nomenclatural reasons *Sphacelaria reticulata* (formerly *Disphacella reticulata*) must be chosen as type-species of the genus *Sphacelaria*.

The descriptions of family, genera and sections are usually short, but the descriptions of the species are comprehensive and contain a formal description and a list of dimensions. The paragraphs on distribution start with summaries of coastal regions where the species occur. Each summary is followed by an extract of the list of collections and relevant references. Distribution maps are added. Full lists of collections and references for all species are published separately. Important taxonomic conclusions occur in *Sphacelaria reticulata* (was *Disphacella reticulata* (Lyngb.) Sauv.), in *S. radicans* (ecad *libera* found in the Baltic), in *S. nana* (= *S. britannica* Sauv.) which include *S. saxatilis* and which is different from *S. rigidula* (= *S. furcigera* Kütz.), in *S. plumigera* (unattached growthform = ecad *pinnata*, found in the Baltic), in *S. mirabilis* (was *Battersia mirabilis* Reinke ex Batt.), in *S. fusca* (different from *S. rigidula*), in *S. cirrosa* (includes *S. bipinnata* (Kütz.) Sauv. and *S. hystrix* Suhr ex Reinke which are incorporated amongst the five different ecads of the species) and in *S. sympodiocarpa* (which cannot be incorporated into one of the described subgenera). Most details of morphology are depicted.

INTRODUCTION

For the taxonomy of the *Sphacelariaceae* we still largely depend on the taxonomic conceptions held by Sauvageau (1900–1914) and his previous century predecessors in phycology.

Lyngbye, who introduced the name *Sphacelaria*, included in 1819 nine species in this genus, of which eight (including two varieties) were described in detail. Four of these described taxa (and the undescribed one) are still accepted as *Sphacelaria* species, while all taxa of Lyngbye are still included in *Sphacelariales.* Lyngbye transferred several species of *Conferva* and *Ceramium* of other authors to his genus *Sphacelaria*, and he added three new species. His herbarium is still preserved in Copenhagen and lectotypes of most taxa could be there located. Most of Lyngbye's taxa can still be considered as separate entities. C. Agardh (1824, 1828), Bonnemaison (1828), Harvey (1833), Kützing (1843, 1845, 1849, 1855) and J. Agardh (1848) revised the genus *Sphacelaria* worldwide or for smaller geographic areas. Reinke (1890a, 1891) was the first author who studied all species of the *Sphacelariales* (as *Sphacelariaceae*) in detail. His work was not intended as a taxonomic monograph, but most other contemporary phycologists used it as such. Rather, his papers were contributions to comparative anatomy and morphology of *Sphacelariales* as were earlier works by Geyler (1866), Magnus (1873b) and Pringsheim (1874). Sauvageau's publications (1900–1914) were, again, intended as contributions to the anatomy and morphology of *Sphacelariales*, but were in fact used as a standard taxonomic monograph by all later phycologists.[1]

New insights and new methods in taxonomy, as well as results of revision of the genus *Sphacelaria* in several geographic areas in Europe (Goodband, 1968, 1971, Great Britain; de Haas-Niekerk, 1965, The Netherlands; Irvine, 1956, Great Britain; Kylin, 1947, Sweden; Lund, 1950, Denmark; Waern, 1945, 1952, Sweden) resulted in a need of a new critical revision of the family. The present volume is the first genuine taxonomic revision of the European *Sphacelariaceae.*

The total number of species of European *Sphacelariaceae* recorded by Reinke was 13. Sauvageau recorded 19 different species for Europe and in the present study I reduce the number to 17 and the number of genera from five to two.

Some authors included genera in the *Sphacelariales* which are now considered belonging to other orders. These genera are *Myriotrichia* (Decaisne, 1842) (now in the *Myriotrichiaceae*, *Ectocarpales*) and *Ballia* (now in the *Rhodophyceae*). For details of the history of classification in the *Sphacelariales* see table I.

In my investigation of the taxonomy of the European representatives of the *Sphacelariaceae* s.s. I worked along the following lines:

(1) Study of living material in its natural habit (at different times of the year, if possible), with comparative observations on morphology of the species growing in one locality.

(2) Study of the morphology in unialgal cultures (kept under approximately constant

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[1] The bibliographic status of Sauvageau's work 'Remarques sur les Sphacélariacées' is rather complicated. A large part of this work was published in separate papers in the Journal de Botanique (1900–1904). When published as a separate publication the pagination of the collected papers was changed. In references to the Remarques I will first give the date and page of the original publication in the Journal de Botanique, followed by a reference to the page in the collected Remarques (as: = R. and the relevant page number).

TABLE I. Classification in Sphacelariales

		Genera
Reinke (1890a) (Sphacelariaceae)	Sphacelariaceae crustaceae	1
	Sphacelariaceae hypacroblastae	2, 3, 5, 7
	Sphacelariaceae acroblastae	9, 13
Oltmanns (1904 (Sphacelariaceae)	Tribus Sphacelarieae	1–5
	Tribus Cladostepheae	7
	Tribus Stypocauleae	9–13
Sauvageau (1903, 1906) (Sphacelariaceae)	Hemiblastées (1903)	1–5
	Dichoblastées (1903)	6
	Polyblastées (1906)	7
	Acroblastées (1903)	8
	Holoblastées (1903)	9–13
Svedelius (1911) (Sphacelariaceae)	Tribus Sphacelarieae	1–5
	Tribus Disphacelleae	6
	Tribus Cladostepheae	7
	Tribus Alethocladeae	8
	Tribus Stypocauleae	9–13
Oltmanns (1922) (Sphacelariales)	Sphacelariaceae	1–6
	Cladostephaceae	7
	Stypocaulaceae	(8), 9–13
Fritsch (1945) (Sphacelariales)	Sphacelariaceae	1–6
	Cladostephaceae	7
	Stypocaulaceae	8–13
	Choristocarpaceae	14, 15
Prud'homme van Reine (1971) (Sphacelariales)	Sphacelariaceae	1–5
	Disphacellaceae	6
	Cladostephaceae	7
	Stypocaulaceae	8–13
	Choristocarpaceae	14, 15
Prud'homme van Reine (the present publication) (Sphacelariales)	Sphacelariaceae	1–6
	Cladostephaceae	7
	Stypocaulaceae	8–13

Genera:

1. Battersia. Is Sphacelaria mirabilis in the present publication.
2. Sphacella.
3. Sphacelaria.
4. Sphaceloderma = Sphacelaria caespitula. Not mentioned by Reinke (1890a).
5. Chaetopteris. Is Sphacelaria plumosa in the present publication.

Table I (continued)

6. Disphacella. Is Sphacelaria reticulata in the present publication. Not mentioned by Reinke (1890a) and Oltmanns (1904).
7. Cladostephus.
8. Alethocladus. Not mentioned by Reinke (1890a) and Oltmanns (1904).
9. Anisocladus. Incorporated into the genus Halopteris by Sauvageau and subsequent authors.
10. Halopteris.
11. Stypocaulon. Incorporated into the genus Halopteris by Sauvageau, Svedelius, and Fritsch.
12. Phloiocaulon (often cited as Phloeocaulon).
13. Ptilopogon.
14. Choristocarpus.
15. Discosporangium.

conditions) of strains isolated from widely varying material taken from as widely varying habitats and from areas as geographically distant as possible.

(3) Study of the reproduction, of the life-histories, and of the morphology of the reproductive bodies.

(4) Study of herbarium material.

(5) Formulation of taxonomic criteria and delimitation of the taxa using the above four methods.

(6) Critical investigations of the type-material of as many taxa as possible in order to establish the correct epithets and the synonymy.

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I must also record my indebtedness to the Netherlands Organization for the Advancement of Pure Research (Z.W.O.), the Centre National de la Recherche Scientifique (C.N.R.S.), the National Museum of Natural History at Leiden, the Beijerinck-Popping Fund of the Royal Dutch Academy of Sciences and the State University at Leiden for providing grants for visits to marine biological institutes, botanical institutes, and marine coasts all over Europe.

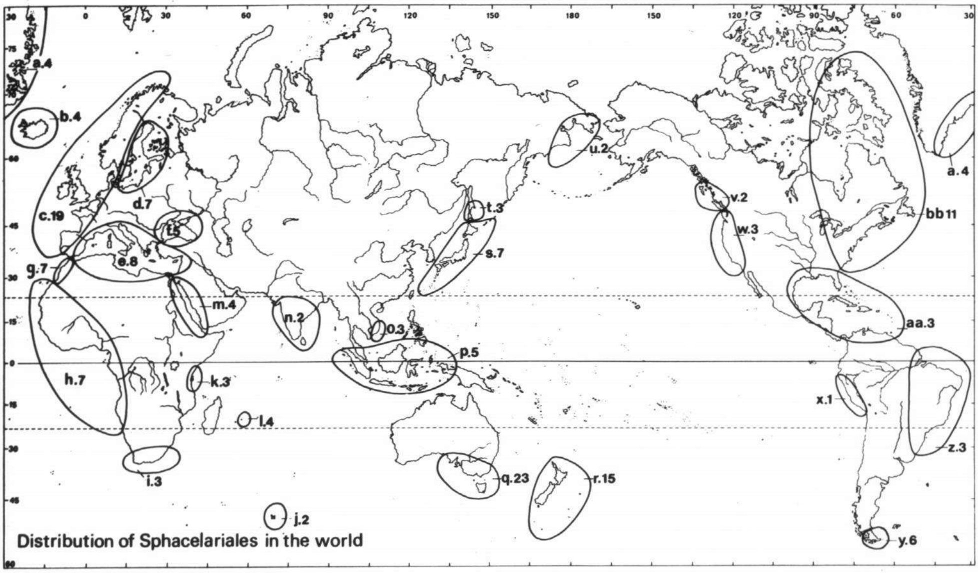


Fig. 1. Distribution of *Sphacelariales* in the world. Geographical areas are marked with a letter (see table II), and the total number of species of each area is given.

SPHACELARIALES Migula

Ordo *Sphacelariales* Migula (1909) 237; Oltmanns (1922) 83; Setchell & Gardner (1925) 390; Newton (1931) 188; Steinecke (1931) 287; Hamel (1938) 240; Fritsch (1945) 260 (p.p.); Lund (1950) 5; Papenfuss (1955) 172 (p.p.); Lindauer, Chapman & Aiken (1961) 152; A. Zinova (1967) 146 (p.p.); Prud'homme van Reine (1971) 151, (1974) 171; Russell & Fletcher (1975) 778; Prud'homme van Reine (1978) 301.—Type: Familia *Sphacelariaceae* Decaisne emend. Oltmanns.

See also the list of references and synonyms published for the *Sphacelariaceae* (p. 31) and the relevant notes on nomenclature of the *Sphacelariaceae*.

Small (<2 cm) to relatively large (30–40 cm) marine plants (one species of *Sphacelaria* in fresh water). The heterotrichous plants consist usually of a basal part and erect filaments with apical growth. The walls of all cells blacken when treated with bleaching liquid.

The basal parts consist of monostromatic or polystromatic discs, of creeping filaments (rhizoids, stolons, or tuberculous filaments) or of irregularly aggregated cells endophytic in a host. They are rarely unattached or without erect filaments.

The terete, articulate, erect filaments are subsimple to bushy, quite rigid to flaccid, provided with sparse to many, determinate or indeterminate, branched or unbranched, acroblastic or hypacroblastic laterals, which are distichous, helicoid, whorled, or irregularly placed.

Segments cut off from the usually conspicuous cylindrical apical cell of the erect filaments are each transversely divided once before longitudinal segmentation. The secondary segments may have secondary growth in length and width and secondary transverse divisions in the cells of the secondary segments may be frequent or absent. Some species have rhizoids which may corticate the erect filaments and may be divaricate. Hairs are present in several species.

All coloured cells of the thallus contain many disc-like and mostly parietal chloroplasts. In surface-view they are rounded, elliptical, or more or less irregular in shape.

Reproduction takes place by means of propagules, plurilocular isogametangia, or anisogametangia, neutral plurilocular zoidangia, unilocular oogonia, or unilocular zoidangia.

Distribution. The geographic distribution of the *Sphacelariales* in the world is given in fig. 1 and in table II. Only the genus *Sphacelaria* is a real cosmopolitan genus, but the genera *Halopteris* (*Stypocaulon* included) and *Cladostephus* have also been found in many localities all over the world. The monotypic genera *Sphacella*, *Alethocladus*, and *Ptilopogon* can be found in limited areas only and the genus *Phloiocaulon* (with three species) has been found in southern Africa and southern Australia.

The main centres of distribution of the *Sphacelariales* are Europe, southern Australia, and New Zealand. For Japan see discussion in the section on distribution of *Sphacelaria* (p. 54).

Notes on morphology and descriptive terminology (see also the glossary, p. 262)

Herbarium specimens could be made to resume their original form by soaking them in a few drops of a saturated solution of detergent (washing powder). No heating of the material was necessary to make the specimens regain their natural form, and so the morphology of the

TABLE II. Distribution of Sphacelariales in the world

code	area	main source	year	Sphacella	Sphacelaria	Alethocladus	Halopteris + Stypocaulon	Phloiocaulon	Ptilopogon	Cladostephus	Total
a	E. Greenland	Jönsson	1904	-	4	-	-	-	-	-	4
b	Iceland	Munda	1972b	-	4	-	-	-	-	-	4
c	Atl. Europe and North Sea	Prud'h. v. R.	-	-	16	-	2-3	-	-	1	19-20
d	Baltic	Pankow	1971/1976	-	6^x	-	1	-	-	-	7
e	Mediterranean	Prud'h. v. R.	-	1	4	-	2-3	-	-	1	8-9
f	Black Sea	A. Zinova	1967	-	3	-	1	-	-	1	5
g	Morocco	Dangeard	1949	-	4	-	2	-	-	1	7
h	Trop. W. Africa (incl. Canary Isl.)	Price et al.	1978	-	1^x	-	2	-	-	1	7
i	S. Africa	Simonds	1977	-	1	-	1	1	-	-	3
j	Kerguelen Isl.	Papenfuss	1964	-	1	1	-	-	-	-	2
k	Tanzania	Jaasund	1976	-	3	-	-	-	-	-	3
l	Mauritius	Børgesen	1941	-	3^x	-	-	-	-	-	3
m	Red Sea	Papenfuss	1968	-	3^x	-	1	-	-	-	4
n	India	Misra	1966	-	2	-	-	-	-	-	2
o	Vietnam	Pham-Hoang	1969	-	3^x	-	-	-	-	-	3
p	Indonesia	Weber-van Bosse	1913/1928	-	4^x	-	1^x	-	-	-	5
q	S. Australia	Womersley	1967	$-^x$	15	-	4	2	1	1	23
r	New Zealand	Lindauer et al.	1961	-	7	-	6^x	-	1	1^x	15
s	Japan	several	several	-	6^x-23	-	1	-	-	-	7-24
t	S. Sachalin	Tokida	1954	-	2^x	-	1	-	-	-	3
u	Beering Sea	Vinogradova	1978	-	2	-	-	-	-	-	2
v	W. Canada	Scagel	1957	-	2	-	-	-	-	-	2
w	W. coast of U.S.A.	Setchell & Gardner	1925	-	3^x	-	-	-	-	-	3
x	Peru	Acleto	1973	-	1	-	-	-	-	-	1
y	Fuegia	Papenfuss	1964	-	2	1(?)	3	-	-	1^x	6-7
z	Brazil	Taylor	1931	-	3^x	-	-	-	-	1(?)	3-4
aa	Caraibean	Taylor	1960	-	3^x	-	-	-	-	-	3
bb	E. coasts of U.S.A. and Canada	Taylor	1957	-	9^x	-	1	-	-	1^x	11

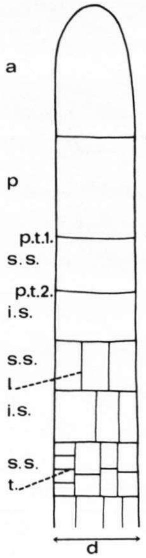
x = number of species in this table differs from the number given by the cited author because of addition of new data or new taxonomic concepts.

? = doubtful

specimens could be studied. Sections of living specimens have been made by hand and thin sections of dried-and-soaked specimens and of specimens preserved in fluids have been made by the common microtome procedures and also by sectioning with an ultra-microtome.

Herbaria from which material was investigated are indicated in the text by the abbreviations borrowed from the Index Herbariorum (Holmgren & Keuken, 1974). Not incorporated in this list are herbaria in the Biologische Anstalt Helgoland (HELG), the Portsmouth Polytechnic (PORT), and the Bibliothèque Municipale de Quimper (QUI).

Segmentation and growth: One of the main characters of the *Sphacelariales* is the growth of the erect filaments by a prominent elongate apical cell (fig. 2; plate 2d). This apical cell cuts off segments parallel to its base. When the apical cell has reached a certain length, a transverse septum (fig. 2, p.t.1) separates a primary segment from the apical cell



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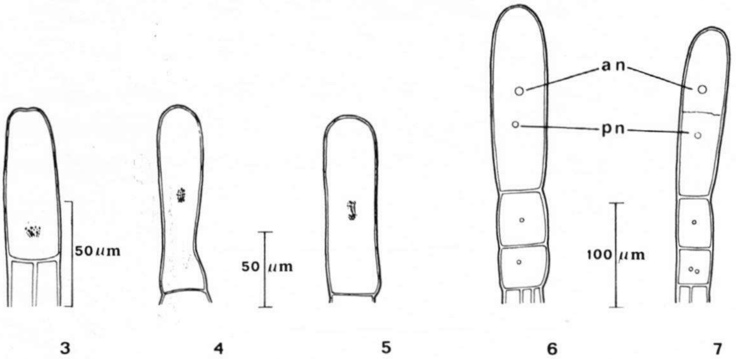


Fig. 2. Diagram of apical growth of an unbranched filament (based on *Sphacelaria* sp.). a = apical cell; d = diameter or width; i.s. = inferior secondary segment; l = longitudinal cell-wall; le = length; p = primary segment; p.t. = primary transverse wall; s.s. = superior secondary segment; t = (secondary) transverse cell-wall.

Fig. 3–7. Apical growth in *Sphacelaria.* Microslides from culture of specimens from Hoek van Holland, *Van den Hoek*, spring 1960, coloured with acetocarmine. In fig. 3–5 dividing nuclei in apical cells. In fig. 6 and 7 in the apical cell a large superior nucleus (an) and a smaller nucleus of the future primary segment (pn).

proper. The large nucleus of the apical cell divides into a large nucleus of the new apical cell and a much smaller nucleus of the primary segment. When continued cell-divisions produce smaller and smaller cells the nuclei also become smaller (fig. 3–7). A primary segment divides again by a transverse septum (fig. 2, p.t.2) into two secondary segments which are usually of equal size. Both the superior secondary segment and the inferior secondary segment divide further to produce the mature polysiphonous filament. The first longitudinal wall (primary longitudinal wall) is usually radial and median in the cylindrical secondary segments of the filaments, and subsequently more radial and often also periclinal walls are formed. In several species the long cells formed in the secondary segments by these longitudinal walls are divided by one or more transverse walls. These transverse walls are often called secondary transverse walls to distinguish them from the walls which separate the segments (fig. 2).

In many *Sphacelariales* the segments exhibit almost no further enlargement after their formation. In these so-called leptocaulous *Sphacelariales* the diameter of the segments of the filaments equals or slightly exceeds the diameter of the apical cell at the time of formation of these segments (fig. 2d; 8a). Chapman (1962, p. 124) and Goodband (1971, p. 964) stated that the small increase of the diameter of the filaments is due to the formation of these segments (fig. 2d; 8A). Chapman (1962, p. 124) and Goodband (1971, walls. The length of the secondary segments does not alter in the leptocaulous *Sphacelariales*

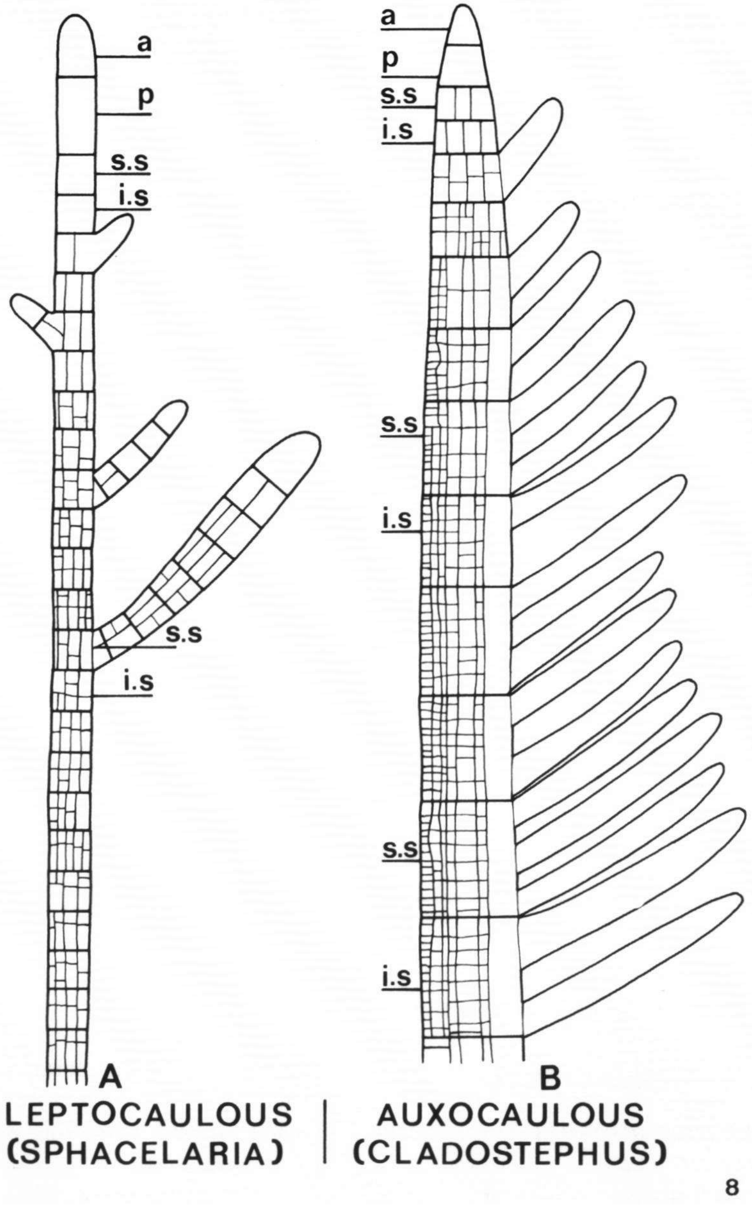


Fig. 8. Diagram of leptocaulous and auxocaulous growth. For explanation of the abbreviations, see text to fig. 2.

(fig. 8A). In another group of *Sphacelariales*, called auxocaulous, the secondary segments can enlarge conspicuously both in length and diameter (fig. 8B).

The only means of conspicuous secondary enlargement for the leptocaulous *Sphacelariales* is by downward growing corticating filaments that originate from the peripheral cells of the axial filaments. Many of these cortical filaments may extend down to the basal system and spread over it, thus functioning as a part of the attachment organ. Actually, such cortical filaments are specialized rhizoidal filaments. In my descriptions I will use the denomination 'rhizoids' for these structures.

Branching: Two different patterns in the formation of the laterals can be distinguished within the *Sphacelariales.* In the *Sphacelariaceae* laterals are formed as outgrowths of secondary segments (fig. 9k, m). In the other families branching is more complex. There the apical cell cuts off a small apical lenticular branch-initial (fig. 9a–c). In an early stage this branch-initial divides horizontally, cutting off a small cell on its upper side (fig. 9e, f). The lower and larger cell of the branch-initial forms the lateral, while the upper and smaller cell may give rise to a bundle of hairs, to one or more sporangia, to one small lateral, or to a group of resting cells. The larger part of the original apical cell, located below and to one side of the small lenticular cell, elongates and functions again as the apical cell of the main axis so that the small lenticular branch-initial is pushed into a lateral position (fig. 9, b–f).

In the *Sphacelariaceae* the apical cell can also cut off a small lenticular cell. In this family such a lenticular cell is nearly always a hair-initial.

Nägeli (1844) was the first author who studied the growth of a member of the *Sphacelariales* in detail. In *Stypocaulon scoparium* (as *Sphacelaria scoparia*) he described the cutting off of a small (semi-) lenticular cell by an oblique wall, a little to one side of the tip of the apical cell. As the latter elongates, the small cell comes to occupy a lateral position. When the large apical cell divides, the transverse wall meets the convex wall of the lenticular cell approximately at a right angle. The lenticular cell divides horizontally at an early stage and cuts off a small cell on its upper side. Nägeli also shortly described the formation of primary and secondary segments and he stated that growth of *Cladostephus* is quite similar.

Cramer (1864) and his pupil Geyler (1866) considered the small lenticular branch-initial occurring in many *Sphacelariales* as a lateral outgrowth of the apical cell. According to these authors this lateral outgrowth can be observed before a wall separates the lenticular wall from the large apical cell. According to Geyler hairs in *Sphacelaria tribuloides* have a similar origin. Thus growth of *Stypocaulon scoparium* as described by Nägeli can be considered as sympodial, while growth of *Sphacelariales* as described by Geyler has to be considered as monopodial. Authors e.g. Kny (1872a, for *Halopteris filicina*), Pringsheim (1874), Reinke (1890a), and Ginsburg-Ardré & Chadefaud (1964) followed Geyler, but other authors, e.g. Magnus (1872a and 1873b), Reinke (1891, for *Stypocaulon scoparium*), Sauvageau (1900, p. 215 = R. 3, 1903, p. 83 = R. 254, and p. 333 = R. 268), and Hommersand (1963) followed Nägeli. Strasburger (1892) and Swingle (1897) observed that the nuclear spindle in the apical cell of *Stypocaulon scoparium* has an oblique position before any asymmetry can be observed in the form of this apical cell. Swingle proposed to consider the formation of laterals from the apical cells as entirely different from the formation of the segments of the main axes. In that case, he declared, the growth of *Stypocaulon scoparium* can be considered monopodial.

Recently the morphology of the *Ceramiaceae* and *Rhodomelaceae* (both *Rhodophyta*) has been discussed by several authors. They often also discussed branching of *Sphacelaria* and '*Halopteris*' in their publications. For their discussion of '*Halopteris*' they used observations by earlier authors on *Halopteris filicina* as well as on *Stypocaulon scoparium*, but

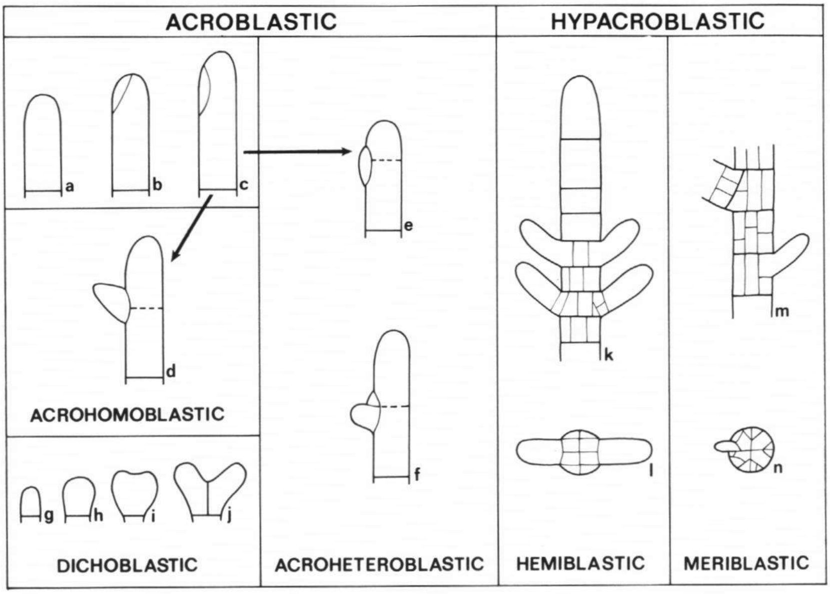


Fig. 9. Diagram illustrating descriptive terminology used for the mode of branching. a–j. acroblastic branching, longitudinal sections; a–c. forming of the lenticular cell. The arrows point to further possible development of this lenticular cell; d. direct outgrowth (acrohomoblastic), or e–f, formation of two cells from which different structures develop (acroheteroblastic); g–j. growth of the apical cell in case of dichoblastic branching; k–n. hypacroblastic branching; k,m. longitudinal sections (in m only the lower lateral shows meriblastic branching); l, n. transverse sections.

usually without citation of these authorities.

Hommersand (1963) considered the sympodial branching of the *Dasyaceae* (*Rhodophyta*) and of the *Rhodomelaceae* similar to that of '*Halopteris*'. Ginsburg-Ardré & Chadefaud (1964), however, considered the branching pattern of '*Halopteris*' as monopodial and that of *Polysiphonia* (a member of the *Rhodomelaceae*) as sympodial. Later Ginsburg-Ardré (1966) described branching of the latter as pseudo-sympodial and monopodial. The designation 'monopodiale pseudosympodiale' is also used by l'Hardy-Halos (1971) to characterize the branching pattern of *Callithamnion* spp. (*Rhodophyceae*). Branching of '*Halopteris*' she considered, however, as unequal dichotomy. The concept of dichotomy in apical cells of *Sphacelariales* has also been proposed by Kny (1871, 1872a, 1872b) and Pringsheim (1874) to elucidate the mode of branching of the main axes of *Cladostephus* spp. According to Magnus (1872b, 1873a, 1873b), however, the preparation on which Kny based his concept, was a damaged main axis of which the cells of a subapical segment were transformed into apical cells.

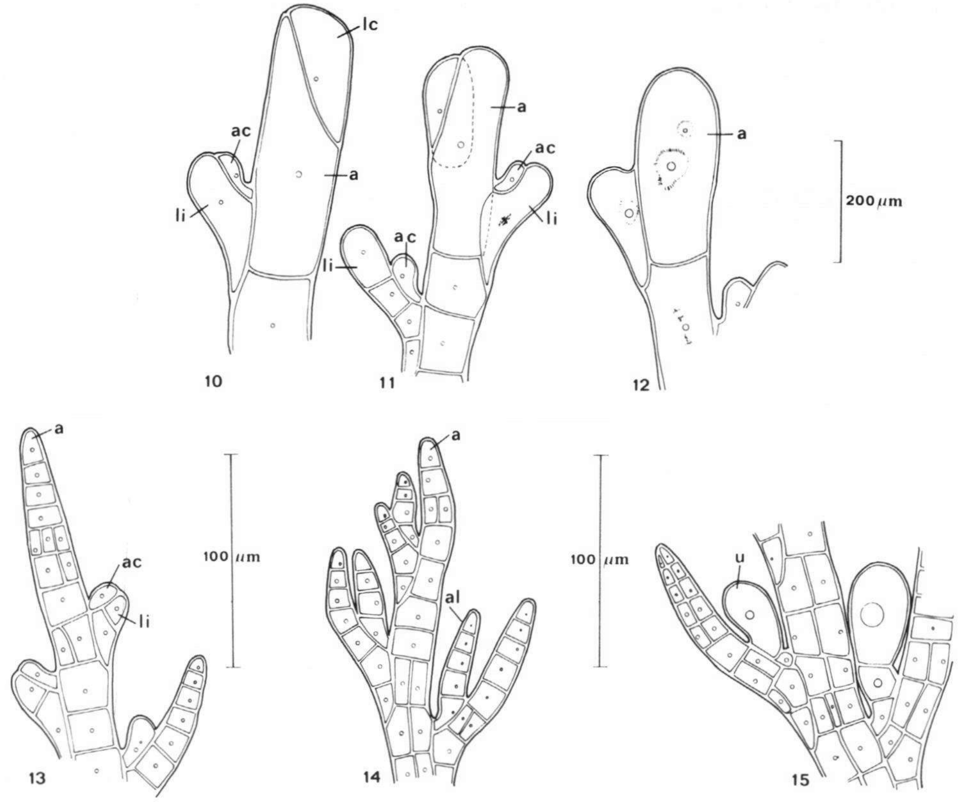
Sauvageau (1906) detected that the indeterminate laterals of *Cladostephus* spp. are usually formed by modified hemiblastic branching ('plagioblastic'). True dichoblastic branching was described by Sauvageau (1903, p. 338 = R. 273) for *Sphacelaria reticulata* (as *Disphacella reticulata*).

The concept of unequal dichotomy was based by l'Hardy-Halos (l.c.) on an incorrect figure by Chadefaud (1960, p. 292). She wrongly copied this as her figure 7F. In this figure the laterals of the first and second order are not opposite the primary transverse walls of the axis or the lateral of the first order, but they are figured as if they sprout from a superior secondary segment. In the apical cell of this figure 7F the oblique wall between the small lenticular cell and the remaining part of the original apical cell is almost longitudinal and the direction of the nuclear spindle is suggested to be perpendicular to it and so transverse in the cell. In a letter (l'Hardy-Halos, personal communication, 1972) she suggested considering the branching pattern of '*Halopteris*' as 'monopodiale pseudosympodiale'. This branching differs, however, from the branching of the same name in the *Rhodophyceae* by the tardy outgrowth of the lateral in the *Sphacelariales*. In my figures 10–20, stages of the development of the lenticular cell and of the remaining part of the original apical cell of *Halopteris filicina* and of *Stypocaulon scoparium* are given. The designation 'pseudo-sympodial and monopodial' can be used for the acroblastic branching pattern in the *Sphacelariales*. However, the small lenticular cell of the *Sphacelariales* is a unique morphological element within the *Phaeophyceae*. When one tries to incorporate the acroblastic branching in one of the categories 'sympodium' or 'monopodium' it results in rather complicated and in fact unnecessary designations. The term 'acroblastic' as such is adequate.

Denffer & Fricke (1968) investigated the polarity of the apical cells of *Stypocaulon scoparium*. Isolated apical cells were found to be distinctly polarized as soon as the small lenticular cell had been formed. Younger isolated apical cells did not show this polarity. Polarity of these large apical cells is probably induced by the presence of neighbouring cells. In most *Sphacelariales* all cells can grow into a filament with a distinct apical cell. When a part of a main filament is cut away, the undamaged cells of the nearest secondary segment all grow into new filaments. Often the largest cells, which are usually medullar cells, grow into indeterminate filaments and the peripheral cells into determinate filaments or into rhizoids. When only the apical cell of a filament died, the undivided subapical primary segment or the subapical superior secondary segment directly starts to function as the apical cell of this filament. If in the superior secondary segment already one or more longitudinal walls were formed, the new cells may each form a new filament.

Terminology used for different types of branching: In 1890 Reinke divided the majority of the *Sphacelariales* into two groups (see table I). His '*Sphacelariaceae* acroblastae' comprised all types of *Sphacelariales* in which branching is mainly initiated in the apical cell, and his '*Sphacelariaceae* hypacroblastae' comprised all types in which the laterals sprouted from cells below the apical cell. Sauvageau (1900–1914) introduced many other terms. In 1903 (p. 334 = R. 269) he criticized the use of the concept 'acroblastae'. According to him in most cases the laterals do not originate from the apical cell proper, but from only a part of the lenticular cell formed from this apical cell. He considered the small upper cell, cut off from this lenticular cell, as the genuine apical cell of the branched filament. The other part of the lenticular cell was considered to be a primary segment. Since the basal part of the laterals originated from these undivided primary segments, Sauvageau called them 'rameaux hologènes' and described the method of branching as 'holoblastique'. The notion 'acroblastique' is used by Sauvageau in a much more limited sense, i.e., only when the undivided lenticular cell gives rise to a lateral.

Fritsch (1945, p. 273) used the term 'holoblastic' in a much broader sense. In the termi-



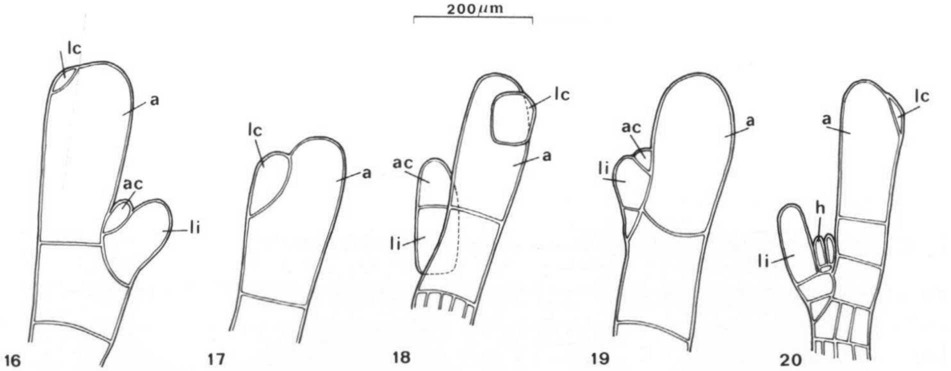


Fig. 10–15. Acroheteroblastic branching in ***Halopteris filicina***. Microslides of specimens from Banyuls-sur-Mer, *Prud'homme van Reine*, 6/9/1967, coloured with acetocarmine. In the apical cell (a) of fig. 10 a small lenticular cell (lc) is formed, which is pushed into a lateral position by the elongation of the remaining part of the original apical cell in fig. 11 and 12. This small cell divides into an axillary cell (ac) and an initial for a lateral (li). The axillary cell can grow into an axillary lateral (al) or a unilocular zoidangium (u).

Fig. 16–20. Acroheteroblastic branching in ***Stypocaulon scoparium***. Microslides from Tremiti, *Pignatti* (TSB). Code as in fig. 10–15. In fig. 20 young axial hairs (h).

nology of Fritsch this term does not only cover all acroblastic branching sensu Reinke, but also the formation of hairs from apical cells. Since the term 'holoblastic' used by Fritsch is so different from the concept used by Sauvageau, this term cannot be used any longer. However, the term 'acroblastic' (sensu Reinke) can be expanded also to the *Sphacelariales* with hair-initials.

Where only one kind of structure (a hair, or a lateral for instance) is formed from the lenticular initial cell, I introduce the term 'acrohomoblastic branching' for this type of branching. Where the lenticular initial cell gives rise to two different structures (both a hair and a lateral for instance) I introduce for this the term 'acroheteroblastic branching'. A special case of acrohomoblastic branching is dichotomy occurring in the apical cell ('dichoblastic branching').

In the hypacroblastic type of branching (sensu Reinke) the basal part of the lateral is often as broad as the whole length of a secondary segment. Sauvageau (1903, p. 332 = R. 267) used the term 'hemiblastique' for this. For a lateral of which the base is only as broad as a part of the length of a secondary segment Sauvageau (1904, p. 478) used the term 'meriblastique'. In that case the lateral is formed as outgrowth of a cell that was already divided by second ary transverse walls. Sauvageau also introduced the terms 'microblastique' (1906, p. 84) for the small fertile laterals of *Cladostephus*, formed as outgrowths of small peripheral cells and 'plagioblastique' (1906, p. 91) for indeterminate laterals of *Cladostephus*. Since microblastic branching seems to be a special case of meriblastic branching, and plagioblastic branching is a normal or somewhat tardy hemiblastic branching, I do not accept these latter terms of Sauvageau. The terms used by me to describe branching in *Sphacelariales* are illustrated by fig. 9.

Hommersand (1963) used the terms acroblastic and holoblastic for the description of branching of *Rhodophyceae*. However, he had to adapt these terms so much that they have little in common with their original meaning.

In the majority of *Sphacelariales* filaments of limited growth occur beside filaments of which the growth is not distinctly delimited. The former filaments are here called 'determinate filaments,' the latter 'indeterminate filaments.' In the determinate filaments the apical cell soon ceases to function and often persists as a small cell (fig. 228). In many genera the main axes are indeterminate and the laterals for the greater part determinate. In the leptocaulous forms, some of the normally determinate laterals may become indeterminate, but in the auxocaulous forms in most cases the indeterminate laterals are formed in another way than the determinate ones.

The laterals that normally rise from or directly below the apical cell of the main axis and the indeterminate laterals are termed primary laterals (fig. 21c–h). Laterals that arise from peripheral cells (dormant branch-initials, the pericysts) or rhizoids in a later stage of development, or laterals that arise from subapical segments when the apical cell is damaged or killed, are termed secondary laterals (fig. 21 l). The term 'proliferations' is used for small outgrowths if these are formed from all or most peripheral cells of axes and laterals (fig. 21k).

If thick indeterminate filaments are perennial and after rest form new primary or secondary laterals, these newly formed laterals are referred to as 'laterals of the second generation (fig. 21n, o).

The primary laterals sprouting from the main axis are called '(primary) laterals of the first order' (fig. 21c, d). Laterals sprouting from these primary laterals of the first order are

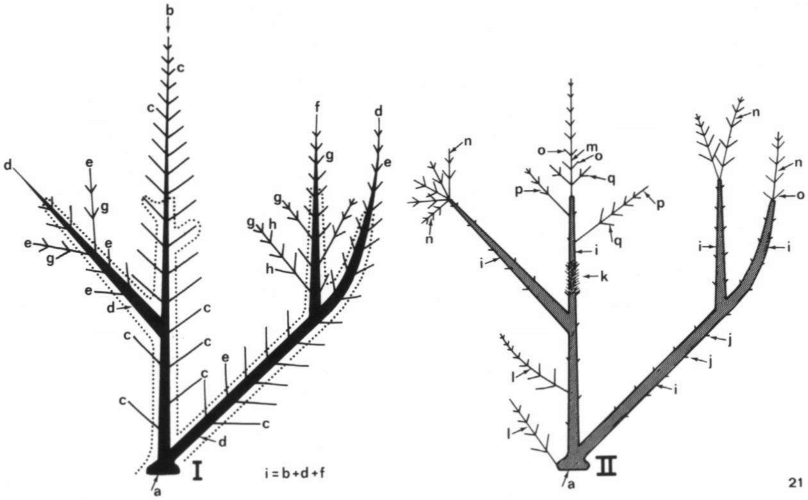


Fig. 21. Diagram explaining the descriptive terminology used for hierarchy of branching (based on *Sphacelaria plumosa*). I. First year of growth. a. basal disc; b. main axis; c. primary determinate lateral of the first order; d. primary indeterminate lateral of the first order; e. primary lateral of the second order (more or less determinate); f. primary indeterminate lateral of the second order; g. primary lateral of the third order (more or less determinate); h. primary determinate lateral of the fourth order; i. (= b + d + f) the main (erect indeterminate) filaments (in *S. plumosa* covered by rhizoids), c and h can also be called ultimate laterals, e and g are ultimate laterals, and in part penultimate laterals. Many filaments break off in winter. Next spring only the parts inside the area bordered by the dotted line are supposed to remain. II. Second year of growth (the perennial parts are shaded), a and i as in I. j. remains of determinate laterals (often difficult to observe in living specimens); k. proliferations or meriblastic laterals (fertile in *S. plumosa*); l. secondary indeterminate lateral of the first order; m. axis of the second generation; n. new branch functioning as axis of the second generation; o. primary determinate lateral of the first order and of the second generation; p. primary determinate lateral of the first order that survived the winter and became a primary indeterminate lateral of the first order and of the second generation; q. primary determinate lateral of the second order and of the second generation.

termed 'laterals of the second order,' and so on (fig. 21e–h). The branching system is often terminated by determinate laterals, the ultimate laterals. Sometimes the term 'penultimate laterals' will be used for the determinate laterals on which the ultimate laterals are formed.

Some of the laterals of the first order, and often also some laterals of a higher order, can exhibit indeterminate growth. In particular the larger indeterminate laterals are often very difficult to discern from the main axis. These complex structures will be described as 'the main (erect indeterminate) filaments' (fig. 21i).

Rhizoids are laterals or proliferations with negative geotropic growth. Stolons are creeping filaments, arising from the marginal cells of basal discs, from the upper cell layers of the basal holdfast, or from erect filaments or rhizoids when in contact with a suitable substrate.

Formation of hairs: Hairs are usually formed by acroblastic branching. Exceptionally hemiblastic hairs have been observed (see fig. 310). Solitary hairs arise usually by acrohomoblastic branching. The lenticular hair-initial may grow directly into a hair, but often the hair-initial divides to form two or four small cells which each grow into a hair. Exceptionally, one of these initial cells in *Sphacelaria* grows into an erect filament (see fig. 70; 77). Branched hairs are exceptional (see fig. 107; 108), normally hairs are unbranched.

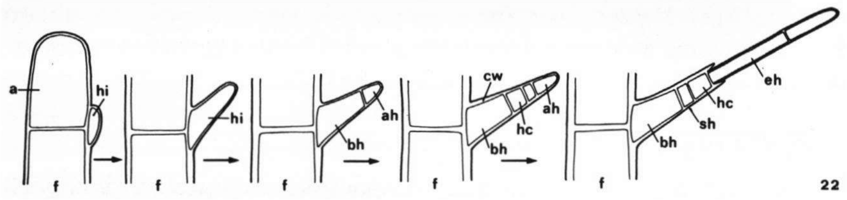


Fig. 22. Formation of a solitary hair in *Sphacelaria.* Semi-diagrammatic. In the filament (f) with apical cell (a) the hair initial (hi) grows into a basal cell of the young hair (bh) and a small apical cell of the young hair (ah). The basal cell forms new cells (hc) and the original cell-wall (cw) bursts to form a sheath (sh) while the cells of the hair elongate (eh).

The lenticular hair-initial (or the cells formed from it) protrudes and divides into a small apical cell (fig. 22ah) and a larger basal cell (fig. 22bh). The apical cell of the young hair does not divide further, but the basal cell starts meristematic activity. When a few more cells are formed by this apical cell the original cell-wall ruptures and the small young cells start to elongate (fig. 22eh). The remnants of the original cell-wall can be found as a sheath (fig. 22sh) around the base of these endogenous hairs. The cells of the hairs grow only in length, not in width. The growth of hairs can be conceived as the reverse of apical growth, supplemented by elongation of the cells.

Prostrate parts: The prostrate part of the plants can be described as the basal holdfast. Often this basal holdfast is a basal disc, which can be monostromatic or polystromatic. When several polystromatic discs grow over each other a basal crust can be formed, which can be covered by rhizoids. Complex basal holdfasts can be formed by intricate growth of erect filaments, arising from rhizoids, stolons, and small or larger basal discs. In some species the basal holdfast is formed by short, swollen stolon-like filaments only (the tuberculous basal parts of *Sphacelaria plumula*) or by irregular masses of cells growing endophytic in another alga (the basal parts of *Sphacella subtilissima*).

Branching in the basal holdfast is usually less regular than in the erect filaments. When basal discs are formed directly after attachment of zoids or zygotes they consist of radially arranged, creeping, coalescent filaments. The prostrate filaments show pseudodichotomous branching.

The creeping filaments have apical growth, but the formation of secondary segments is often less regular than in erect filaments. Frequently the division of secondary segments is lacking in many or all filaments of the discs. As described for *S. mirabilis* (p. 000) in polystromatic discs all cells of the creeping filaments proliferate to form upright files of cells which can be considered as determinate laterals. In some species the apical cells of these crowded upright files of cells can divide, resulting in dichotomous or pseudodichotomous branching of these files. Usually the competition for room in these polystromatic discs is so sharp, that the cells resulting from the division of the apical cells of the upright files have to be much smaller than the lower and undivided cells of these files. When the cells of an upright file grow much faster than the surrounding upright files an erect filament can be formed which sprouts from the basal holdfast. When several neighbouring upright files present this faster growth, a new polystromatic disc can be formed over an older one, resulting in a thick basal crust. Rapid growth of marginal cells of basal discs can result in the production of a stolon or in a new lobe of the basal disc.

Ultrastructure: Methods used for preparing *Sphacelaria* filaments for ultrastructural studies were the same as described by Lokhorst (1978) for *Ulothrix*. For results see the section 'Notes on morphology' of the genus *Sphacelaria* (p. 50).

Notes on ecology

Most *Sphacelariales* are genuine marine plants. One species (*Sphacelaria fluviatilis* Jao) has been found in fresh water in China and the U.S.A. Several other species occur in brackish waters, but often the specimens found in these habitats are sterile or they are not attached to a substrate. In the marine environment *Sphacelariales* can be found in many habitats. They occur in Europe in supralittoral habitats as well as in deep water (100–120 m depth), and have been found growing in salt-marshes as well as on rocky shores or in seagrass-meadows. They are often epilithic but have also been found growing on (and partly in) wood, on clay, peat, and on other plants. The basal parts of several species can be partly endophytic in parenchymatous *Phaeophyceae*. In *Codium* several species of *Sphacelaria* form long rhizoids which grow in between the utriculi of the host. The variation in habitats is largest in the *Sphacelariaceae*. In the other families most species are usually epilithic.

Form range and cultures

The early phycologists, like the Agardhs and Kützing regarded any morphological variant as a distinct taxon. They did not appreciate the morphological variation in appearance of plants either at different seasons or growing under different conditions. Harvey, on the other hand, had a much better understanding of the morphological plasticity of marine algae. Pringsheim (1874) described the variation in what he supposed to be one species (*Sphacelaria olivacea*). It is a pity that his *S. olivacea* has to be regarded as an amalgamation of at least three distinctly different species (*S. caespitula, S. rigidula*, and *S. radicans*; perhaps also *S. nana*).

Morphological plasticity in *Sphacelariales* was much better understood by Reinke (1890–1892) and Sauvageau (1898–1914). Many later authors (for example Waern 1945 and 1952, Kylin 1947, Lund 1950, and Irvine 1956) mainly based their work on the 'Remarques sur les Sphacélariacées' of Sauvageau. Their study of living material collected from nature and often also of a considerable number of herbarium specimens combined with their understanding of variability of these algae resulted mainly in changes in the delimitation of several species in the genus *Sphacelaria*.

Sauvageau studied several *Sphacelariales* in culture. He mainly studied the dehiscence of zoidangia and gametangia and occasionally also the germination of attached zoids and the development of the germlings. De Haas-Niekerk (1965) was the first investigator who grew *Sphacelaria*-species in unialgal cultures under relatively constant conditions in order to eliminate the influence of several environmental conditions on the morphology of these algae. Later Goodband (1971) used the same methods during his study of British *Sphacelaria* species. In other genera of the *Sphacelariales* culture-methods have only been used in studies of the life-histories.

Goodband (l.c.) was the first investigator who used a simple statistical approach to study the variation in morphological characters in three *Sphacelaria* species. He concluded that his investigations revealed that not all the criteria previously used to delimit these species were taxonomically valid. Considerable overlap between the species was found in the expression of several characters, for example in apical cell dimensions, dimensions of sub-apical cells, in the form of the arms of propagules, and in the number of these arms. He also demonstrated by his culture experiments that environmental factors play a large part in the observed variation. For *S. cirrosa* he suggested that no sub-specific taxa should be maintained within this species. *Sphacelaria fusca* and *S. furcigera* are, according to Goodband, almost indistinguishable on the basis of most of the characters considered in his investigation. He stated, however, that a number of characteristics which could not be treated statistically clearly distinguish these two species. All specimens of *S. fusca* and of *S. furcigera* studied by Goodband belonged to *S. rigidula*, however. Consequently the presuppositions on which Goodband based his investigations on the two supposed species were wrong and this part of his study is less valuable.

In the *Stypocaulaceae* no recent studies about the form range of species or infraspecific taxa have been published in Europe, apart from notes on the unattached *Stypocaulon scoparium* found in the Baltic and Denmark (Waern, 1945 and 1952, Lund, 1950). Moore (1953) and Lindauer, Chapman & Aiken (1961) for New Zealand as well as Womersley (1967) for southern Australia based their studies on the *Stypocaulaceae* mainly on the previous works of Sauvageau.

In the *Cladostephaceae* I (Prud'homme van Reine, 1972) suggested to unite all European taxa into one species. The differences between the two former main taxa, usually called *Cladostephus spongiosus* and *C. verticillatus* in European marine floras, were all considered to be gradual and probably caused by external factors. Occurrence of genetic differences cannot yet be excluded, however.

Unialgal cultures — methods: As many plants as possible representing a form range as large as possible were collected from different habitats and from geographically distant localities. Living material of 12 out of 17 species was collected during a number of excursions to the Baltic coast near Trosa, the coasts of Norway near Bergen and Oslo, the west coast of Sweden, several localities in Denmark, Heligoland, the coast of the Netherlands, and northern France (Boulonnais–Quiberon), the east coast of Scotland near St. Andrews, the Orkney Islands, the coasts of Eire near Galway and Dublin, the Mediterranean coast near Banyuls, and to several islands in Macaronesia (Madeira and surrounding islands, Salvage Islands, and Canary Islands).

Unialgal cultures were obtained by cutting off, under a binocular dissecting microscope, a number of apparently clean apical fragments of filaments with 6–10 secondary segments. Subsequent superficial cleaning was carried out by dragging the fragments with a sterile needle made of a thin wolfram filament through a semisolid sterile medium of seawater with 2, 2.5, or 3% agar. The cleaned fragments were put separately into culture tubes filled with sterile medium and plugged with a sterile but ventilating stopper. Several weeks later the contaminated cultures were cleaned or discarded and the unialgal ones were grown further in culture tubes, in petri-dishes, or deeper culture vessels (glass boxes) and were used for observations on morphology and life-history.

Algal and fungal spores possibly present in the medium were killed by heating the medium in a steam-chamber or by pasteurizing it by heating to 72°C in a water-bath three times over a three-day period.

Three media were used concurrently. Two of them were modifications of Erdschreiber medium both prepared in exactly the same way but one with aged natural sea-water and one with sea-water made from sea-salt (35 g Meeressalz Wimex HW, from Spezialfabrikation für Meeresaquaristik H. Wiegandt, 415 Krefeld 1, B.R.D. in 1000 ml demineralized water). In the Erdschreiber medium (Föyn, 1934) the Na of the additions was substituted by K and the pH was adjusted between 7.8 and 8.2 by the addition of some drops of a 10% KOH solution or a 1N HCl solution. A stock solution of 500 ml soil extract with 0.2 g K_2HPO_4 and 1.0 g KNO_3 was made up; of this 5 ml was added to 1000 ml sea-water to obtain the diluted modified Erdschreiber medium. In less diluted Erdschreiber medium growth was rather stunted. To the medium 1 ml of a solution of 3.7 mg Na_2 EDTA. $10H_2O$ in 1020 ml sea-water was added, together with 0.5 ml of a Fe-EDTA solution and 1 ml of the PII-solution. Both additive solutions were prepared as described by Provasoli (1968) for his ES medium.

The third medium used was Provasoli's (1968) Enriched Seawater Medium (= ES medium). Its preparation, including the preparation of a Fe-EDTA solution and the PII-trace-element solution was not modified. For isolation of specimens from nature or for cleaning of contaminated cultures often 3 mg germanium dioxide were added to a litre of medium to prevent growth of diatoms. Blue-green algae were checked by adding massive doses of penicillin (1000 unit/ml) or 3 mg bacitracin/1. Artificial media (mainly Provasoli's ASP6 and ASP12-NTA) have also been used in preliminary studies. Growth of most *Sphacelariales* in these media was quite poor and so these artificial media were not suitable for my purposes.

In the three different media concurrently used growth of *Sphacelariales* differed distinctly. In Erdschreiber medium based on natural sea-water (DH medium) the plants were usually dark-brown and branching and proliferations were usually rich. In the Erdschreiber medium based on sea-salt (N medium) most plants were light-brown and branching and proliferations were less rich or occasionally scarce. In Provasoli's ES medium (PR medium) both colour and branching were intermediate. In vegetative growth and in the forming of propagules and zoidangia individual cultures of the same species (occasionally from specimens collected in the same habitat and locality) often exhibited different reactions in the different culture media used. Therefore I cannot say that one of these three media was distinctly better than the other two. For that reason, and also to prevent loss of cultures in case of mispreparation or severe contamination of culture media, I grew subcultures of all numbers in all three media.

The cultures were grown in constant temperature rooms at a distance of 18–21 cm from a series of white fluorescent tubes (20 Watt, Philips TLD 33) (code 'L' in table III). Several cultures were covered by white paper to reduce light intensity and other cultures were only illuminated by a small amount of diffuse light (code 'D' in table III). For a synopsis of the conditions in the culture rooms see table III. At higher temperatures growth of the *Sphacelariales* (and also of the contaminating organisms) is usually faster, so at higher temperature the medium has to be replenished more frequently than at the lower temperatures (see table III). Occasionally cultures were grown in other conditions, in an oscillator or in a tide simulating apparatus.

Fragments from unialgal cultures, generally in series of 3 to 5 culture tubes, were grown further for observations on their morphology and reproduction. In many strains these observations were repeated several times during the years I cultured these algae. So possible differences in morphology resulting from different properties of the media, prepared at various times, could be noted. Differences in growth rate may be due to differences in the

TABLE III. Conditions in culture rooms

temp. (°C) and code	light intensity in Lx	covered by white paper	light/dark regime in hours	period in weeks between replenishment of media
4° L	1400–2800	no	8/16	5
4° D	88–500	no	8/16	5
12° L	700–1400	yes	16/8	4
12° D	175–700	no	16/8	4
20° L	2000–2400	yes	16/8	3
20° D	185–500	no	16/8	3

properties of the soil extracts prepared at different times, to differences in the sea-water and to differences in light intensity within the culture rooms. These differences in growth rate, however, may be considerable also in one series of cultures. The fragments which serve as starting points for the cultures, are often disparate as they are cut off from different plants or different parts of plants. When forming of propagules, zoidangia, or of hairs sets in, growth can also be inhibited and after dehiscence of zoidangia occasionally whole plants or parts of plants die off. Apart from fragments of vegetative filaments cultures can also be started from propagules or from zoids. In the case of propagules the same methods can be used as described for fragments of filaments. When unialgal cultures could be established from zoids the hanging drops method was used, as described by Wynne (1969, p. 3).

Results of culture experiments: The results of most culture experiments are summarized in the sections on form range and cultures of the separate species. Under the culture conditions described above the thalli appeared to have a normal morphology. Fragments of species with a large number of free rhizoids (*S. arctica*, *S. radicans*) or stolons (*S. nana*, *S. rigidula*) often attach to the wall of the culture tube and form a new basal holdfast. Species without rhizoids (*S. caespitula*, *S. mirabilis*) or with tightly packed cortex-forming rhizoids (*S. plumosa*, *S. plumigera*) usually do not form a new basal holdfast or do not attach to a substrate. Attached specimens of these species occurred after germination of zoids. In nature unattached specimens are usually sterile, but in culture unattached specimens often form zoidangia. In several species it appeared that the general morphology could vary extremely, especially in the number of rhizoids and erect filaments formed, when the salinity of the culture medium was changed (see *S. arctica*, p. 158). Unattached specimens of *Sphacelaria* and *Cladostephus* from nature often grew into plants which were very similar to plants grown from originally attached plants. In *Stypocaulon*, however, the unattached specimens in culture remained different from the originally attached specimens. In some species of *Sphacelaria* (*S. cirrosa*, *S. rigidula*) the number of arms of propagules in culture was often lower than in nature.

Reproduction and life-history

Some (C. Agardh, 1817; Lyngbye, 1819) but not all (Dillwyn, 1802–1809) early authors considered the conspicuous apical cells as fructifications and only halfway through the nineteenth century were zoidangia (in *S. cirrosa*, *Halopteris filicina*, and *Stypocaulon scoparium*) and propagules (in *S. cirrosa* and *S. tribuloides*) recognized as the true reproductive structures (J. Agardh, 1836, 1842, 1848; Decaisne, 1841, 1842; Kützing, 1843; Meneghini, 1843). Nevertheless Wuitner (1946, p. LIII) still stated for *Stypocaulon scoparium* 'les sommets sphacélés contiennent les spores'.

Janczewski (1872) described the development of propagules of *Sphacelaria cirrosa* and their germination. The occurrence of vegetative propagation by propagules in *Sphacelaria* species has never been doubted since.

Pringsheim (1855) described 'antheridia' in *Sphacelaria tribuloides* and in *Cladostephus spongiosus*. Later (1874) he admitted that these supposed antheridia were apical cells containing a parasitic chytrid. He described, however, in this later publication unilocular and plurilocular zoidangia of *S. caespitula* (as '*S. olivacea*'). He thought that there were intergrades between the unilocular and the plurilocular zoidangia in this species, but according to Sauvageau (1900, p. 217 = R. 5) this was based on incorrect observations. Pringsheim (1874) also described the unilocular and plurilocular zoidangia of *Cladostephus verticillatus*. He observed that the plurizoids escape by a small pore from the individual loculi of the plurilocular zoidangia of *Cladostephus*, whereas he correctly observed dehiscence by a common apical pore in the plurilocular zoidangia of *S. caespitula*. Subsequent authors like Askenasy (1888) and Reinke (1890–1892) considered all plurilocular zoidangia as neutral sporangia or as isogametangia, but Sauvageau (1898) observed plurilocular zoidangia with different dimensions of the loculi in '*Sphacelaria hystrix*'. The zoidangia with small loculi he called 'antheridia', those with larger loculi 'sporanges pluriloculaires'. He observed the zoids but no copulations or fused zoids with two eye-spots were detected. Nevertheless he suggested sexual reproduction. Subsequent research on life-histories was usually incomplete and on the basis of these incomplete observations the life-histories of the *Sphacelariales* and of *Sphacelaria* in particular were generally inferred to be isomorphic diplohaplontic until the publication of Van den Hoek & Flinterman (1968). Earlier evidence regarding the life-history of *Sphacelaria* was given by Clint (1927) and Papenfuss (1934). For a discussion of the results and conclusions of these earlier investigations see Van den Hoek & Flinterman (l.c.), who also discussed the investigations by Sauvageau (1898) on *S. hystrix*, by Sauvageau (1931), Mathias (1935), and Ernst-Schwarzenbach (1957) on *Halopteris filicina*, by Sauvageau (1907a) and Higgins (1931) on *Stypocaulon scoparium* and by Moore (1951) on five species of *Halopteris* from New Zealand.

A few other investigations have not been discussed by Van den Hoek & Flinterman. Sauvageau (1907b, 1908, 1914, 1931) described the similarity in germination of unizoids and unfused plurizoids of *Cladostephus* '*verticillatus*'.

Schreiber (1931) observed fusion between immobilized 'female' isogametes and mobile 'male' isogametes of *Cladostephus* '*verticillatus*' but he did not further follow the development of the germlings of zygotes and parthenogametes. Kuckuck (1912) and Schreiber (1931) unsuccessfully tried to observe fusions in *S. caespitula* (as *S.* '*olivacea*').

All these investigations were incomplete especially with regard to karyological evidence. Clumping and fusion of zoids cannot be considered indisputable evidence for the gametic nature of zoids. The investigations by Van den Hoek & Flinterman gave evidence of a slightly heteromorphic diplohaplontic life-history in *S. rigidula* (fig. 23). They found a distinct influence of temperature on sexual and vegetative reproduction. For details see also

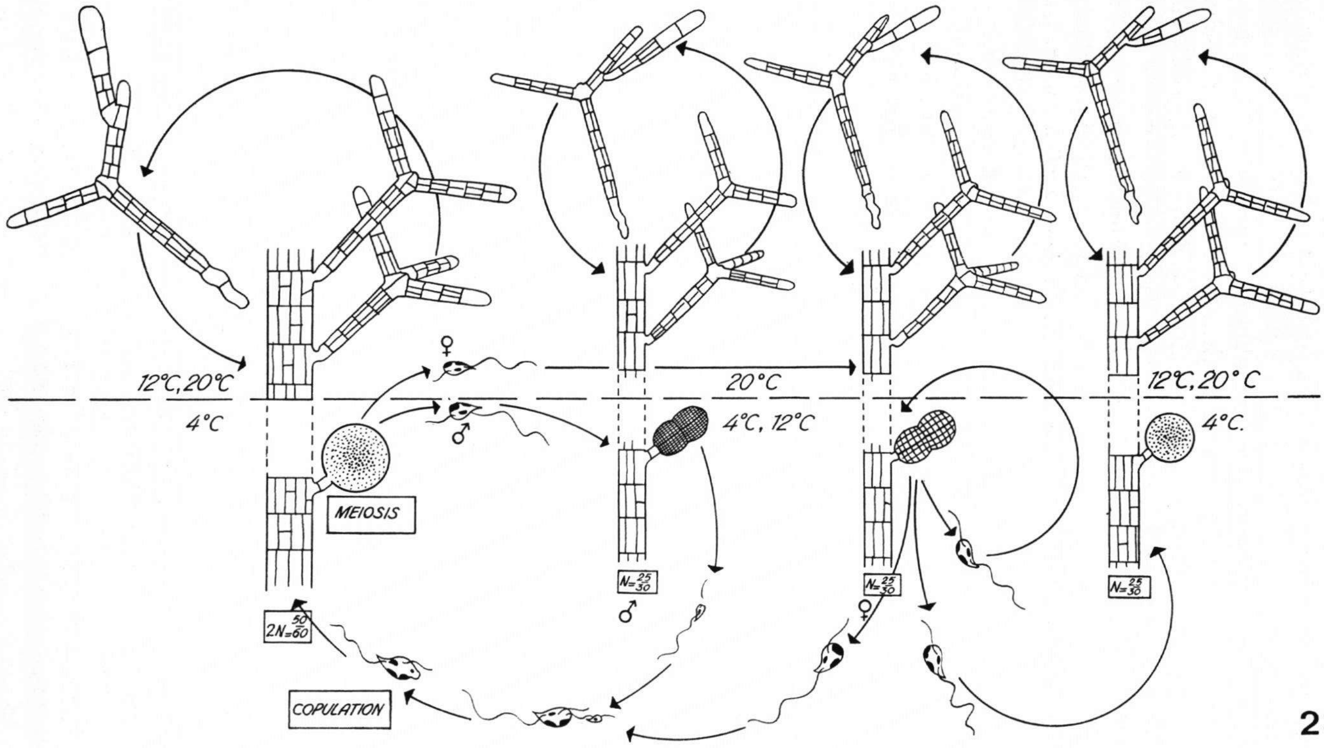


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Fig. 23. Diagram of the life-history of ***Sphacelaria rigidula*** according to Van den Hoek & Flinterman (1968).

my section on reproduction and life-history of *S. rigidula* (p. 214). Later Colijn & Van den Hoek (1971) demonstrated a distinct influence of the daylength on the life-history of that species. The results of the investigations of John & De Graft-Johnson (1975) on *S. brachygonia* do not provide new insights.

Van den Hoek & Flinterman obtained haploid plants on which at 4°C small unilocular zoidangia were formed. These small unilocular zoidangia (for which I use the designation mini-zoidangia) were never observed to reach maturity and to produce viable zoids. The authors stated that these haploid plants with mini-zoidangia do not form part of the main life-history of *S. rigidula.* I observed similar mini-zoidangia for *S. nana* (p. 110). Van den Hoek & Flinterman observed quite a few unilocular zoidangia which released their contents as one spherical 'monospore'. These spherical structures never grew out in their cultures. It is possible that the use of sodium alginate as aid for the observation of dehiscence of zoids is the main cause for the existence of these 'monospores'. The ova of *Halopteris* species from New Zealand, as described by Moore (1951) are not comparable to these 'monospores'.

In their discussion of the investigations of the life-history of *Phaeophyceae* Van den Hoek & Flinterman (l.c.) compared the chromosome numbers as found for *Ectocarpus siliculosus* by Knight (1929), Papenfuss (1934), and Schussnig & Kothbauer (1934) with those found by Müller (1966, 1967). Müller found a haploid chromosome number of about 25, and a diploid chromosome number of about 50. These numbers make it unlikely that the earlier much smaller counts (n = 8, 2n = 16) were correct. A similar comparison for members of the *Sphacelariales* is not yet possible. In the *Sphacelariales* only few chromosome counts have been published. Knight (1929) mentioned (without further information) n = 16 and 2n = 32 for *Halopteris filicina*, *Sphacelaria bipinnata,* and *Stypocaulon scoparium.* Earlier Escoyez (1909) counted 32 chromosomes in apical cells of *Stypocaulon scoparium* and Higgins (1931) observed 16 chromosomes in this species in unilocular zoidangia after meiosis. Later Ernst-Schwarzenbach (1957) found n = 8 and 2n = 16 for *Halopteris filicina* from Naples. She thought that the *H. filicina* populations studied by Knight (l.c.) could be diploid/tetraploid and her own specimens haploid/diploid, and that comparable differences in ploidy-level possibly existed between different populations of *Ectocarpus siliculosus.* Evidence available, however, does not support this hypothesis.

Cole (1967) tentatively assigned a basic chromosome number of 8–12 to the *Sphacelariales*, but from her table 1 a basic chromosome number of 8 is more probable. Van den Hoek & Flinterman (l.c.), however, found a haploid number of 20–30 and a diploid number of 50–60 in *Sphacelaria rigidula.* Since they investigated another species than earlier authors, nothing can be said about the reliability of these earlier counts.

Methods for chromosome counts: Counting of chromosomes in the *Sphacelariales* is usually very difficult. In favourable cases the chromosomes can be seen as small spheroid or discoid bodies after staining with acetocarmine (or other caryological methods) and they are often so numerous that it is usually only possible to make an approximate count. In *Stypocaulon scoparium,* for example, Swingle (1897, p. 318) estimated a number of 20–40 chromosomes in somatic cells. Escoyez (1909, p. 191) counted up to 32 chromosomes in these cells, and Higgins (1931, p. 349) estimated a diploid number in the order of 30. She managed, however, to count exactly the haploid number in unilocular zoidangia as 16 (see also her f. 12). This number is in agreement with Knight (1929), who gave no details of the methods and material she used. Van den Hoek & Flinterman (1968, p. 197) published a detailed description of the karyological methods they used. I used exactly the same methods for my investigations. For results see section 'Chromosome numbers' of the genus *Sphacelaria* (p. 55).

Review of life-histories in *Sphacelariales:* On the basis of the results of the investigations of Van den Hoek & Flinterman and the (mostly incomplete) evidence in other publications an isomorphic or slightly heteromorphic diplohaplontic life-history as in *S. rigidula* can be hypothesized for all *Sphacelariales.* Vegetative propagation by propagules, however, occurs only in the subgenus *Propagulifera* of the genus *Sphacelaria.* Neutral plurilocular zoidangia, which can be supposed to be of diploid nature, probably occur when unilocular and plurilocular zoidangia can frequently be found together on the same plants, as in *Sphacelaria plumigera* or in *S. cirrosa* ecad *bipinnata.* Combination of all available data results in the following generalizations:

Cladostephaceae: Isomorphic diplohaplontic life-history with isogametes (isomorphic, but physiologically differentiated) and perhaps also neutral plurilocular zoidangia. Parthenogenesis and ephebogenesis, implying germination of unfused female as well as male gametes, have been observed.

Stypocaulaceae: Isomorphic diplohaplontic life-history with anisogamy or oogamy. Parthenogenesis and ephebogenesis have been observed.

Sphacelariaceae: Isomorphic or slightly heteromorphic diplohaplontic life-history with isogamy or anisogamy. Occurrence of neutral plurilocular zoidangia is probable in several species. Parthenogenesis has been observed and vegetative propagation by propagules occurs in several species.

Chytridiaceous fungi in *Sphacelariales*

The chytridiomycete *Anisolpidium sphacellarum* (Kny) Karling infects apical cells of *Sphacelariales* and causes their swelling (Kny, 1871; Sparrow, 1960, p. 747). The zoids released by this fungus have been incorrectly interpreted as spermatozoids of the alga (Pringsheim, 1855) and the swollen apices as unilocular zoidangia (Pringsheim, 1874, p. 172, t. IX, f. 9 & t. X, f. 5–7). The characteristic feature of *S. apicalis* Takamatsu (1943), the swollen apical cells, is probably the result of a fungus infection (cf Tokida, 1948, p. 113). I have often observed such swollen apical cells in *S. caespitula* (fig. 149).

In *Sphacelaria caespitula* and *S. radicans* curious proliferations (fig. 110, 147) may also be caused by Chytridiaceous fungi, probably by a species different from *Anisolpidium sphacellarum.*

Systematic position

Taxa: In the order *Sphacelariales* one can distinguish families, genera, subgenera, sections, species, and a few forms. In some species populations occur with slightly different morphologic characteristics. It is not possible to state, on basis of the present state of knowledge of these algae, whether these populations are genetically different, or whether the differences are mainly expressions of reactions to ecological factors in the different habitats. In the present study I consider the algae of these populations as growth-forms of the relevant species. These entities (see Vink, 1970, p. 301) have no taxonomic status, but, since the occurrence of the presumed growth-forms is possibly caused by ecological factors, they can be called ecological growth-forms or ecads (see also Heywood, 1959).

Criteria used for the distinction of taxa: Most taxonomic criteria used in the more recent publications dealing with the taxonomy of *Sphacelariales* are derived directly from the investigations of Sauvageau or indirectly from the publications of Geyler, Magnus, Pringsheim, and Reinke.

Sauvageau's formal descriptions are usually comprehensive and fairly complete. Of the many criteria used by Sauvageau and subsequent authors the most useful ones have been discussed in an earlier paper (Prud'homme van Reine, 1978). A list of characters used for numerical taxonomic methods is given in the same paper. A list of characters with their apomorphous and plesiomorphous expressions, suitable for the construction of a cladistic system, is given in table IV of the present publication.

The validity of a number of taxonomic criteria will be discussed below.

Endophytism. Reinke (1890a, 1891) used endophytism of the basal parts of *Sphacelaria* species as a main criterion in that genus. On the basis of the presence or absence of endophytic filaments in host-plants (usually larger *Phaeophyceae*) Reinke divided the species of the genus *Sphacelaria* into 'Sphacelariae autonomae' and 'Sphacelariae parasiticae'. The presence of endophytic filaments does not prove genuine parasitism, however. According to Sauvageau (1900, p. 223 = R. 11) the division made by Reinke into autonomous and parasitic *Sphacelaria* species is artificial. In *S. rigidula* (as *S. furcigera*) he observed that the occurrence of endophytic filaments is dependent on the nature and structure of the substrate. Sauvageau still used the designation 'parasitism', however. He observed that the middle-lamellae of the walls of the cells of the host-plants adjacent to endophytic filaments of a *Sphacelaria* species blacken when treated with bleaching liquid. He supposed that a substance is formed in the walls of the *Sphacelaria* which can diffuse into middle-lamellae of the cells of the host-plants and which can turn black when reacting with bleaching liquid (Sauvageau, 1900a). The nature of that substance is still unknown.

Chemin (1922) and Goodband (1973) both came to the conclusion that there is no physiological dependence between the partly endophytic *S. cirrosa* ecad *bipinnata* and its host *Halidrys siliquosa.* Penetration into the host is mainly by pushing apart the host cells. Most European *Sphacelaria* species which can have endophytic basal parts (like *S. caespitula, S. rigidula, S. cirrosa,* and the rare *S. sympodiocarpa*) can usually grow as strictly epiphytic as well as epilithic plants. In the rare and very small species *Sphacella subtilissima* only specimens with endophytic basal parts are known. This will possibly change when more specimens of this tiny alga can be collected.

Endophytism as such is not a discriminating criterion in *Sphacelaria.* Since many species of *Sphacelaria* are never endophytic, the presence of a partly endophytic basal part can nevertheless be used as a character and the presence of the ability to grow partly endophytic may be genetically defined.

Colour. The colour of living specimens is often so variable, that it cannot be used as a character of taxonomic value. Brown and Richardson (1968) found a distinct effect of light

TABLE IV. Apomorphous (a.) and plesiomorphous (p.) states of expression of characters, and transformation series

number	series	
1	walls	blackening of cell-walls when treated with bleaching liquid: a.; not so: p.
2	segments 1	primary segments of filaments with transverse divisions (occasionally transverse divisions may be absent in a few segments): a.; always without transverse divisions of primary segments: p.
3	segments 1	all primary segments with transverse divisions: a.; several primary segments without transverse divisions: p.
4	segments 1	all or most secondary segments with longitudinal cell-walls: a.; no longitudinal cell-walls present: p.
5	segments 1	periclinal pattern: a.; radial pattern: p.
6	segments 1	with tangential primary wall: a.; with median primary wall: p.
7	segments 2	secondary transverse cell-walls frequent: a.; secondary transverse cell-walls scarce or absent: p.
8	segments 2	marked pericysts present: a.; marked pericysts absent: p.
9	branching 1	hemiblastic laterals arise close to the apical cell: a.; laterals arise from peripheral cells and distant to the apical cell: p.
10	branching 2	cell division in the intact apical cells of erect filaments results in formation of filaments or hairs and filaments: a.; cell division in the intact apical cells of erect filaments results in formation of hairs only: p.
11	branching 2	dichoblastic branching: a.; acroheteroblastic branching: p.
12	branching 3	hairs in bundles of 2 or 4: a.; hairs in solitary: p.
13	branching 4	branches arising in a distichous pattern: a.; branches arising in a helicoid pattern or irregularly placed: p.
14	disc	specialized (not a real disc): a. (two different apomorphies present); normal rounded disc: p.
15	disc	disc polystromatic: a.; disc monostromatic: p.
16	rhizoids	rhizoids appressed to the erect filaments: a.; rhizoids divaricate: p.
17	rhizoids	appressed rhizoids form a cortex: a.; no cortex formed: p.
18	rhizoids	cortex closed and regular: a.; cortex open and irregular: p.

Table IV (continued)

number	series	
19	rhizoids	rhizoids arise from particular cells only: a.; rhizoids may arise from all peripheral cells: p.
20	propagules	propagules present: a.; propagules never present: p.
21	propagules	two different apomorphies present: propagules with short, broad arms: a.1; propagules with long, narrow arms: a.2; propagules small, without arms: p.
22	propagules	propagules with apical cell and without apical hair: a.; propagules usually with apical hair: p.
23	zoidangia	two different apomorphies present: zoidangia on long, often branched, stalks: a.1; zoidangia in cymose stands: a.2; zoidangia on short, usually unbranched stalks, or sessile: p.
24	zoidangia	zoidangia sessile: a.; zoidangia always stalked: p.

intensity on the pigmentation of a *Sphacelaria* species. This difference in pigmentation is probably related to the number of packets of thylakoids in the chloroplasts. The greenish colour in sicco of species such as *Sphacelaria caespitula* and *S. nana* is not suitable to characterize these species, since specimens of e.g. *S. radicans* and *S. rigidula* can also turn greenish when dried. In herbaria all four species can often be found under the name *S. olivacea.* Sauvageau (1902, p. 384 = R. 196) used the reddish-brown colour of herbarium specimens of *S. cirrosa* ecad *bipinnata* (as *S. bipinnata*) to separate them from the usually olivaceous specimens of dried *S. cirrosa* ecad *cirrosa.* In the many herbarium specimens I studied I found olivaceous specimens of *S. cirrosa* ecad *bipinnata* as well as reddish-brown specimens of *S. cirrosa* ecad *cirrosa.* The number of reddish-brown specimens of *S. cirrosa* ecad *bipinnata* is much higher, however. Nevertheless colour in *Sphacelaria* (and other *Sphacelariales*) cannot be used as a reliable character. The colour suggested by its name for *Sphacelaria fusca* can be found in many other species.

Height of plants. The maximum height of a plant is surely characteristic. It has to be realized, however, that all large plants start as small ones and that species which can grow into large plants under quiet conditions may remain very small in wave-exposed localities.

The general habit of the plant. Though very variable, the general habit of the plant can often be used to separate taxa in the field. The compact semiglobular epilithic cushions formed by *Sphacelaria tribuloides*, *S. brachygonia*, and *S. fusca* are quite different from the softer and less compact epilithic cushions formed by *S. radicans*, *S. racemosa*, and *S. rigidula*. The asymmetrical broom-like tufts of *S. arctica* are characteristic and differ from the usually complanate tufts of *S. plumosa.* The thick broom-like tufts of *Stypocaulon scoparium* are usually easily discerned from the more complanate tufts of *Halopteris filicina* and the pipe-cleaner habit of *Cladostephus spongiosus* is undeniable.

Basal holdfast. This character is certainly of taxonomic value. See table IV and Prud'homme van Reine (1978).

Ramification. Many features of the ramification can be used as taxonomic criteria. See table IV and Prud'homme van Reine (1978). The angle of branching, though variable, can also provide a valid criterion. Branching in *S. nana* is usually perpendicular and in *S. radicans* (attached specimens) laterals are often almost parallel to the main filaments. In the pinnate specimens the angle of branching of *S. arctica* is much smaller than that of *S. plumula.* See also Goodband (1971, p. 970).

Dimensions of filaments. Though variable, the diameter of the main filaments can be considered as characteristic for a species. The difference in dimensions of main axes and determinate laterals can also be used in several cases. For length of filaments see 'height of plants' above.

The rigidity of the filaments. This is a result of the thickness of the cell-wall and the number of longitudinal walls and it is a character of taxonomic value in, e.g., *S. nana, S. rigidula, S. tribuloides*, and *S. cirrosa*. See also Goodband (1971, p. 964).

Hairs. The absence of hairs has usually no taxonomic impact, but presence of hairs can be used as a criterion. It is true that in *Sphacelaria caespitula* hairs are unknown and that in *S. nana* hairs are very rare, but in many other species hairs may be lacking in one specimen and be present in another specimen. See also table IV and Prud'homme van Reine (1978).

Rhizoids and cortication. These are certainly characters of taxonomic value. Absence of these structures is reported in many species. In species which usually have these structures, they may be absent in individual specimens. See also table IV and Prud'homme van Reine (1978).

Length to width ratio of apical cells and segments. These measurements cannot be used without comment as taxonomic criteria. The apical cells of the *Sphacelariaceae* and many *Stypocaulaceae* are the main meristematic cells of the filaments. Their length is very variable and depends on the moment the primary transverse wall has been formed to separate the subapical primary segment from the apical cell proper. See also Goodband (1971, p. 960). The length to width ratio of segments depends mainly on the vitality of the apical cell and the interval between the formation of primary segments. Goodband (l.c., p. 964) detected that segments showed a change in the length to width ratio due to an increase in width rather than a decrease in length. This increase in width corresponds to the sum of the widths of the newly formed longitudinal walls.

Growth and mode of division of segments. These are certainly important characters to distinguish taxa. See table IV and Prud'homme van Reine (1974, 1978) and observations made by Goodband (1971).

Pericysts. The presence or absence of pericysts is a useful criterion. See also table IV and Prud'homme van Reine (1978).

Free-floating plants. This condition was thought to be of systematic value by Sauvageau. Culture experiments indicated that most unattached plants are growth-forms (ecads) of attached plants.

Chloroplasts. The size of chloroplasts was considered to be a useful criterion by De Haas-Niekerk (1965). From my measurements I cannot confirm this.

Reproduction. Very useful criteria can be obtained from the occurrence, the arrangement, and the form of propagules and unilocular and plurilocular zoidangia. Many other features of the life-history can provide important taxonomic criteria. Information on the reproduction and life-history of most species is very scanty, however. See also table IV and Prud'homme van Reine (1978) and Goodband (1971).

Delimitation of the order: Kützing (1843) and J. Agardh (1848) were among the first authors who separated *Sphacelaria* and *Cladostephus* from the other filamentous brown algae and placed them together in the family *Sphacelariaceae.* Both agreed that this family was well defined. Later Migula (1909) raised the status of this group to the level of an order. Fritsch (1945), who included the *Choristocarpaceae* (with the monotypic genera *Choristocarpus* and *Discosporangium*) in the *Sphacelariales* stated: 'the *Sphacelariales* form a clearly defined group which is almost certainly a natural one....'. Steinecke (1931), using serological methods, came earlier to the same conclusions as Fritsch. Russell & Fletcher (1975, p. 778), in a numerical taxonomic study of the British *Phaeophyta* concluded about the *Sphacelariales* (incl. *Choristocarpus*): 'There seems no reason to question either the validity or the circumscriptions of this Order'. I agree with the above-mentioned authors about the naturalness of the order (see also Prud'homme van Reine, 1974 and 1978), but not with the inclusion of the *Choristocarpaceae* amongst the *Sphacelariales.* Unique features of the *Sphacelariales* are the apical growth and subsequent separation of primary segments into secondary segments and the blackening of the cell-walls when treated with bleaching liquid. Both features are missing in *Choristocarpus*, which therefore cannot be incorporated into this natural order. Thus the systematic status of *Choristocarpus* and *Discosporangium* has to remain uncertain.

Classification

For a historical survey of classification in the *Sphacelariales* see table I; the reasons why the *Choristocarpaceae* are not incorporated in the *Sphacelariales* are mentioned above.

In all classifications the mode of branching is used as the main criterion. Most classifications are mainly based on the investigations of Sauvageau. The incorporation of *Alethocladus* into the *Stypocaulaceae* has not been studied in detail by me. This incorporation can be justified, however, as the typical acrohomoblastic branching, as found in *Alethocladus*, has also been observed in specimens of *Halopteris filicina* (Sauvageau, 1903, p. 396 = R. 306). For the reasons for incorporation of the only species of *Disphacella* in the genus *Sphacelaria* see p. 41. All known species of *Sphacelariales* can rather easily be incorporated in one of the three families.

KEY TO THE FAMILIES[2]

1a. All laterals arise by direct or tardy hypacroblastic (occasionally dichoblastic) branching; no secondary growth of segments (exceptions: occasional acroheteroblastic branching in *Sphacelaria radicans* and absence of erect filaments in *S. mirabilis*) . . . . Sphacelariaceae

b. At least some of the laterals show acroblastic branching; secondary growth of segments absent or present 2

2a. Laterals from the main axes arise by hypacroblastic branching; determinate laterals arranged in whorls and with acroblastic laterals of the second order; segments of the main axes grow in length and in width by secondary growth . . . . Cladostephaceae

b. The majority of the laterals arise by acroblastic branching; secondary growth of segments absent in European species . . . . Stypocaulaceae

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[2] For terminology see the glossary, p. 262.

SPHACELARIACEAE Decaisne emend. Oltmanns

Familia *Sphacelarieae* Decaisne (1842) 329 (p.p.); Kützing (1843) 291 (p.p.), (1845) 238 (p.p.); J. Agardh (1848) 27, 'Ordo' (p.p.); Harvey (1849) 54, 'sub-order' (p.p.); Areschoug (1850) 387 (p.p.); Geyler (1866) 479, 'Sphacelarieen' (p.p.); Falkenberg (1881) 220, 'Sphacelarieen' (p.p.); Reinke (1889) 38 'Gruppe' or 'subfamilia' (p.p.).—Familia *Sphacelariaceae* Cohn (1872) 17 (p.p.); Kjellman (1890) 63 (p.p.); Reinke (1890a) 203 (p.p.), (1891) 2, 'Sphacelariaceen' (p.p.); De Toni (1895) 497 (p.p.); Sauvageau (1898) 1672 (p.p.); Oltmanns (1904) 349 (p.p.); Migula (1909) 237 (p.p.); Svedelius (1911) 151 (p.p.); Oltmanns (1922) 85; Setchell & Gardner (1925) 391; Newton (1931) 188; Hamel (1938) 247 (p.p.); Fritsch (1945) 300; Lund (1950) 5 (p.p.); Schussnig (1954) 199, 'Sphacelariaceen' (p.p.); Papenfuss (1955) 172; Lindauer, Chapman & Aiken (1961) 153; Christensen (1962) 108; A. Zinova (1967) 147 (p.p.)—Tribus *Sphacelarieae* J. Agardh (1842) 27, '*Sphacellarieae*' (p.p.); Hauck (1885) 342 (p.p.); Oltmanns (1904) 407; Svedelius (1911) 151.—*Sphacelariaceae* genuinae Reinke (1890a) 205 (p.p.), (1891) 3 (p.p.).—*Sphacelariaceae* hypacroblastae Reinke (1890a) 206 (p.p.), (1891) 3 (p.p.).—Sphacélariacées section Hémiblastées Sauvageau (1903) 332 = R. 266.—Type: *Sphacelaria* Lyngbye. See also notes on nomenclature 1–4.

Sphacelariaceae crustaceae Reinke (1890a) 205.—Type: *Battersia* Reinke ex Batters.

Sphacélariacées section Dichoblastées Sauvageau (1903) 338 = R. 272.—*Sphacelariaceae* tribus *Disphacelleae* Svedelius (1911) 151.—*Disphacellaceae* Prud'homme van Reine (1971) 151 (nom. inval.). —Type: *Disphacella* Sauvageau. See also the section on classification of the genus *Sphacelaria* (p. 56).

Small (<2 cm) to medium-sized (up to more than 10 cm high) *Sphacelariales* which form subglobose, hemispherical, penicillate, or complanate tufts or spreading mats. The usually hypacroblastic laterals are distichous, helicoid, or irregularly placed. Secondary segments have no secondary growth.

Distribution. For the geographic distribution of the *Sphacelariaceae* in the world see table II. The genus *Sphacelaria* is cosmopolitan and *Sphacella subtilissima* has only been found in the Mediterranean. See also the sections on distribution of the genera *Sphacelaria* (p. 51) and *Sphacella* (p. 44).

Notes on nomenclature

(1) Decaisne (1842) definitely indicated that he considered the *Sphacelarieae* as a family. J. Agardh (1842) published his paper a few months earlier than Decaisne. Agardh did not indicate a definite rank to his *Sphacelarieae*, but when he subdivided his familia *Florideae* in the same work (l.c. p. 66–68) he used the designation Tribus for the subdivisions of that familia. For that reason Decaisne has to be cited as the author of the family.

Before Oltmanns (1922, p. 85) divided the *Sphacelariales* into three families, the designation *Sphacelariaceae* (or *Sphacelarieae*), was used in the majority of studies (with exception of the cited papers by Oltmanns (1904) and Svedelius) for all algae now incorporated in the order *Sphacelariales*. Even Migula (1909, p. 237) when proposing the new order *Sphacelariales*, distinguished only one family in this order. Of later authors still using the name *Sphacelariaceae* to cover all *Sphacelariales* only Hamel (1938), Lund (1950), Schussnig (1954), and A. Zinova (1967) are included in my list. Papenfuss (1955) p. 172 incorrectly cited the name of the family as *Sphacelariaceae* J. Ag. orth. mut. Cohn.

(2) Reinke's *Sphacelariaceae* genuinae and his *Sphacelariaceae* hypacroblastae covered more genera of *Sphacelariales* than the *Sphacelariaceae* Decaisne emend. Oltmanns. Svedelius

expanded the name *Sphacelariaceae* hypacroblastae to include all *Sphacelariales* except his tribi '*Disphacelleae*' (= *Sphacelaria reticulata*) and '*Alethocladeae*' (= the monotypic genus *Alethocladus*).

(3) The Sphacélariacées Hémiblastées of Sauvageau have the same definition as the *Sphacelariaceae* Decaisne emend. Oltmanns.

(4) To separate *Sphacelariaceae* Cohn (= *Sphacelariales* Migula as now understood) and *Sphacelariaceae* Decaisne emend. Oltmanns (= familia *Sphacelariaceae* as now understood) I will use the designation *Sphacelariaceae* s.s. for the latter group.

Systematic position

Delimitation of the family. Reinke (1890a, p. 203) included both the *Sphacelariaceae* (s.s., but excluding *Sphacelaria mirabilis* as '*Battersia mirabilis*') and the *Cladostephaceae* in his '*Sphacelariaceae* hypacroblastae'. Oltmanns (1904) p. 407 was the first author to separate the *Cladostephaceae* (as 'Tribus *Cladostepheae*') from the *Sphacelariaceae* s.s. (as 'Tribus *Sphacelarieae*'). Sauvageau, using a different nomenclature, agreed with Oltmanns in this respect. Many subsequent authors, however, still use the designation *Sphacelariaceae* to cover all species in the order *Sphacelariales.* I shall only discuss the *Sphacelariaceae* s.s. here. This family is less well defined than the order. It includes all *Sphacelariales* which do not exhibit secondary growth in length and width of secondary segments of erect filaments and in which laterals arise by hypacroblastic branching. Aberrant branching occurs in *Sphacelaria reticulata*, in *S. radicans*, and in *Sphacella subtilissima.* In *S. reticulata* the dichoblastic branching of the filaments is unique. When the dichoblastic filaments of this unattached species are considered as modified parts of the attachment system, however, this mode of branching is not so exceptional any more. In *S. radicans* occasionally a cell of a subdivided hair-initial grows into a filament instead of a normal hair. According to Sauvageau (1909, p. 67 and f. 11B) the longitudinal wall, which usually divides the hair-initial into two, is curved and so a smaller hair-cell is separated from the larger branch-initial. Sauvageau considered this branching as a primitive stage of acroblastic branching (as 'holoblastique') and so as related to the ancestors of the *Stypocaulaceae.* In *Sphacella subtilissima*, and rarely also in *Sphacelaria radicans*, laterals may arise as outgrowths of primary segments. This branching is very similar to hemiblastic branching, but in these cases the primary segments are not subdivided into secondary segments. Isolation between the *Sphacelariaceae* and the *Choristocarpaceae* is complete (see also fig. 24). For isolation between the *Sphacelariaceae* on one side, and the *Cladostephaceae* and the *Stypocaulaceae* on the other side, I have no such evidence. Except for *Sphacelaria radicans* (and perhaps *S. reticulata*) no algae are known which possess characters fit for incorporation in more than one of these families.

Classification

Relationship of genera, subgenera, sections, and species. In an earlier paper (Prud'homme van Reine, 1978) I constructed a phenetic system of *Sphacelariales* based upon a numerical taxonomic approach, which for *Sphacelaria* resulted in the distinction of groups agreeing well with subgenera distinguished on the basis of 'intuition'. Here I will try to construct a phyletic-cladistic system of the *Sphacelariaceae* based, in principle, upon methods developed by Hennig (1950). There is a voluminous and mainly zoological literature on this subject, but see for the history and the complications of the phyletic-cladistic approach a review of Dupuis (1979). The procedure of the phyletic-cladistic system (the 'phylogenetic reconstruction') is explained by Bremer & Wanntorp (1978). Below I shall explain my own methods employed in this effort.

I only incorporated data of all species of *Sphacelaria* known from European localities, as well as data of *Sphacella subtilissima* and *Choristocarpus tenellus.* I did not incorporate information about other families of *Sphacelariales.* In speciation a phyletic line, formerly represented by a single species (the mother species), bifurcates into two separate lines, each represented by a species (daughter species). The daughter species may also separate into new ('younger') daughter species. The younger daughters of a daughter species together form a sister group. Each daughter species will develop new features, which separate them from each other as well as from the mother species. A new feature is based on a change in the expression of a given character. In the mother species and one of the daughters this character will still be in the primitive or plesiomorphous state; in the other daughter species the character will be in the derived or apomorphous state. The Hennigian cladistic phylogeneticists use comparative morphology as basis of their phylogenetic reconstruction. Only the joint possession of apomorphy (a synapomorphy) indicates cladistic relationship and species with synapomorphies can be considered belonging to a monophyletic group, i.e. in the cladistic approach a group derived from a common ancestor and comprising all descendants of that ancestor. Apomorphies only occurring in a single taxon can be called autapomorphies. The joint possession of a plesiomorphy (a symplesiomorphy) leads to a so-called paraphyletic group, i.e. a grouping excluding one or more descendants of the common ancestor. Occasionally the state of a character may switch independently to a given apomorphous state in separate phyletic lines (parallelism). In that case the synapomorphy is false and grouping taxa on basis of this false synapomorphy leads to a polyphyletic group. Polyphyletic groupings based on false synapomorphies could also be the result of convergence, i.e. development of apparently similar apomorphies from different plesiomorphous states.

The first stage in the procedure of a phyletic-cladistic system is to define apomorphous and plesiomorphous character-states (see table IV). Analysis of the possible evolution of various organs results often in the detection of possibly irreversible steps, which can be arranged in transformation series (table IV). Several independent transformation series may occur during evolution of a given organ (for example two independent series for 'segments', see table IV). Occasionally switches in character states can only be arranged in transformation series of one step (see characters 9, 12, and 13 in table IV, the series 'branching 1', 'branching 3', and 'branching 4' each consist of one step only). A data matrix with all taxa and their apomorphous character states will result from the applied procedure.

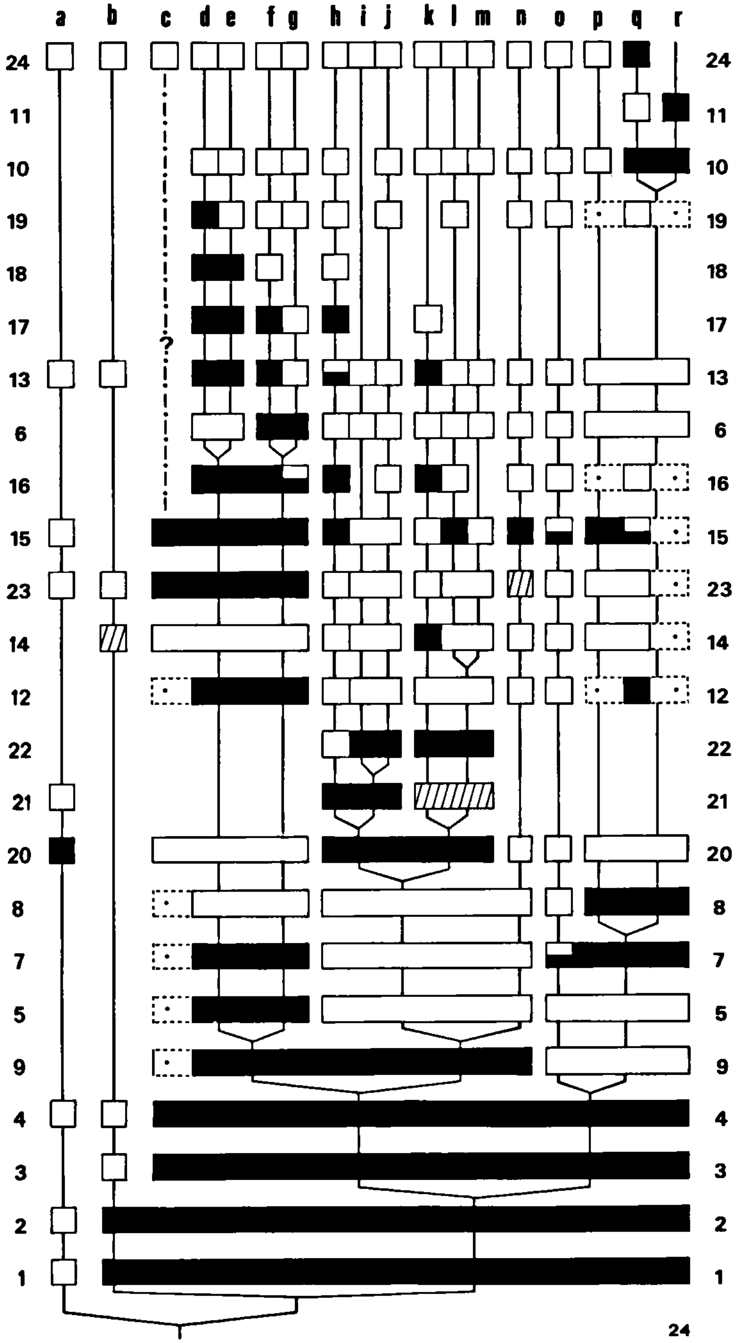
Now the search for the sister groups is started by surveying the apomorphies. The procedure is facilitated if it is started with the taxon possessing most of the apomorphous states. Of course the sequence of the character states in the transformation series must be maintained. This procedure results in the construction of the argumentation scheme (fig. 24) and the phylogenetic diagram (fig. 25). When a character was not present in one or more species (for example laterals in the crustose *S. mirabilis*, a basal disc in the unattached *S. reticulata* or characters of rhizoids or hairs in specimens without these structures), dots

Fig. 24. Argumentation scheme for a cladistic phylogenetic system of the *Sphacelariaceae.*

a = *Choristocarpus tenellus*
b = *Sphacella subtilissima*
c = *Sphacelaria (Battersia) mirabilis*
d = *S. plumigera*
e = *S. plumosa*
f = *S. arctica*
g = *S. racemosa*
h = *S. cirrosa*
i = *S. fusca*
j = *S. rigidula*
k = *S. plumula*
l = *S. brachygonia*
m = *S. tribuloides*
n = *S. sympodiocarpa*
o = *S. nana*
p = *S. caespitula*
q = *S. radicans*
r = *S. (Disphacella) reticulata*

For characters 1–24 see table IV.

■ ▨ apomorphous
☐ plesiomorphous
⬓ partly apomorphous, partly plesiomorphous in one species
• or | character not present



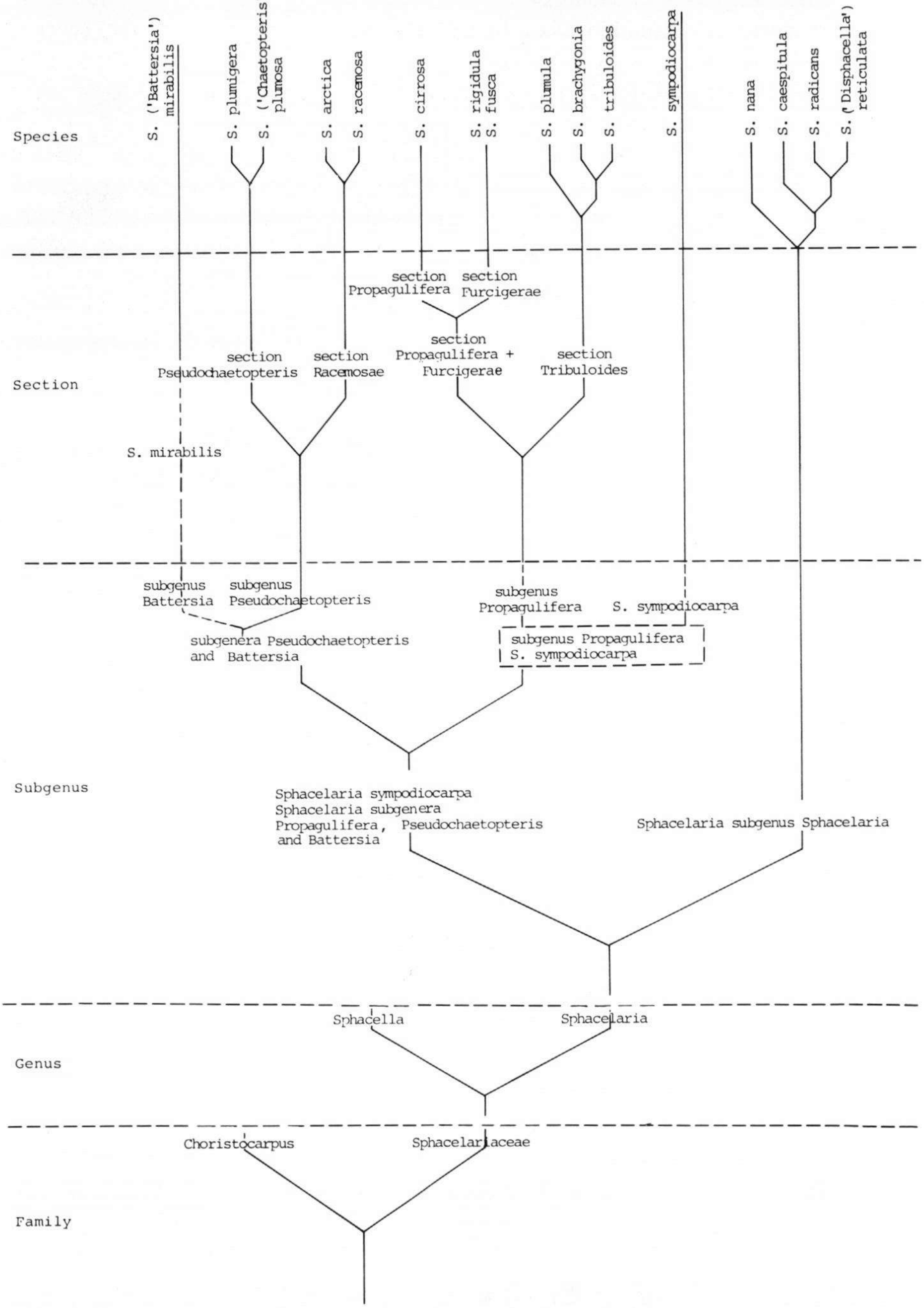


Fig. 25. **Phylogenetic diagram for a cladistic system of the *Sphacelariaceae*.**

are inserted on relevant places in the argementation scheme or an uninterupted line will be drawn between the white or black blocks of the relevant characters. For the aberrant species, like the ones formerly separated from *Sphacelaria* in the genera *Battersia* and *Disphacella*, many dots had to be inserted. For *S. caespitula* also several of these dots had to be used. Occasionally a character is present in only a part of the specimens of a species. In *S. cirrosa* distichous branching does not occur in all specimens and a polystromatic basal disc can only be found in a part of the populations of *S. nana*. In *S. racemosa* rhizoids can be divaricate or appressed. In *S. nana* secondary transverse walls varying in number from a few to many may occur in the secondary segments. In the last-mentioned species the number of walls is often very variable in the filaments of a single tuft, but tufts which are almost devoid of secondary transverse walls are not uncommon. These five cases, where a character can be present in the apomorphous as well as in the plesiomorphous state, are mentioned in the argumentation scheme.

Apomorphous and plesiomorphous character states. For a list see table IV.

(1) The blackening of the cell-walls is only observed in the *Sphacelariales* and it does not occur in any other group of *Phaeophyceae* (nor in other plants as far as I know). Therefore I define it as being apomorphous, characteristic of *Sphacelariales*.

(2) In all *Sphacelariales* the cell cut off from the apical cell functions as a primary segment and usually it will be divided into two secondary segments and later usually into more and smaller cells. This characteristic feature of *Sphacelariales* is supposed to be the apomorphous state.

(3) The apomorphous state of character 2 can be of irregular occurrence. A consistent occurrence of this apomorphous state seems to be apomorphous with respect to its irregular occurrence. Regression cannot be excluded here. In *S. radicans*, occasionally, a few of the primary segments do not form secondary segments.

(4) The occurrence of longitudinal walls in secondary segments is defined apomorphous.

(5) When longitudinal walls in secondary segments are present, the primary longitudinal wall is usually median and the subsequent longitudinal walls will be perpendicular to it or form other angles with the primary wall. If the angle is not perpendicular, a radial pattern will be formed. Thus the occurrence of only perpendicular longitudinal walls can be considered apomorphous.

(6) A non-median primary longitudinal wall of a secondary segment is considered apomorphous. In the radial pattern the primary longitudinal wall in the main erect filaments is always median.

(7) The frequent occurrence of secondary transverse walls in the cells of the secondary segments is considered apomorphous.

(8) Marked pericysts occur only in specimens with many secondary transverse walls. The presence of these special meristematic cells can be considered apomorphous.

(9) When the apical cell dies off or when an erect filament is more proximally truncated it can often be observed that each peripheral cell can grow into a lateral (or a rhizoid). So all peripheral cells can proliferate. In young secondary superior segments, however, only a few large cells may grow into hemiblastic laterals, which are often arranged in a distinct pattern. This hemiblastic branching is here considered apomorphous.

(10) Acroblastic branching in *Sphacelaria* usually results in the formation of hairs. When

filaments can also be formed from cells separated from the apical cells, this can be considered apomorphous.

(11) Dichoblastic branching can be considered as unique and apomorphous (autapomorphous for *S. reticulata*).

(12) When hairs are formed in bundles, the lenticular meristematic hair-initial must divide before the formation of the hairs. This is probably apomorphous in comparison to solitary hairs. The presence of hairs as such cannot be considered apomorphous or plesiomorphous: it varies too much in most species.

(13) When branches arise in a distichous pattern, the direction of the division of the superior secondary segments by longitudinal walls is determined. This is probably apomorphous.

(14) Germlings in *Phaeophyceae* usually form a basal disc and erect filaments. In some species no disc will be formed, but a specialized mode of attachment occurs. This can be considered apomorphous. Specialization in the partly endophytic *Sphacella subtilissima* may be regressive and is distinctly different from the tuberculous holdfast of *Sphacelaria plumula.*

(15) When a normal basal disc is formed, a polystromatic structure is likely to be apomorphous.

(16) When rhizoids are present they can be divaricate or appressed to the erect filaments. Presence or absence as such is too variable to be useful. Appressed rhizoids can be considered apomorphous.

(17) The formation of a cortex is probably apomorphous.

(18) A closed and regular cortex is probably the apomorphous state of this character.

(19) When rhizoids arise from particular cells only, this is considered apomorphous.

(20) Propagules are specialized structures for vegetative propagation. They are known to occur in one particular group of *Sphacelaria*-species, in *Choristocarpus* and in a few other algae. They are considered apomorphous.

(21) In *Sphacelaria* the two types of propagules with arms can both be considered apomorphous with regard to armless propagules.

(22) Occurrence of a small apical cell (instead of an apical hair) in propagules is considered apomorphous. On old and germinating propagules of *S. tribuloides* in culture the apical cell occasionally forms a hair, but in mature propagules found in nature no hairs have been observed.

(23) Zoidangia are often lacking in *Sphacelaria* and in several species they have only rarely or even never been observed. For that reason only a few characters of zoidangia can be used for comparison of species. The branched specialized laterals on which zoidangia with long stalks can be found in several *Sphacelaria* species, and the cymose stands of unilocular zoidangia found in *S. sympodiocarpa* are two different apomorphous character states of branching of the stalks of zoidangia.

(24) The sessile zoidangia of *S. radicans* can be considered autapomorphous.

The argumentation scheme (fig. 24). *Choristocarpus* (a in fig. 24) cannot be considered to belong to a monophyletic group together with the *Sphacelariaceae*, but the monophyletic origin of *Sphacelariaceae* seems warranted by two synapomorphies, viz. in characters 1 and 2. *Choristocarpus* has only one apomorphy of its own (character 20, convergence with the synapomorphy of this character in the taxa h–m is probable).

The apomorphous state of characters 1–4 is characteristic for most *Sphacelariales*, but the characters 3 and 4 are nevertheless plesiomorphous in *Sphacella subtilissima* (taxon b). This forms a sister group to the remaining taxa within the *Sphacelariaceae* (the genus *Sphacelaria*). Character 14 can be considered an autapomorphy for *Sphacella*, but this is the only apomorphy in this sister group. All other characters (if present) are in the plesiomorphous state in this taxon. The synapomorphies in the characters 3 and 4, but also these in 1 and 2 will also occur in all other *Sphacelariales*. To separate the *Sphacelariaceae* (and the genus *Sphacelaria*) from the other families and genera in the *Sphacelariales* other characters must be used.

Information for a number of characters is lacking for *Sphacelaria mirabilis* (c in fig. 24) but in the characters 15 and 23 a synapomorphy can be observed with the species of the subgenus *Pseudochaetopteris* (d–g). Further information about the phylogenetic relationship of *S. mirabilis* to the other species in the subgenus *Pseudochaetopteris* is lacking. In that subgenus *Pseudochaetopteris* two sister groups can be observed. The synapomorphy occurring between one species (f = *S. arctica*) and the other sister group (d, e) can be explained by occurrence of convergence in the characters 13 and 17 (also found in species n and m which are part of other monophyletic groups) or by occurrence of parallelism in character 6.

Sphacelaria sympodiocarpa (n) and the species of the subgenus *Propagulifera* (h–m) form together a paraphyletic group, only based on symplesiomorphy. The subgenus *Propagulifera* itself seems to be a monophyletic group, based on synapomorphy of character 20 (presence of propagules). However, occurrence of propagules may also be a convergence, as can be seen from the occurrence of propagules in *Choristocarpus tenellus* (a), although this is not very probable. The correct place of *S. sympodiocarpa* in this system is questionable and this problem cannot be solved without detailed study of extra-European *Sphacelaria* species. In the subgenus *Propagulifera* most species can easily be separated from the others, but in *S. rigidula* (j) and *S. fusca* (i) this is not possible in this scheme.

In the subgenus *Sphacelaria* (o–r) the place of *S. nana* (j) is questionable. It is not possible to relate *S. nana* to other groups in European *Sphacelaria* however. In this case the possibility of reduction of the apomorphous expression of character 12 (hairs in bundles or not) can be considered, as well as the plesiomorphous expression of character 8 (no marked pericysts), a result of the relatively scarce occurrence of secondary transverse walls (character 7) in *S. nana*. The other species in the subgenus *Sphacelaria* (p–r) form a monophyletic group, but their coherence as a group is not very obvious, due to the absence of several of the discussed characters in *S. caespitula* and even more in *S. reticulata*. The possibility of the occurrence of convergence resulting in false apomorphies in the characters 13, 17, and 20, as well as a similar convergence in the characters 7 and 16 is suggested in the argumentation scheme. In the character 15 the apomorphies may also be false, possibly resulting from convergence or from parallelism. The apparent synapomorphies in character 12 between the taxa d–g on one side, and q on the other side are possibly inferred from parallelism and the synapomorphy of character 10 may also be based on parallelism.

Sister groups in the argumentation scheme formed by one single taxon are not always warranted as such by an autapomorphy. These autapomorphies are missing in the taxa c, e, g, m, o, and p. For the taxa i and j the synapomorphy in character 22 may be considered a joint autapomorphy, but the apomorphy of character 15 cannot be used as an autapomorphy for taxon o.

Alternatives and refinements. The sequence of characters, as given in the argumentation scheme resulted from the procedure described before as the 'search for sister groups'. During this procedure many decisions are to be made. I will now discuss the changes which would occur in the argumentation scheme when I should have made another decision. The first three alternatives will affect the sequence of characters between 4 and 16 in fig. 24.

ALTERNATIVE a. Start the sequence above character 4 with character 7, followed by 9, 20, 21, 22, 14, 15, and 8. After these the characters 5, 12, 23 will follow. The mutual sequence of the last three numbers is indifferent in this alternative scheme. In this alternative the sequence of the species must also be changed and this will result in a slight change in the cladistic diagram on subgenus level. The subgenus *Propagulifera* (h–m in fig. 24) and the species *S. sympodiocarpa* (n) will form a sister group in this alternative, warranted by a synapomorphy in character 9. This character, however, also has a synapomorphy in the subgenus *Pseudochaetopteris* (d–g in fig. 24). Thus in this alternative convergence or parallelism has to be suggested inferring in character 9. The arrangement of species in sections and subgenera in the genus *Sphacelaria* will not be altered by this alternative. I prefer the original scheme because I consider convergence in character 7 more probable than convergence or parallelism in character 9.

ALTERNATIVE b. The sequence above character 4 also starts with character 7. In alternative b (and also alternative c), however, the appreciation of the apomorphous and plesiomorphous state of character 9 is changed. Hemiblastic branching is considered the plesiomorphous state in these alternatives b and c, and thus laterals arising from peripheral cells and distant to the apical cells are to be considered apomorphous. Doing this, further sequence of the characters in the argumentation scheme will be 12, 20, 21, 22, 14, 15. The mutual sequence of the next five characters (5, 8, the altered 9, 16, and 23) is indifferent in this alternative. The consequences of this alternative for the cladistic diagram are considerable.

The subgenera *Battersia* (c in fig. 24), *Pseudochaetopteris* (d–g), and *Sphacelaria* (o–r) will have a synapomorphy in character 7. The subgenus *Propagulifera* (h–m) and the species *S. sympodiocarpa* (n), however, form a paraphyletic group, based on symplesiomorphies only. The species *S. nana* (o) is separated from the other genera of the large group because character 12 is plesiomorphous in this species. It has no apomorphies of its own, however, since apomorphies in the characters 9 and 15 are possibly inferred by convergence or parallelism. The monophyletic origin of the subgenus *Pseudochaetopteris* (d–g) is warranted by synapomorphies in 5, 23, and 16 and the monophyletic origin of the remaining part of the subgenus *Sphacelaria* by a synapomorphy in 8. In this alternative *S. nana* has to be considered the only species of a separate subgenus. I prefer the original scheme because I consider convergence in character 7 more probable than convergence or parallelism in the altered character 9. Moreover, I still want to consider hemiblastic branching apomorphous. Establishing a new monotypic subgenus for *S. nana* seems undesirable.

ALTERNATIVE c. This differs from alternative b in the place of the character 12 in the mutual sequence. In alternative c the sequence above character 4 is 7, 20, 21, 22, 14, 15, 12. Then follow the characters 5, 8, the altered 9, 16, and 23 in a sequence which is indifferent in the scheme. The consequences of this alternative are similar to alternative b.

ALTERNATIVE d. The sequence of the characters 6, 13, 17, 18, and 19 is not altered by one of the above-mentioned alternatives. The sequence as given in fig. 24 can be altered by insertion of character 6 on other positions in this sequence. Moreover, the appreciation of the apomorphous and plesiomorphous state of character 6 can be changed. Occurrence of a tangential primary wall can be considered plesiomorphous, and thus a median primary wall will then be considered apomorphous. This change of appreciation is indifferent when the original sequence has not been changed. Insertion of character 6 on other positions in the sequence results in separation of the subgenus *Pseudochaetopteris* (d–g in fig. 24) into a group of three species (d–f) and the single species *S. racemosa* (g). When the appreciation of character states in section 6 is changed as described above, and when the sequence will be 13, 17, 18, 6, 19 the relevant part of the argumentation scheme will be as in fig. 26. As can be seen from this figure the species (except d) have still no autapomorphies and are thus not warranted as monophyletic groups. I prefer the original scheme because I consider convergence in the characters 13 and 17 not improbable. Moreover, I still consider apomorphy of the tangential primary wall most probable. Separation of the subgenus *Pseudochaetopteris* into two comparable sections still seems desirable.

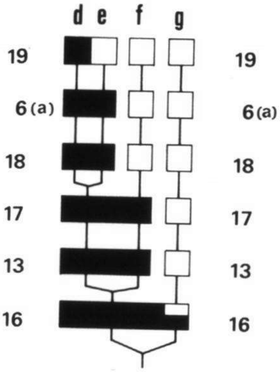


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Fig. 26. Phylogenetic diagram for a cladistic system of the *Sphacelariaceae*—alternative d (detail).

Discussion of the list of character states results in the following remarks.

For *S. nana* (p) the apomorphous as well as the plesiomorphous state of character 7 may occur. To refine the argumentation scheme character 7 in table IV may be changed as follows:

Secondary transverse cell-walls usually present and often frequent: a.

Secondary transverse cell-walls usually absent: p.

Add character 7′:

Secondary transverse cell-walls present in all filaments: a.

Secondary transverse cell-walls not present in all filaments: p.

For character 16 a similar refinement can be introduced for *S. racemosa* (g). The consequences of that action will be similar to the alternative d published above. For the characters 15 (for *S. nana*; o) and 13 (for *S. cirrosa*; h) similar refinements are indifferent to the scheme.

The characters with two different apomorphous states (characters 14, 21, and 23) can also be subdivided when desired. Character 11 can possibly also be subdivided into two separate characters, resulting in an apomorphous state for acroheteroblastic branching as well as for dichoblastic branching. Change of appreciation of states in character 14 will result in establishing a separate subspecies for *S. plumula* (k), which is most undesirable. In the characters 16, 18, and 22 change of appreciation of states is possible and indifferent to the scheme.

The phylogenetic diagram (fig. 25). *Choristocarpus* (as a typical member of the *Choristocarpaceae*) and the *Sphacelariaceae* can be considered to belong to separate families (and possibly also to separate taxa of higher order). *Sphacella* and *Sphacelaria* are sister groups and the genus level can be considered having been reached here. The next two sister groups are composed of the subgenera *Propagulifera* and *Pseudochaetopteris* together with *S. sympodiocarpa* and *S. mirabilis* (subgenus *Battersia*) in one group, and the species of the subgenus *Sphacelaria* (including *S. nana* and *S. reticulata*) in the other group. In the largest sister group the next splitting is in the subgenera *Pseudochaetopteris* and *Battersia* on one side and a paraphyletic group composed of the subgenus *Propagulifera* and *S. sympodiocarpa* on the other side. The latter group being only based on symplesiomorphy, has no value in justifying a supposition of close phylogenetic relationship. After separation of *S. sympodiocarpa* from this group the remaining species of the subgenus *Propagulifera* form a monophyletic group. So the subgenus *Sphacelaria* is a sister group of the remaining European species in *Sphacelaria* and the subgenera *Pseudochaetopteris* and *Battersia* together form a sister group of the paraphyletic group composed of the remaining *Sphacelaria* species, of which the subgenus *Propagulifera* forms a new monophyletic group. According to the principles of classification used by Hennigian phylogenetic systematicists sister groups must be given equal rank. On the other hand I do not like to multiply the ranks used in the classification of the genus *Sphacelaria*. For that reason, and because much information is still lacking, I like to consider the larger monophyletic groups as subgenera. The localisation of the exact position of the separation of the subgenera *Battersia* and *Pseudochaetopteris* remains uncertain.

In the subgenus *Propagulifera* two sister groups can be found: the section *Tribuloides* and a sister group composed of *S. cirrosa, S. rigidula* and *S. fusca*. Of these the two last-mentioned species are found together in the next sister group (section *Furcigerae*) of which *S. cirrosa* forms the other sister (section *Propagulifera*). Theoretically it is more correct to consider the two last-mentioned sister groups as having a lower rank than the section *Tribuloides*. In view of the discussion about the rank of the subgenera, I like to consider all these small sister groups as sections.

In the subgenus *Sphacelaria S. nana* is separated from the other three species in an early stage. I do not propose a special infrageneric rank for this species, which can probably be considered as a species with reduction of the apomorphous expression of characters. The loose coherence of the remaining group is discussed above.

From my cladistic exercises I learned that the monotypic genera *Battersia* and *Disphacella* cannot be considered as genera separate from the genus *Sphacelaria. Battersia mirabilis* is a member of a monophyletic group together with the four species of the subgenus *Pseudochaetopteris*. I consider *S. mirabilis* a representative of a separate monotypic subgenus. *Disphacella reticulata* is a member of a monophyletic group (subgenus *Sphacelaria*) together with *S. radicans, S. caespitula*, and perhaps also *S. nana*. The loose coherence of this group prevents the separation of the subgenus into consistent sections.

The results of the phyletic-cladistic procedure can be tested against the geographical distribution patterns. As discussed in the section on distribution of the genus *Sphacelaria* (p. 51 and fig. 42) the subgenera *Pseudochaetopteris* and *Propagulifera* vicariate nicely. The subgenus *Sphacelaria* is in an intermediate position and the knowledge of the geographical distribution of the genera *Choristocarpus* and *Sphacella*, the subgenus *Battersia*, and the species *Sphacelaria sympodiocarpa* is inadequate. Thus the distribution of the three main subgenera in the genus *Sphacelaria* is not in contradiction with the results of the phyletic-cladistic procedure as given in the figures 24 and 25). I do not claim that these figures represent the only possible theoretical phylogenetic system in the European *Sphacelariaceae.* In the section on alternatives and refinements (p. 39) I explained this already. Other problems in the interpretation of the results of this procedure are discussed by Bremer & Wanntorp (1978). Nevertheless I consider my results as a first step towards a more reliable phylogenetic system in the *Sphacelariales.*

The genera in the Sphacelariaceae. The monotypic genus *Sphacella* can easily be separated from the genus *Sphacelaria* on the basis of the absence in the former genus of longitudinal walls in the segments of the erect filaments and because the primary segments of that genus only irregularly subdivide into secondary segments. Presence of longitudinal walls, and regular subdivision of primary segments, however, occurs in all other *Sphacelariales*, except in *Sphacelaria mirabilis*, which is devoid of erect filaments. Absence of secondary growth in length and width of segments can be used as a distinction with respect to the auxocaulous *Sphacelariales.* Occurrence of acroblastic branching resulting in the formation of filaments (or filaments and hairs, but not only hairs) can be considered as a criterium to separate the leptocaulous *Stypocaulaceae* from the species of the genus *Sphacelaria.* True hemiblastic branching occurs only in the *Sphacelariaceae*, but tardy hypacroblastic branching from pericysts or from peripheral cells can also be found in most other *Sphacelariales.* From this discussion it appears that it is not yet fully possible to define the genus *Sphacelaria* as a unity. Future research may result in fission of this genus into smaller genera.

KEY TO THE GENERA[3]

1a. All or most secondary segments subdivided by longitudinal walls or without erect filaments .... **Sphacelaria**
b. Segments not subdivided by longitudinal walls .... **Sphacella**

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[3] For terminology see the glossary, p. 262.

SPHACELLA Reinke

Sphacella Reinke (1890a) 206; (1891) 35; De Toni (1895) 499; Newton (1931) 192; non Clayton (1974) 800.—Type: *Sphacella subtilissima* Reinke.

Very small plants (less than 2 mm high), forming subglobose dense tufts on other algae, attached by irregular filaments which are endophytic in the species' hosts. The terete and articulate, branched, erect filaments are quite rigid and provided with only a few or occasionally many, irregularly placed laterals, which are very similar to the main erect filaments. Segments from the cylindrical apical cell are once transversely divided or they remain undivided. Longitudinal segmentation and secondary transverse divisions in the segments do not occur. Rhizoids, hairs, propagules, and plurilocular zoidangia are unknown. Chloroplasts are small, lenticular, and occur in small numbers. Reproduction takes place by unilocular zoidangia.

Systematic position

The monotypic genus *Sphacella* can easily be separated from *Sphacelaria*, the only other genus in the *Sphacelariaceae*. *Sphacella subtilissima* is a *Sphacelaria*-like alga lacking the regular formation of secondary segments as well as longitudinal division in these segments. Sauvageau (1900, p. 249 = R. 24 and 1903, p. 93 = R. 264) discussed the relationship of *Sphacelaria* and *Sphacella*. He considered *Sphacella subtilissima* as a *Sphacelaria* species with segments without longitudinal walls. He compared *Sphacelaria pulvinata* from New Zealand with *Sphacella subtilissima* and he considered them to be very similar. However, in this *Sphacelaria pulvinata* all primary segments are divided into secondary ones and longitudinal walls in the secondary segments are common. Thus the two species discussed do not show a closer relationship than between any other *Sphacelaria* species and *Sphacella subtilissima*. The two genera can still be considered as distinctly separate.

In the argumentation scheme for the cladistic system (fig. 24) it can be seen that most characters for *Sphacella subtilissima* are plesiomorphous. Exceptions are two characters which are characteristic for all *Sphacelariales* and one (autapomorphous) character of the basal holdfast. If the characters of *Sphacelaria pulvinata* should be added to this argumentation scheme, it would not affect the distinct separation of the two genera.

Womersley (1967, p. 194, fig. 1) incorporated *Cladophora ferruginea* Harvey in Hooker into the genus *Sphacella*. Clayton (1974, p. 800. fig. 33) described *Sphacella ferruginea* (Harvey) Womersley in detail. She also published a new description of the genus *Sphacella* and she incorporated this genus within the *Ectocarpales*. Her genus-description was mainly based on *S. ferruginea*. Delépine & Asensi (1975, p. 296, fig. 5) incorporated *S. ferruginea* in the new genus *Asteromena* on basis of the stellate arrangement of the chloroplasts. However, in *Sphacella subtilissima* the chloroplasts in the preserved specimens are not stellate arranged. On the other hand the cell-walls of *Asteronema* do not turn black in bleaching liquid. For this reason I follow Delépine and Asensi in removing *S. ferruginea* from the genus *Sphacella*. Consequently the genus-description by Clayton must be excluded as well. There are no reasons to transfer the genus *Sphacella* from the *Sphacelariales* to the *Ectocarpales*.

ACCEPTED SPECIES

1. Sphacella subtilissima Reinke—Fig. 27–38

Sphacella subtilissima Reinke (1890a) 206; (1891) (5, t. 2); De Toni (1895) 499; Sauvageau (1900) 229 (= R. 17), f. 3–5; Funk (1927) 353; Hamel (1938) 247; Funk (1955) 43; Prud'homme van Reine (1978) 303.—Type: *Rodriguez s.n.* Menorca, on *Carpomitra costata*, 3/1/1888 (KIEL).

Plants forming small, dense, subglobose tufts on *Carpomitra costata* (fig. 29) and *Sporochnus pedunculatus* (fig. 27; 28). Colour of fresh specimens is not known. Many erect filaments arise from a basal part which is endophytic in its host.

The basal parts consist of intricate, irregular filaments which form small or quite extensive irregular multicellular endophytic structures (fig. 30; 31).

The erect parts of the plant are composed of many erect main filaments which are unbranched or from which few to many unbranched laterals arise (fig. 31–35). The sharply divaricate laterals arise in an irregular pattern. There is no difference in growth or dimension of axes and laterals. The dimensions of the short or elongate apical cells and of the segments are very variable. Transverse walls subdividing the primary segments are often lacking (fig. 35) or they arise very irregularly or late (fig. 36; 37). Segments are 1–5 times longer than they are wide, occasionally they are shorter than they are wide.

Hairs and rhizoids are not known.

The ovoid unilocular zoidangia are formed on small 1–3 celled stalks arising along the whole length of the filaments or they are terminal on the main filaments and the laterals (fig. 31; 34; 35; 38). Plurilocular zoidangia and propagules are not known.

Dimensions: Plants 1–2 mm high, diam. irregular endophytic structures 100–300 μm. Angle of ramification 15–45 (–60)°. Diam. of erect filaments 12–17 (–20) μm. Height of secondary segments 15–60 μm. Unilocular zoidangia 50–60 X 30–35 μm. Unizoids 5–7 μm according to Sauvageau (1900).

Distribution. Mediterranean coasts of Spain and Italy, See also fig. 43.

SPAIN. Baleares. Menorca: probably Hacia Canutells, 110 m deep, on *Carpomitra cabrerae* (= *C. costata*), *Rodriguez 641*, 3/1/1888 (KIEL, PC). *Ibidem*: Hacia Cala Covas, 120 m deep, *Rodriguez 608A*, 18/10/1887 (PC); Binidalí, 95 m deep, *Rodriguez 608B*, 15/11/1887 (PC) and without exact locality, on *Carpomitra*, *Rodriguez*, 30/9/1890 (coll. Sauvageau in PC).

ITALY. Liguria. Porto Maurizio: on *Sporochnus*, *Strafforello 240*, 1890 (PC). Campania. Ischia: Punta S. Angelo (Funk, 1927, p. 353).

Notes on morphology. In the segments of *Sphacella subtilissima* usually no longitudinal walls are formed. Both Reinke (l.c.) and Sauvageau (l.c.) found occasional longitudinal walls in this species.

The form and dimensions of the chloroplasts could not be observed in the preserved specimens, but Reinke (1891) described them as small and lenticular. Laterals arise often as extensions of the stalks of unilocular zoidangia. The remnants of the walls of the dehisced zoidangia can often be found on the proximal parts of these laterals (fig. 32; 33). In specimens from Porto Maurizio I did not observe laterals (fig. 31; 35; 36; 38).

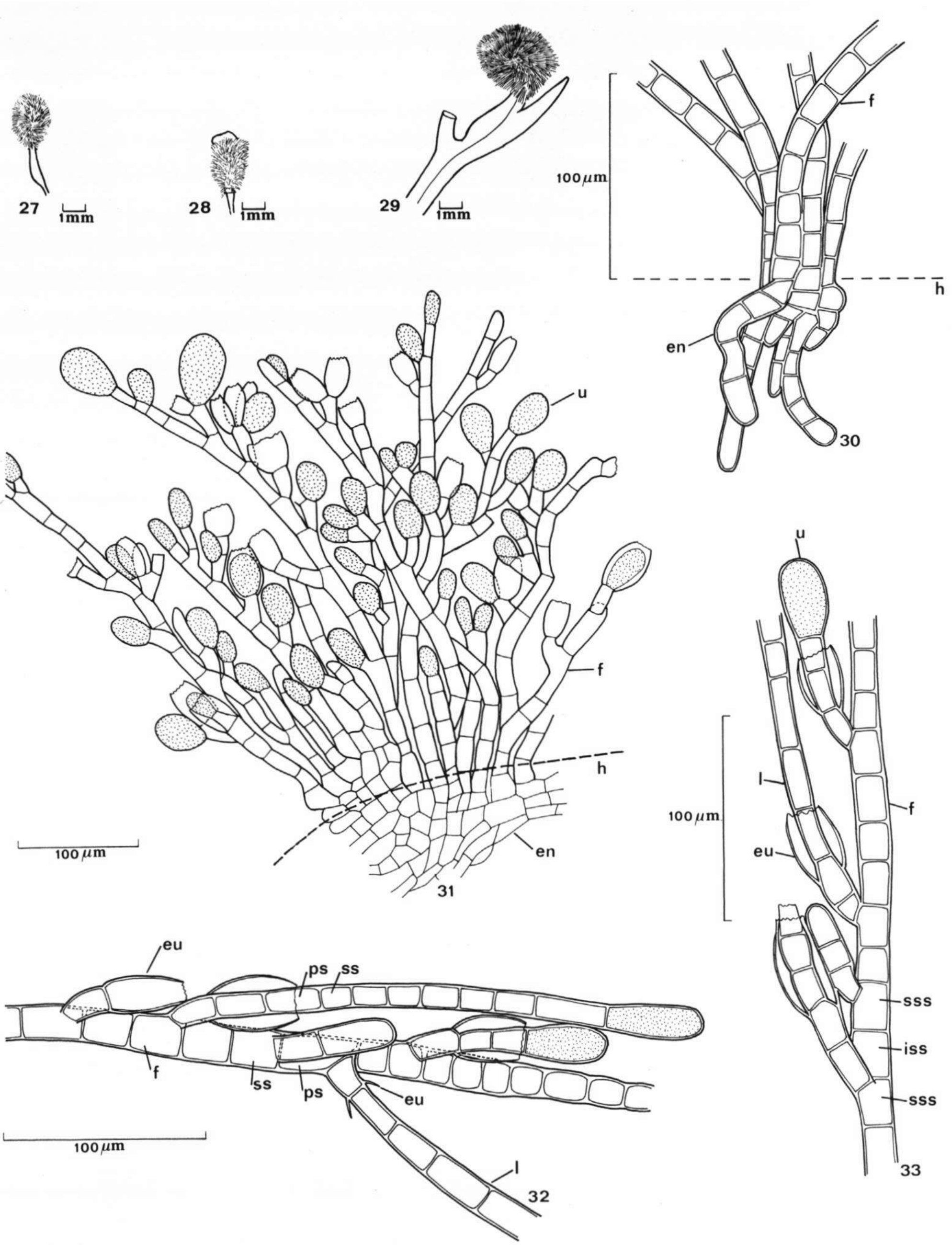

Fig. 27–33. Sphacella subtilissima. 27–29 Habits. en. endophytic part; eu. empty unilocular zoidangium, solitary or arranged in small sympodes; f. erect filament; h. host; l. lateral; ps. primary segment; ss. secondary segment; u. unilocular zoidangium. 27, 28, & 31. on laterals of *Sporochnus pedunculatus*, Porto Maurizio, *Strafforello 240* (PC, soaked); 29, 30, 32, & 33 on *Carpomitra costata*, Menorca, *Rodriguez* (PC, in alcohol 70%).

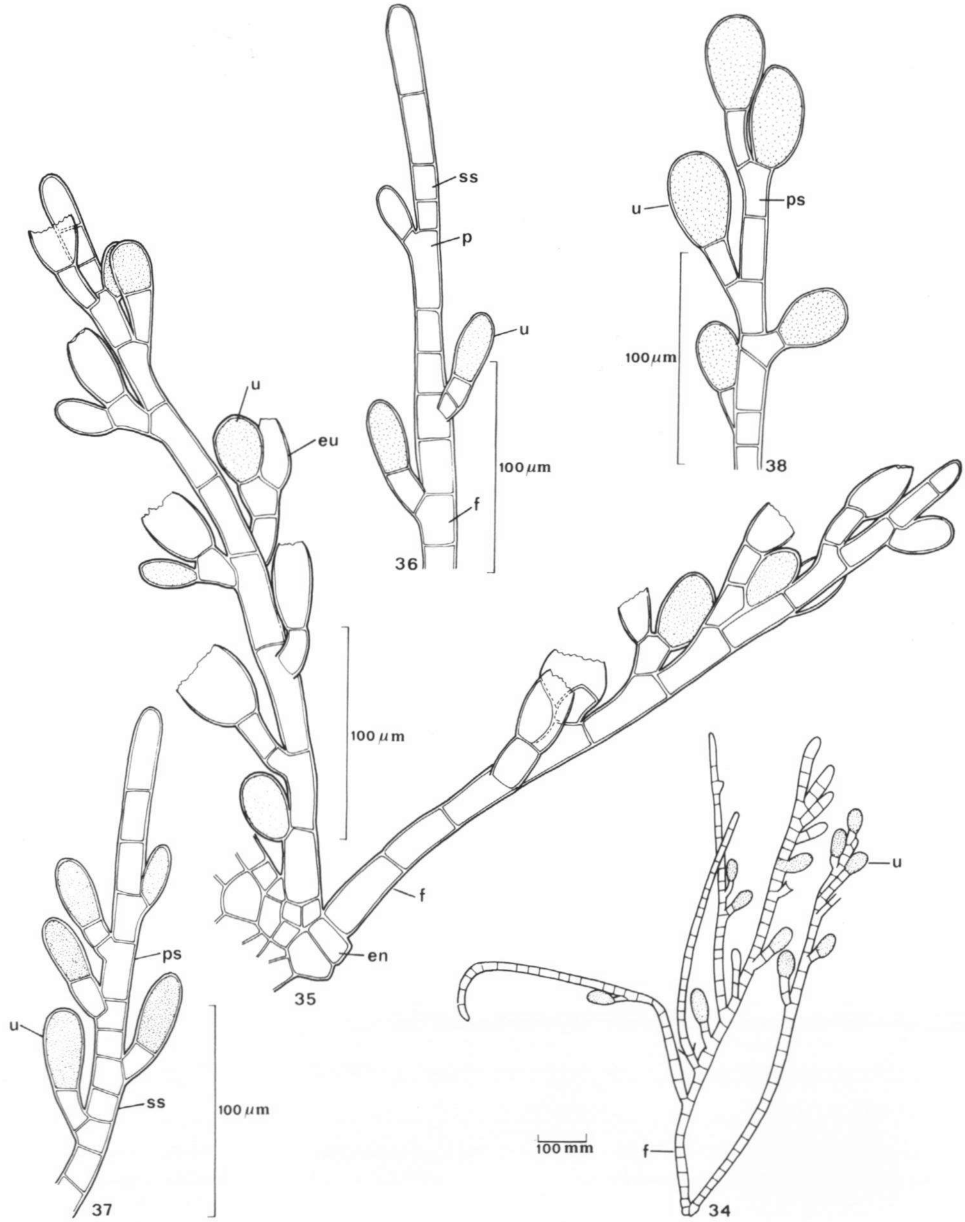

Fig. 34–38. Sphacella subtilissima. Code as in fig. 27–33. 35, 36, & 38 from material as in fig. 27; 34 & 37 from material as in fig. 29.

Division of primary segments into secondary ones by transverse cell-walls is not as constant as it is in other *Sphacelariales*. This division can be absent in many filaments (fig. 31; 35). In other filaments several primary segments are divided into secondary ones, while others are not (fig. 32; 36; 37). Only occasionally are all primary segments of a filament divided (fig. 33). The division of primary segments is less frequent in the specimens from Porto Maurizio, but it is not completely lacking like Sauvageau (l.c.) supposed (see my fig. 36).

The unilocular zoidangia of the specimens from Menorca are usually solitary (fig. 34; 37), but in the specimens from Porto Maurizio they are often arranged in small sympodia (fig. 31; 35), occasionally they are also solitary, however (fig. 38).

Notes on ecology. The few specimens that have been found so far were partly endophytic in the larger *Phaeophyceae Carpomitra costata* and *Sporochnus pedunculatus.* Sauvageau (l.c.) stated that the endophytic part of *Sphacella subtilissima* seriously disorganizes the structure of the thallus of the host plants. On specimens of both host plants, collected from Atlantic coasts, no *Sphacella* has been detected. The rare *Sphacella subtilissima* is probably confined to the deeper sublittoral.

Systematic position. For the position of the genus *Sphacella* within the *Sphacelariaceae* see p. 40 & p. 43.

Sphacella subtilissima var. *anglica* described by Batters (1897, p. 436) and depicted by Newton (1931, f. 120 B & C) is an ectocarpoid alga, possibly a juvenile winter phase of *Spongonema tomentosum*. See also Russell & Fletcher (1975, p. 774).

SPHACELARIA Lyngbye

Sphacelaria Lyngbye in Hornemann (1818) t. 1600; Lyngbye (1819) 103; Gray (1821) 332; Bonnemaison (1822) 189; Bory de Saint Vincent (1823b) 393 (as *Sphacellaria*); Greville (1824a) II, t. 96 (as *Sphacellaria*); C. Agardh (1824) XXX, (1828) 17; Bonnemaison (1828) 107; Brongniart (1829) 537; Sprengel (1831) 752; Harvey (1833) 323; Duby (1832) 333; Kützing (1843) 291; Meneghini (1843) 29; Rabenhorst (1847) 175; J. Agardh (1848) 29; Kützing (1849) 463; Zanardini (1865) 139; Hauck (1885) 342; Kjellman (1890) 66; Reinke (1890a) 206, (1891) 3; De Toni (1895) 499; Sauvageau (1903) 92 (= R. 263); Newton (1931) 188; Hamel (1938) 248; Lund (1950) 9; Irvine (1956) 25; De Haas-Niekerk (1965) 145; Prud'homme van Reine (1974) 172.—Type species: *Sphacelaria reticulata* Lyngbye. See notes on nomenclature 1.

Delisella Bory de Saint-Vincent (1823a) 540, (1824) 389.—Lectotype species: *Delisella pennata* (Dillw.) Bory = *S. cirrosa* (Roth) C. Agardh.

Chaetopteris Kützing (1843) 293, (1845) 241; J. Agardh (1848) 40; Kützing (1849) 468; Hauck (1885) 347; Batters (1889) 64; Kjellman (1890) 65; Reinke (1890a) 209, (1891) 3, (1892) 69; De Toni (1895) 511; Sauvageau (1903) 93 (= R. 264); Newton (1931) 193.—Type species: *Chaetopteris plumosa* (Lyngbye) Kützing = *S. plumosa* Lyngbye.

Sphacelaria (subgenus ?) *Eusphacelaria* Hauck (1885) 342.—Type: not indicated.

Battersia Reinke ex Batters (1889) 59; Reinke (1890a) 205, (1891) 4; De Toni (1895) 499; Sauvageau (1900) 224 (= R. 12), (1903) 79 (= R. 249); Newton (1931) 191.—Type species: *Battersia mirabilis* Reinke ex Batters = *S. mirabilis* (Batters) Prud'homme van Reine.

Sphaceloderma Kuckuck (1894) 232; De Toni (1895) 498.—Type species: *Sphaceloderma helgolandicum* Kuckuck = *S. caespitula* Lyngbye.

Disphacella Sauvageau (1903) 345 (= R. 280) nom. illeg., Oltmanns (1922) 90.—Type species: *Disphacella reticulata* (Lyngbye) Sauvageau = *S. reticulata* Lyngbye. See notes on nomenclature 2.

Plants varying in height from less than 2 cm to more than 10 cm, forming subglobose, hemispherical, penicillate, or complanate tufts or spreading mats, attached by monostromatic or polystromatic basal discs or by stolons and rhizoids ramifying on or penetrating into the support. They are rarely unattached or without erect filaments. The terete, articulate, isodiametric, erect filaments are subsimple to bushy, quite rigid to flaccid, provided with sparse to many, determinate or indeterminate, branched or unbranched, usually hemiblastic laterals, which are distichous, helicoid, or irregularly placed. Segments cut off from the usually conspicuous cylindrical apical cell are each transversely divided once before longitudinal segmentation. Secondary transverse divisions in the secondary segments may be frequent, infrequent, or entirely absent. Some species have rhizoids which may corticate the erect filaments or may be divaricate. Hairs are present in several species. Many small discoid parietal chloroplasts occur in each cell. Reproduction takes place by means of propagules, plurilocular gametangia, neutral plurilocular zoidangia, or unilocular zoidangia. These various types of reproductive structures occur on separate specimens; or several kinds of reproductive structures occur together on one and the same plant or tuft.

Notes on nomenclature

(1) The publication of the new genus *Sphacelaria* by Lyngbye (in Hornemann 1818) was valid and legitimate at that time since the description of *S. reticulata* can be considered as a descriptio generico-specifica. The author placed nine other species in his new genus in 1819, eight of which were described in detail. Several later authors selected a lectotype for the genus *Sphacelaria*: all without regard to the earlier typification by Lyngbye. Bonnemaison (1822, p. 190) and Brongniart (in Bory, 1829, p. 537) selected *Conferva scoparia* L.

(= *Stypocaulon scoparium* (L.) Kütz.); Pfeiffer (1874, p. 1216) cited *Ceramium pennatum* Fl. Dan. (= *Sphacelaria plumosa* Lyngbye) as the lectotype and De Toni (1891, p. 180) proposed *S. radicans* (Dillw.) C. Agardh as the type. The last-mentioned species was not included in the original treatment of *Sphacelaria* by Lyngbye. None of these authors should be followed when selecting the type of the name of the genus *Sphacelaria.*

(2) Sauvageau (1903, p. 345 = R. 280), when separating *S. reticulata* from all other species of *Sphacelaria*, acted against article 63.1 of the International code of botanical nomenclature (Stafleu *et al.*, 1978). Therefore the genus name *Disphacella* is nomenclaturally superfluous and illegitimate.

Notes on morphology

In the *Sphacelariaceae* the secondary segments have no secondary growth. They are, however, usually divided by longitudinal walls, and often also by transverse walls. In transverse sections of the polysiphonal secondary segments two different patterns of division by the longitudinal walls can be observed: a radial pattern and a periclinal one. In both patterns the first longitudinal wall is in principle radial. The two next walls are usually perpendicular to the primary longitudinal wall. In the radial type later walls form acute angles with the ones formed before (fig. 39), but in the periclinal type all walls are perpendicular to each other (fig. 40). For aberrant patterns see Prud'homme van Reine (1974, f. 3, 4, 6, and 7).

Ultrastructure. The ultrastructure of the *Sphacelariales* has not been studied very often. All studies deal with *Sphacelaria* species. Bisalputra and collaborators published several papers in 1969 and 1970 in which they carefully described all details of the chloroplasts of an unidentified *Sphacelaria* species. Galatis, Katsaros & Mitrakos (1977) described the fine structure of vegetative cells of *Sphacelaria tribuloides.* Evans (1966) studied the pyrenoid of zoids of *S. cirrosa* ecad *bipinnata* (as *S. bipinnata*), and Parker (1970) figured cellulosic microfibrils in the cell wall of a *Sphacelaria* species. Bouck (1965) was the first author to describe the general details of fine structure in the cells of brown algae. His diagram of a hypothetical brown alga cell can be found in several modern handbooks. All subsequent studies of the ultrastructure of the *Phaeophyceae* are based on Bouck's paper. The main part of my studies of the ultrastructure of *Sphacelaria* spp. will be published separately (Prud'homme van Reine & Star, 1981). A few remarks will be published here.

Near the apex of the apical cell the cell wall is narrowest (plate 1a). In fast growing filaments of *Sphacelaria* species this apex may become so thin, that the apical cell bursts very easily. The weight of a cover slip may be heavy enough to cause this (see also fig. 41). Van den Hoek & Flinterman (1968, p. 215, 216) suggested that apical cells may show some properties of unilocular zoidangia and that they may release their (undivided) protoplast through an apical pore. Their observations (their figures 6 and 54) were possibly on apical cells with very thin and vulnerable apices.

Young outer cell walls consist of four layers: a narrow electron dense outer layer, an amorphous vesiculated layer, an outer fibrillary layer, and an inner fibrillary layer (plate 1b). Small quantities of silica, as detected by Parker (1968, 1969) occurring in cell walls of several *Phaeophyceae*, may be responsible for the traces made by the knife during preparation of the ultra thin slices (plate 2d), see also Bisalputra & Bisalputra, 1969, f. 3).

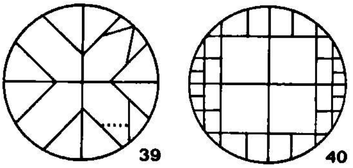

Fig. 39, 40. Sphacelaria spp. Transverse sections of mature erect filaments. 39. Radial type; 40. Periclinal type.

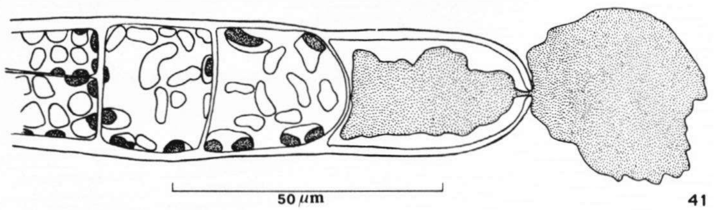

Fig. 41. Sphacelaria arctica. The apical cell of an erect filament is killed by the pressure of a cover-slip and the contents escape through an artificial pore in the thinnest part of the wall.

In the chloroplasts usually three thylakoids can be observed in each photosynthetic lamella. Occasionally, however, lamellae may consist of only one thylakoid (plate 1b).

Microbodies (peroxisomes ?) have often been observed in *Sphacelaria* species (plate 1b), as well as paramural bodies in the space between the plasmalemma and the cell wall (the paramural space).

Other inclusions of the cytoplasm (unstructured electron-dense vesicules, physodes, supposed fucoidan-vesicles and vacuoles) may be present in growing apical cells (plate 2d).

Notes on distribution

The geographic distribution of the European species of *Sphacelaria* is given in a number of maps in this paper.

Figure 42 shows that the subgenus *Propagulifera* is, with a few exceptions, restricted to the warm temperate coasts of Europe and the subgenus *Pseudochaetopteris* to the cold temperate (boreal) coasts (with an exception for *S. plumigera*, see fig. 308). The species of subgenus *Sphacelaria* do not enter the cold waters as far and as much as the species of subgenus *Pseudochaetopteris*. The southern borders of the areas of these two subgenera are broadly the same. Because the northern borders of the areas (which cannot be given in fig. 42) are so different, I consider the distribution of subgenus *Sphacelaria* as intermediate between the subgenera *Pseudochaetopteris* and *Propagulifera*. For the distribution of the monotypic subgenus *Battersia* see the map for *S. mirabilis* (fig. 43), on which the distribution of the aberrant species *S. sympodiocarpa* is also given.

Of the 16 European *Sphacelaria* species nine (subgenera *Sphacelaria*, *Pseudochaetopteris*, and *Battersia*) have mainly or exclusively been found in the northern and northwestern part of Europe. The remaining seven species (subgenus *Propagulifera* and *S. sympodiocarpa*) occur mainly or exclusively in southwestern Europe. Of these only four species have been found in the Mediterranean. In Great Britain 12 different species of *Sphacelaria* have been

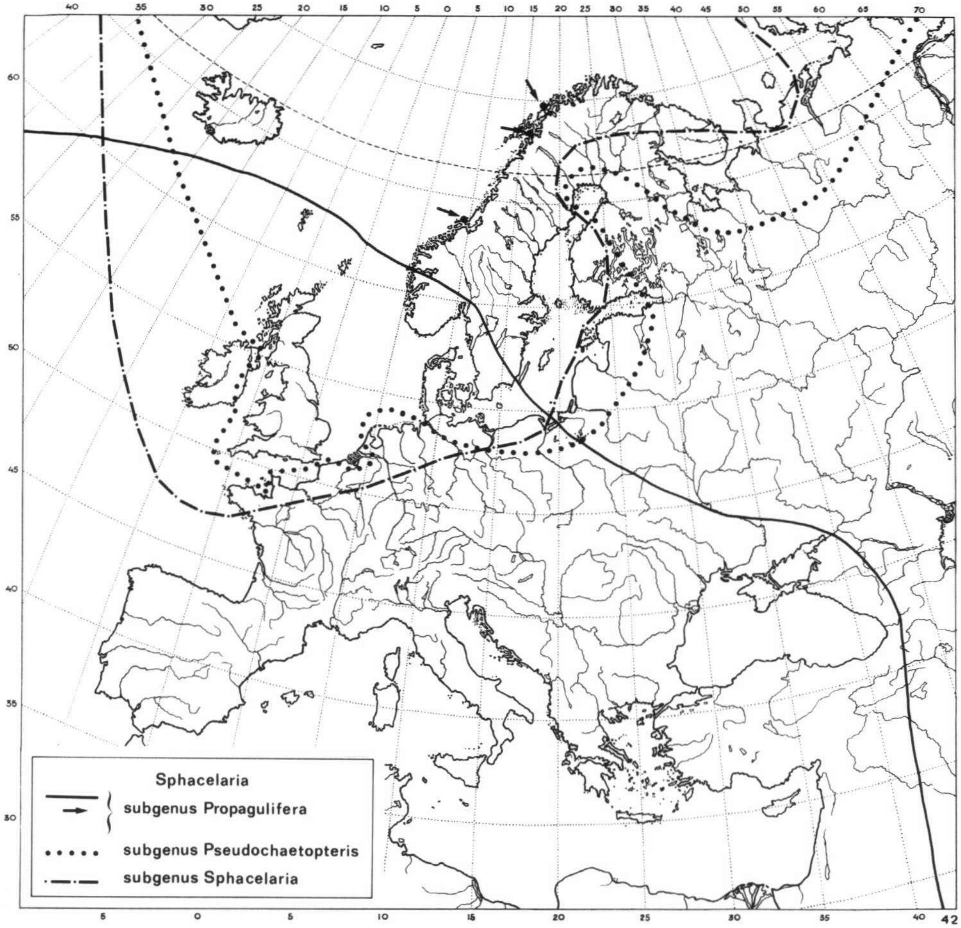

Fig. 42. Geographical distribution of the subgenera of the genus *Sphacelaria*.

—— Northernmost border of occurrence of the subgenus *Propagulifera.*
→ Isolated localities for members of the subgenus *Propagulifera.*
•••••• Southernmost border of occurrence of the subgenus *Pseudochaetopteris.*
•—•— Southernmost border of occurrence of the subgenus *Sphacelaria.*

found, of which *S. arctica* only in the extreme north (The Shetland Isles).

For the distribution of the subgenera *Pseudochaetopteris* (as 'periclinal type') and *Propagulifera* (as 'radial type') see Prud'homme van Reine, 1974. In that paper, in which I reviewed the distribution of the European *Sphacelaria* species in the world, I wrongly included the species of the subgenus *Sphacelaria* in the 'periclinal type'. This has only a very restricted effect on the results, due to the partial coincidence of the areas of distribution of the subgenera *Sphacelaria* and *Pseudochaetopteris.*

The distribution of the species of the subgenus *Sphacelaria* outside Europe is not well-known. *S. radicans* and *S. nana* have been observed on the northern Atlantic coasts of America and *S. radicans* also in Japan. Some extra-European *Sphacelaria* species with second-

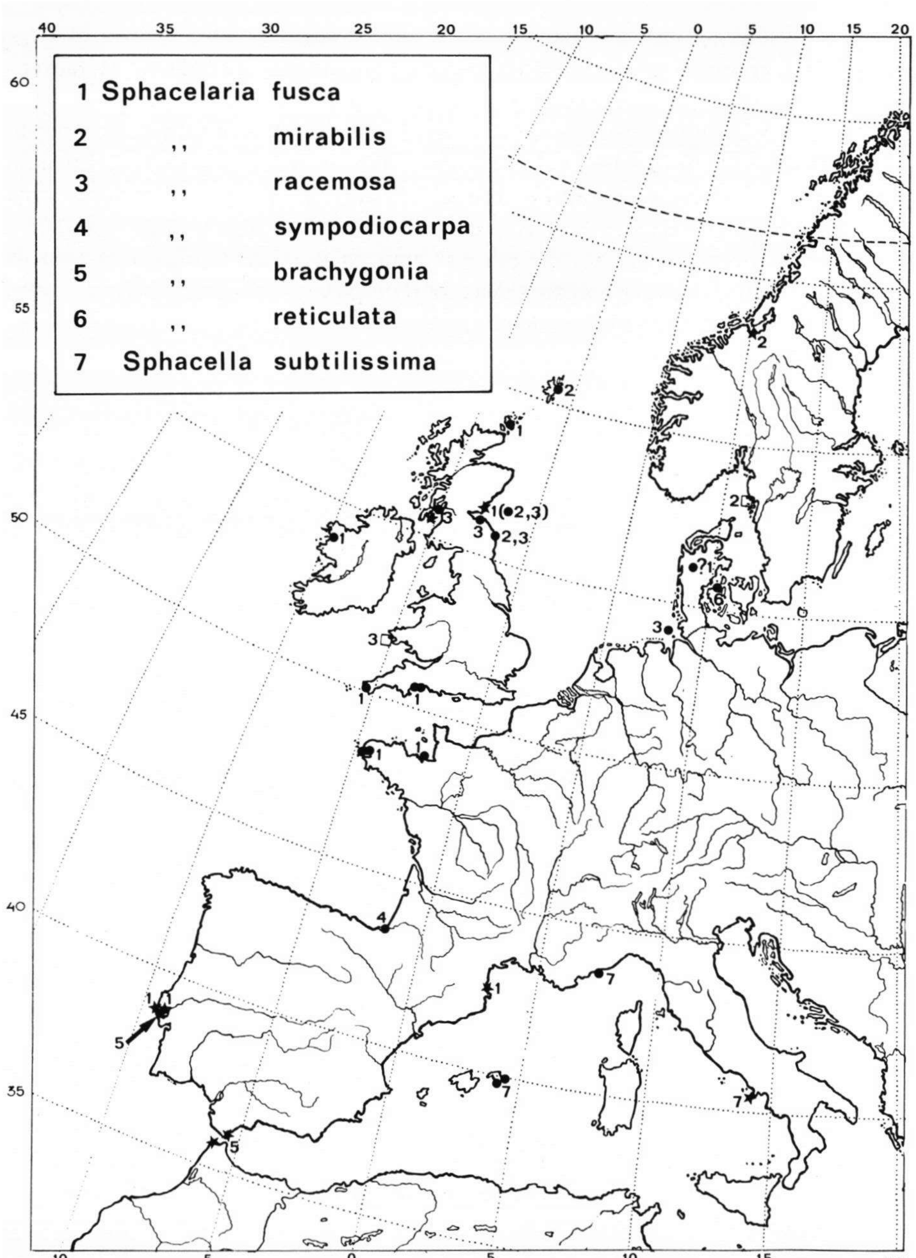

Fig. 43. Distribution of several of the rare species of the *Sphacelariaceae* in Europe.

● = Material seen by the author.
★ = According to literature.
☐ = Uncertain material or locality.

ary transverse cell-walls and pericysts (viz. *S. reinkei* Sauvageau and *S. implicata* Sauvageau) have rarely been collected and hence little is known about their distribution. Moreover, the relationship of these species to the subgenus *Sphacelaria* has not yet been studied.

Sphacelaria is a cosmopolitan genus, but it has its main centres of distribution in Europe (16 species) and southern Australia (15 species according to Womersley, 1967). The number of species occurring in Japan cannot be estimated because of the deviating species concept used by Takamatsu (1943) and Noda (in papers published between 1966 and 1975). In Japan the same subgenera as in Europe can be found. In Australia most species, apart from those fitting the almost cosmopolitan subgenus *Propagulifera*, probably belong to one or two (not yet described) separate subgenera.

Reproduction and life-history

For a survey of observed reproductive structures see table V.

The inadequate knowledge of life-histories in *Sphacelariaceae* only permits preliminary suggestions about possible differences between the subgenera of the genus *Sphacelaria*. In the subgenera *Sphacelaria*, *Pseudochaetopteris*, and *Battersia*, unilocular and plurilocular zoidangia have been observed in most species. Plurilocular zoidangia always had loculi of equal size within one species. Fusion of zoids has never been observed in these subgenera. Occasionally unilocular and plurilocular zoidangia occur on the same plant (*S. plumosa*, *S. plumigera*). In several other species (*S. radicans*, *S. caespitula*, *S. nana*, *S. mirabilis*) plants bearing unilocular zoidangia regularly alternate with plants bearing plurilocular zoidangia. Therefore the occurrence of both neutral (or asexual) plurilocular zoidangia and plurilocular isogametangia can not be excluded in these subgenera.

In the subgenus *Propagulifera*, plurilocular zoidangia with small loculi as well as plurilocular zoidangia with larger loculi have been observed in several species. These appeared to be microgametangia and macrogametangia, respectively, in *S. rigidula* (Van den Hoek & Flinterman l.c.). Earlier Sauvageau (1898) concluded this to be the case for *S. cirrosa* ecad *hystrix* (as *S. hystrix*), but his evidence was incomplete and less convincing. Sizes of loculi mentioned in literature as well as sizes measured in herbarium specimens suggest the occurrence of intermediates between plurilocular micro- and macrozoidangia in *S. rigidula*, *S. tribuloides* and *S. cirrosa* (in the ecads *bipinnata*, *cirrosa*, and *hystrix*). It is imaginable that these intermediates may either represent asexual or neutral plurilocular zoidangia or plurilocular isogametangia. The results of the investigations of Papenfuss (1934) on *S. cirrosa* ecad *bipinnata* (as *S. bipinnata*), though not convincing, suggest the occurrence of both kinds of plurilocular structures in that taxon. In several species (e.g. *S. brachygonia*, *S. plumula*, *S. fusca*) plurilocular zoidangia have not been observed so far. Usually unilocular zoidangia are very rare in these species, but propagules are common. In these species propagation is probably exclusively or almost exclusively vegetative. In other species of subgenus *Propagulifera* (e.g. *S. cirrosa*, *S. rigidula*) in which reproduction by zoids is less exceptional, vegetative propagation by propagules is usually still more common. The successful method of dissemination and multiplication by the vegetative propagules seems to suppress the necessity to maintain the more cumbrous sexual reproduction. In species with a wide geographic distribution and which occur in a wide range of habitats, however, sexual reproduction and asexual reproduction by zoids still occur rather often.

TABLE V. First published descriptions of reproductive structures in Sphacelariaceae

species of Sphacelaria	unilocular zoidangia	plurilocular zoidangia	presumed gametangia	propagules
1. S. reticulata	-	-	-	-
2. S. radicans	Dillwyn 1809	Kuckuck 1894	-	-
3. S. caespitula	Pringsheim 1874	Pringsheim 1874	-	-
4. S. nana	Traill 1887	Kuckuck 1897	-	-
5. S. plumosa	Kjellman 1875	Areschoug 1875	-	-
6. S. plumigera	Dillwyn 1809	Prud'h. v. R. 1968	-	-
7. S. arctica	Kjellman 1877a	Kjellman 1877a	-	-
8. S. racemosa	Greville 1824a	this paper	-	-
9. S. mirabilis	Batters 1889	Wilce & Grocki 1977	-	-
10. S. tribuloides	Sauvageau 1903	Hauck 1878	this paper	Meneghini 1840a
11. S. brachygonia	John & de Graft - Johnson 1974	-	-	Reinke 1891
12. S. plumula	Sauvageau 1901	-	-	Zanardini 1865
13. S. rigidula	Askenasy 1888	Askenasy 1888	Sauvageau 1900	Kützing 1855
14. S. fusca	-	-	-	Harvey 1841
15. S. cirrosa	Dillwyn 1806	Menehini 1843 (?)	Sauvageau 1898	J. Agardh 1836
16. S. sympodiocarpa	Sauvageau 1900	-	-	-
17. Sphacella subtilissima	Reinke 1890a	-	-	-

Chromosome numbers. Earlier chromosome counts in *Sphacelaria* species and methods for chromosome counts have been discussed above (p. 22). My own results were not very satisfactory. Estimates of chromosomes of diploid nuclei of *S. rigidula* (in the same culture as used by Van den Hoek and Flinterman) varied between 35 and 46 (7 counts; see fig. 552; 553) and this is somewhat less than the estimates of Van den Hoek & Flinterman (45–60).

I made incidental chromosome counts of the following species.—*Sphacelaria cirrosa* (22–24 in three counts of one slide: fig. 643, and 28–34 in three counts of another slide: fig. 644).—*Sphacelaria plumigera* (12, presumably the haploid number, seven counts in young unilocular zoidangia: fig. 316).—*Sphacelaria mirabilis* (8, presumably the haploid number, 12 counts in young unilocular zoidangia: fig. 421 and plate 2a).

Systematic position

Delimitation of the genus. The genus *Sphacelaria* can quite easily be separated from *Sphacella*, the only other genus in the family. The aberrant species *S. reticulata* with its dichotomies and *S. mirabilis* which is solely represented by its perennial basal crust, have been placed in separate and monotypic genera by Reinke and Sauvageau respectively. As explained before (p. 41) both species have to be incorporated in the genus *Sphacelaria*. *Sphacella* is a genus in which the only species can be considered as a *Sphacelaria*-like alga lacking regular formation of secondary segments and also lacking longitudinal divisions in the segments. Sauvageau (1903) incorporated the species of the monotypic genera *Battersia*, *Chaetopteris*, and *Sphacella* (but not *Disphacella*) in his descriptions and key to the species of the genus *Sphacelaria*. In this way he suggested that he considered these monotypic genera as aberrant species of the genus *Sphacelaria*. Consequently *Battersia* can be considered as a *Sphacelaria* species with a polystromatic basal crust which has lost its erect filaments. Similar basal crusts, devoid of erect filaments have been found in *S. caespitula*. These basal crusts bore unilocular zoidangia and were originally described as a species in a separate genus: *Sphaceloderma helgolandicum* Kuckuck (1894). From a similar point of view *Sphacella* can be considered as a species in the genus *Sphacelaria* which has not yet developed longitudinal walls or, on the contrary, which has lost its longitudinal walls during evolution. Comparable speculations have been discussed in earlier papers (Sauvageau, 1903, p. 93 = R. 264 and 1903, p. 345 = R. 280; Svedelius, 1911, p. 148; Oltmanns, 1922, p. 85–90).

Using the same concept for a discussion of the genus *Disphacella* may result in considering *Disphacella reticulata* as a *S. radicans*-like member of the genus *Sphacelaria* with dichotomous apical cells.

Classification

In an earlier paper (Prud'homme van Reine, 1978) I constructed a phenetic system in the *Sphacelariales* based upon a numerical taxonomic approach. For *Sphacelaria* this resulted in the distinction of groups quite precisely agreeing with subgenera distinguished on the basis of 'intuition' (compare f. 2 of that paper with its figures 3D, 4D, and 5D).

The phyletic-cladistic system constructed in the present paper (see p. 40 and fig. 25) resulted in the distinction of similar groups in the genus *Sphacelaria*. The inclusion of the former genera *Battersia* and *Disphacella* in the genus *Sphacelaria*, which can be founded on the results of the phyletic-cladistic procedure, is also in agreement with my earlier 'intuitive' classification and for *S.* (*Battersia*) *mirabilis* also with results of some numerical taxonomic procedures (see Prud'homme van Reine, 1978, f. 4D). For unattached taxa (unattached *Sphacelaria* as well as unattached *Halopteris*, *Cladostephus*, and *Disphacella*) the numerical taxonomic procedures gave less usable results.

The subgenera *Pseudochaetopteris* and *Propagulifera* are in all probability well-founded natural groups with consistent sets of joint characters. The coherence of the species in the subgenus *Sphacelaria* is less obvious, but it seems more desirable to unite these 4 species into one single subgenus than to place them into two or more small separate subdivisions of the genus *Sphacelaria*. In the argumentation scheme (fig. 24) and in the subsequent phylogenetic diagram (fig. 25), resulting from the phyletic-cladistic procedure, the place of *S. mirabilis* cannot be established properly, because so many characteristics are missing. A place in the subgenus *Pseudochaetopteris* can be justified because there are two synapomorphies with the other species of that subgenus. Further information about the relationship of *S. mirabilis* to the other species in the subgenus *Pseudochaetopteris* is lacking, however, and thus it is not possible to indicate the exact position of the bifurcation separating *S. mirabilis* its nearest relatives. Since *S. mirabilis*, not possessing vegetative erect filaments, is so different from the other species of *Sphacelaria*, it is desirable to place it in a separate taxon of infra-generic level. This can be a separate subgenus as well as a separate section. Nothing being against it, I consider *S. mirabilis* as the only species of the subgenus *Battersia*.

In the subgenera *Pseudochaetopteris* and *Propagulifera* the distinction of smaller groups (sections) is proposed to express the supposed closer relationships within these sections. It may be expected that several extra-European species will in future become included within sections of subgenus *Propagulifera*.

KEY TO THE SUBGENERA AND SECTIONS IN SPHACELARIA[4]

1a. Erect vegetative filaments absent . . . . **III. Subgenus Battersia**
b. Erect vegetative filaments usually present 2
2a. Structure of main filaments of periclinal type (cross-section); many secondary transverse cell-walls; no propagules (II. Subgenus *Pseudochaetopteris*) 3
b. Structure of main filaments of radial type (cross-section); secondary transverse cell-walls frequent or scarce; propagules absent or present 4
3a. Main erect filaments of attached specimens corticated by a compact sheath of rhizoids; branching pinnate . . . . **IIa. Section Pseudochaetopteris**
b. Main erect filaments of attached specimens not corticated or with quite open or irregular cortication; branching irregular or irregularly pinnate . . . . **IIb. Section Racemosae**
4a. Secondary transverse cell-walls usually frequent (but scarce in *S. nana*); the scarce laterals distant from the apical cell of the erect filaments; no propagules . . . . **I. Subgenus Sphacelaria**
b. Secondary transverse cell-walls usually scarce; laterals scarce or frequent, usually arising near the apical cells of the erect filaments; propagules usually present (propagules are absent in *S. sympodiocarpa*, a species not yet incorporated in a subgenus) (IV. Subgenus *Propagulifera*) 5
5a. Propagules tribuliform . . . . **IVa. Section Tribuloides**
b. Propagules with long arms 6
6a. Propagules with cylindrical arms and without terminal hairs . . . . **IVb. Section Furcigerae**
b. Propagules with fusiform arms or with cylindrical arms which are slightly constricted at their base; usually with terminal hairs . . . . **IVc. Section Propagulifera**

KEY TO THE SPECIES (AND SOME ECADS)[5]

1a. Propagules present 2
b. Propagules absent 7
2a. Propagules with long arms 3
b. Propagules tribuliform or ellipsoid 5
3a. Propagules with constricted arms and usually with terminal hair (see also table XVII; for ecads of *S. cirrosa* see p. 257) . . . . **15. S. cirrosa**
b. Arms of propagules not constricted; no terminal hair 4
4a. Main filaments usually more than 50 µm wide (see also table XVII) . . . . **14. S. fusca**
b. Main filaments usually less than 50 µm wide (see also table XVII) . . . . **13. S. rigidula**
5a. Branching pinnate (see also table XIV) . . . . **12. S. plumula**
b. Branching scarce; irregularly helicoid 6
6a. Propagules solitary and tribuliform or obtriangular (see also table XIV) . . . . **10. S. tribuloides**
b. Propagules often geminate and transverse ellipsoid or transverse fusiform (see also table XIV) . . . . **11. S. brachygonia**
7a. Plants composed of a thick, polystromatic basal crust, without erect filaments when sterile and with sori of unilocular zoidangia on branched or unbranched stalks when fertile (see also the *Sphacelodermа* growth-form of *S. caespitula*) . . . . **9. S. mirabilis**
b. Erect filaments present 8
8a. Branching dichoblastic; plants without basal holdfast . . . . **1. S. reticulata**
b. Branching hemiblastic or laterals arising from peripheral cells; attached or unattached 9
9a. Many secondary transverse cell-walls in the secondary segments of the main filaments 10
b. Secondary transverse cell-walls in the secondary segments of the main filaments scarce or absent 18
10a. Branching pinnate or irregularly pinnate 11
b. Branching irregular or irregularly helicoid 14
11a. Branching strictly pinnate; usually with a thick cortex in the lower parts of the main filaments, formed by coalescent rhizoids firmly attached to each other 12
b. Branching irregularly pinnate; cortex absent or formed by few to many appressed rhizoids, which are loosely attached to each other (see also table XIII, VI, and X) . . . . **7. S. arctica**

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[4] For terminology see the glossary, p. 262.
[5] For terminology see the glossary, p. 262.

12a. Cortex absent; unattached specimens (see also table XIII) . . . . . 6a. S. plumigera ecad pinnata
b. Cortex present; specimens usually attached 13
13a. Cortex formed by rhizoids sprouting from most peripheral cells of the main filaments; zoidangia on special small laterals, which arise from the cortex . . . . 5. S. plumosa
b. Cortex formed by rhizoids sprouting only from the few peripheral cells of the inferior secondary segments which are located in the plane of branching of the erect filaments; zoidangia on specialized laterals which arise from the uncorticated terminal and subterminal erect filaments (see also table XIII and VII) . . . . 6. S. plumigera (excl. ecad pinnata)
14a. Medullar cells present in the main filaments; pericysts not present; zoidangia usually arranged in racemes (see also table VI) . . . . 8. S. racemosa
b. No medullar cells present in the main filaments; pericysts present, conspicuous or inconspicuous; zoidangia solitary or geminate 15
15a. Main filaments usually more than 30 μm wide (but see table X); pericysts conspicuous 16
b. Main filaments usually less than 30 μm wide (see also table X); pericysts usually inconspicuous 17
16a. Attached; laterals often parallel to the main erect filaments; zoidangia geminate (see also table VII, VI, and X) . . . . 2. S. radicans (excl. ecad libera)
b. Not attached; laterals divaricate, often perpendicular to the main filaments; always sterile . . . . 2a. S. radicans ecad libera
17a. Almost all cells of the main filaments with secondary transverse cell-walls; attached by a polystromatic basal crust; zoidangia large and conspicuous; deep water species (see also table VII and X) . . . . 3. S. caespitula
b. Always many cells present without secondary transverse cell-walls; attached by creeping stolons or by a mono- or polystromatic basal disc; zoidangia small and usually inconspicuous; a species found in the upper tidal zone (but deeper in the Baltic) (see also table X and XI) . . . . 4. S. nana
18a. Branching pinnate or irregularly pinnate 19
b. Branching scarce to frequent, helicoid or irregularly helicoid 20
19a. Branching strictly pinnate; main filaments usually more than 75 μm wide; usually found in deep water or in caves . . . . 12. S. plumula
b. Branching irregularly pinnate; main filaments usually less than 75 μm wide; often found in pools in the tidal zone or in shallow water (for ecads of *S. cirrosa* see p. 257) . . . . . . 15. S. cirrosa
20a. Main filaments less than 30 μm wide 21
b. Main filaments more than 30 μm wide 24
21a. Plants forming quite open, felty mats or felty patches, which are quite flaccid; attached by stolons or by a mono- or polystromatic basal disc; zoidangia solitary; usually found in the upper tidal zone (but deeper in the Baltic) (see also table X and XI) . . . . 4. S. nana
b. Plants forming dense bushes, cushions or mats, which are quite rigid; attached on substrates by stolons or by small basal discs or partly endophytic; zoidangia solitary or in secund rows . . . 22
22a. Plants less than 3 mm high; all filaments less than 20 μm wide; zoidangia in secund rows; rare deep-water species of southwestern Europe . . . . 16. S. sympodiocarpa
b. Plants usually more than 3 mm high; main filaments usually more than 20 μm wide; zoidangia solitary 21
23a. Usually few to several laterals transformed into rhizoids; branching scarce to rich (see also table X and XI) . . . . 13. S. rigidula
b. Laterals transformed into rhizoids absent; branching absent to scarce (see also table XI) . . . . 10. S. tribuloides
24a. Laterals usually determinate (but see also table XVII) (for ecads of *S. cirrosa* see p. 257) . . . . 15. S. cirrosa
b. Laterals usually indeterminate 25
25a. Main filaments usually less than 50 μm wide 23
b. Main filaments usually more than 50 μm wide 26
26a. Erect filaments arising from a polystromatic basal holdfast; branching usually scarce; rare species of southern Europe . . . . 11. S. brachygonia
b. Erect filaments arising from monostromatic basal disc; branching scarce to rich; rare species of western Europe (see also table XVII) . . . . 14. S. fusca

ACCEPTED SUBGENERA, SECTIONS, AND SPECIES

I. Subgenus Sphacelaria

Sphacelaria Lyngbye in Hornemann (1818) t. 1600 (as genus).—Type species: *S. reticulata* Lyngbye. Sphacélariacées hemiblastées sous-groupe Acladées Sauvageau (1903) 334 = R. 268, (1909) 67, t. 11.—Sphacélariacées opséblastées Sauvageau (1914) 606.—*Sphacelaria* subgenus *Acladus* Prud'homme van Reine (1978) 309 & 312 (nom. inval.).—Type species: *Sphacelaria radicans* (Dillwyn) C. A. Agardh.

For discussion see the section 'Systematic position' of *S. radicans* (p. 79) and the sections 'Notes on nomenclature' and 'Systematic position' of *S. reticulata* (p. 61 & p. 62).

Thalli plerumque parvi (breviores quam 2 cm), saepe formantes tegetes extensos, ad basin disco unistratoso vel pluristratoso, vel stolonibus repentibus vel crusta pluristratosa praediti, vel liberi. Filamenta lateralia plerumque pauca et indeterminata emersa e segmentis secundariis maturis et ergo distantia a cellula apicali filamentorum erectorum, vel dichotoma emersa e cellula apicali filamentorum. Paucae vel multae parietes secundariae transversales et paucae vel plures parietes longitudinales formantes figuram radialem in segmentis secundariis filamentorum principalum. Pili nulli vel quaterni vel bini, rarius solitarii. Propagula nulla.

Plants are usually small (less than 2 cm high), often forming extensive mats. They are attached by a monostromatic or a polystromatic basal disc, by creeping stolons or by a polystromatic basal crust, or are unattached. The usually scarce and indeterminate laterals arise from the mature secondary segments and as a consequence distantly from the apical cell of the erect filaments or by dichoblastic branching. The secondary segments of the main filaments contain few to many secondary transverse walls and few to several longitudinal walls, which arise in a radial pattern. Hairs are absent or occur in fours or in pairs, rarely solitary. Propagules are absent.

1. **Sphacelaria reticulata** Lyngbye in Hornemann—**Fig. 44–59**

Sphacelaria reticulata Lyngbye in Hornemann (1818) t. 1600; Lyngbye (1819) 106; J. Agardh (1848) 33; Kützing (1849) 465; Areschoug (1850) 393.—*Sphacelaria cirrosa* var. *δ reticulata* C. Agardh (1824) 165; Greville (1827) t. 317; C. Agardh (1828) 28; Hornemann (1837) 694; Reinke (1892) 65.—*Sphacelaria pennata* var. *γ reticulata* Steudel (1824) 377.—*Disphacella reticulata* Sauvageau (1903) 345 (= R. 280), f. 51–53; Lund (1950) 64; Prud'homme van Reine (1978) 302.—Type: *Lyngbye s.n., 'Ceramium ! reticulatum ad interim.* Febr. 1861. *inveni in Fuco plicatos in habitaculis amphibitarum eti ad litt.* Hofmansgave. *Cum fructu legi. Delineari'* (C). See also notes on nomenclature.

Plants forming a minute intricate net-work (fig. 44) between other algae. The colour of fresh specimens is not known. The unattached filaments, without attachment-structures are in the rigid basal region straight or curved and almost unbranched (fig. 45–47; f). The narrow apical parts as well as the scarce laterals are repeatedly divided by dichoblastic branching (fig. 45–55). Most dichotomies are situated in one plane (fig. 48).

The dimensions of the apical cells and of the secondary segments are quite variable. In the main filaments the secondary segments are usually longer than wide or as long as wide (fig. 56; 57); in the dichoblastic filaments most secondary segments are much shorter than they are wide (fig. 48; 54). The superior secondary segments are often shorter than the inferior secondary segments (fig. 56; 57).

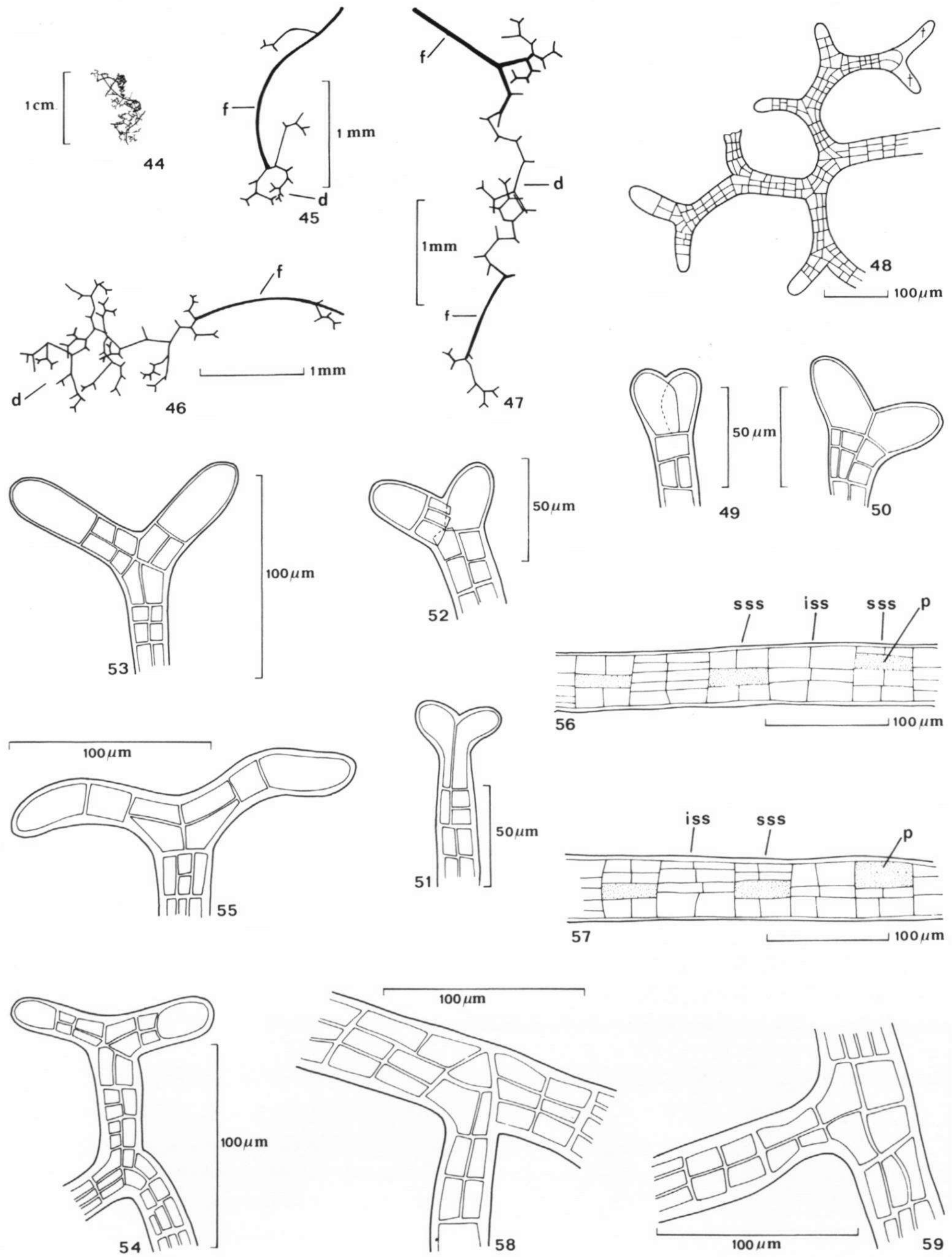


Fig. 44–59. S. reticulata. 44–47. Habit; 48–55. Dichoblastic branching; 56–59. Rigid filaments. d. dichoblastic narrow apical parts; f. rigid main filament; iss. inferior secondary segment; p. pericyst; sss. superior secondary segment. 45. Hofmansgave, *Hofman Bang* (KIEL, dry); 46–50, 52, 53. Hofmansgave between other algae (BR, soaked); 51, 54–59. Hofmansgave (Ag. 45527 in LD, soaked).

The secondary segments of the main filaments are subdivided by radial and transverse walls into a parenchymatic tissue, without a subdivision into a medulla and peripheral cells. In a superior secondary segment one of the larger cells can function as branch-initial or pericyst (fig. 56; 57).

In lateral view 1–4 longitudinal walls can be observed in secondary segments and the narrow peripheral cells are usually subdivided by a transverse wall. Hairs and rhizoids are lacking.

Propagules and zoidangia are not known.

Dimensions: Plants up to 1 cm long (usually less). Angle of ramification of dichotomic branching (80–) 90–120 (–150)°. Diam. of main filaments 40–50 (–55) μm, of dichoblastic filaments 22–30 μm. Height of secondary segments 40–70 μm and 5–25 (–30) μm respectively. Pericysts 40–50 (–53) X 15–25 μm.

Distribution. Only one locality, Hofmansgave near Hasmark, Fyn, Denmark. See fig. 43.

DENMARK. Samsö area. Hofmansgave, washed up, (as *Ceramium reticulatum*), *Lyngbye*, 2/1816 (C, PC) and (as *S. spinulosa*), *Lyngbye*, without date (CN, PC; all mixed with *Stypocaulon spinulosum* and *S. cirrosa* ecad *patentissima*). Nordenstrand, Hofmansgave, washed up (as *S. spinulosa*), *Rosenberg*, 15 & 26/9/1846 (C, mixed with *S. cirrosa* ecad *patentissima*, *S. plumigera* ecad *pinnata* and *Stypocaulon spinulosum*). Hofmansgave, washed up, *Rosenberg*, 3/2/1867 (C, LD).

Notes on nomenclature. (1) Sauvageau (1903, p. 345 = R. 280 and 1904, p. 384) suggested that this alga can perhaps be considered as a variety *patentissima* of a species which is not known in the attached state. He also suggested (p. 384) a connection with *S. olivacea* (= *S. caespitula*).

(2) The short description of *S. reticulata* in 1818 can be considered as a descriptio generico-specifica. All other new species and new combinations in the genus *Sphacelaria* were described later (the earliest by Lyngbye in 1819). So *S. reticulata* is the type species of the genus *Sphacelaria* Lyngbye.

Notes on morphology. The dichoblastic branching was detected and described by Sauvageau (1903, p. 338–339 = R. 272–273 and p. 344 = R. 279). The apical cell enlarges and broadens and divides in two by a longitudinal wall (fig. 49–51). Each half of the original apical cell functions as a new apical cell and forms a new filament (fig. 52–55). This dichotomous branching is repeated several times in the apical parts of the plants (fig. 45–48). Occasionally one of the halves of the original apical cell does not grow out immediately but may do so later. So these halves function as dormant initials (see fig. 53E in Sauvageau, 1903), and are very similar to pericysts.

Most cells in the secondary segments of the rigid main filaments become subdivided by a transverse wall (fig. 56; 57). In the superior secondary segments one large cell will often not become divided. The contents of these undivided cells (pericysts) are much darker than the contents of other cells. These pericysts or dormant branch-initials occasionally form new laterals, which are usually almost perpendicular to the main filament (fig. 58; 59).

Notes on ecology. *Sphacelaria reticulata* has only been found washed ashore on the beaches near Hofmansgave, together with a large amount of leaves of *Zostera marina* and also other *Sphacelariales* viz. *Stypocaulon spinulosum*, *Sphacelaria cirrosa* ecad *patentissima*, and *Sphacelaria plumigera* ecad *pinnata*. These other algae can be found in unattached intricate masses in the *Zostera* beds. So probably *S. reticulata* occurred in the same habitat. This alga has not been found since 3/2/1867. In April 1970 and in August 1977 I visited the coasts near Hofmansgave. I found a lot of *Zostera marina* and in April also many *Zostera* leaves in the drift. I did not find any of the unattached *Sphacelariales*, however. It is possible that the population of unattached *Sphacelariales* in and around Odensefjord has disappeared together with *Zostera marina* as a result of the seagrass-disease occurring after 1930 and has not returned again.

Systematic position. This curious and rare species, of which living specimens were never studied, is characterized by its dichoblastic branching, a unique feature within *Sphacelaria*. Therefore it cannot be considered as a subspecific taxon of *S. cirrosa* (see above).

On the other hand the morphology of its filaments much resembles that of *S. radicans* (compare fig. 75 with fig. 57). One isolate of unknown origin (culture 67-129-2), of an attached *S. radicans* showed occasional dichotomies in culture (fig. 72; 73). The ontogeny of these dichotomies, however, could not be unravelled. Therefore I now place *S. reticulata* in the vicinity of *S. radicans* and this in contrast to my former opinion, according to which the species should be ranged under the genus *Disphacella* of the monotypic family *Disphacellaceae* (Prud'homme van Reine, 1971, 1978). See also the discussion of the cladistic system of the *Sphacelariaceae* (p. 41).

The suggestion by Sauvageau (1904, p. 384) with respect to a possible relationship to *S. olivacea* (= *S. caespitula*) cannot be endorsed because the diameter of the filaments of the latter species is much smaller than in the rigid parts of *S. reticulata.*

2. Sphacelaria radicans (Dillwyn) C. A. Agardh—Fig. 60–117, plate 3a

Conferva radicans Dillwyn (1809) 58, t. C; Smith & Sowerby (1810) t. 2138.—*Sphacelaria radicans* C. Agardh (1824) 165; Harvey (1833) 324, (1848) t. 189; Kützing (1849) 463, (1855) 26, t. 87, f. III; Hauck (1885) 343 (*p.p.*); Traill (1887) 77; Holmes (1887) 80; Reinke (1890a) 207, (1891) 8, t. 3, f. 1; Kuckuck (1894) 229, f. 4; De Toni (1895) 501; Sauvageau (1901) 34 (= R. 63); Batters (1902) 38; Jónsson (1903) 159; Kylin (1907) 62 (*p.p.*); Sauvageau (1909) 64, f. 10, 11; Newton (1931) 189; Hamel (1938) 249; Waern (1945) 400; Kylin (1947) 27; Lund (1950) 17, f. 2; Waern (1952) 96, f. 38, 39; A. Zinova (1953) 114; Sundene (1953) 157; Irvine (1956) 38; Jorde & Klavestad (1960) 99; De Haas-Niekerk (1965) 158, f. 51–63; Jaasund (1965) 68; Pankow (1971) 162 (excl. f. 187–188); Prud'homme van Reine (1974) 174; Russell & Fletcher (1975) 766; Kornmann & Sahling (1977) p. 154, f. 83 (excl. B); Prud'homme van Reine (1978) 303.—*Sphacelaria cirrhosa* var. *ζ simplex* C. Agardh (1828) 29.— *Sphacelaria radicans* forma *typica* Batters (1889) 60.—*Sphacelaria olivacea* var. *radicans* J. Agardh (1848) 31; Areschoug (1850) 395; Crouan (1852) Exsicc. n. 32; Pringsheim (1874) 166.—Lectotype: *Mrs. Hutchins s.n.*, Leg. W. Borrer jr. in Ed. Forster's herbarium (BM sheet 142.832).—See notes on nomenclature 1, 3, and 4.

Conferva olivacea Dillwyn (1809) 57, t. C; Smith & Sowerby (1810) t. 2172; W. Hooker (1821) 83.—*Sphacelaria olivacea* Greville (1824a) t. 96, (1824b) 314 (*p.p.*); C. Agardh (1828) 30; Harvey (1833) 324; J. Agardh (1848) 30 (*p.p.*); Kützing (1855) 28, t. 94, f. 1; De Toni (1895) 500 (*p.p.*); Van den Hoek (1958b) 192.—Type: *Borrer s.n.*, Papa Westray, Orkneys (BM, lecto; LD).—See notes on nomenclature 2, 3, and 5.

Sphacelaria pusilla Kützing (1845) 239, (1855) p. 26, t. 87, f. II.—Type: *Kützing 6b*, Heligoland (L sheet 937.71-485, holo; HBG).

Sphacelaria olivacea var. *caespitosa* Pringsheim (1874) p. 166 (*p.p.* viz. t. X, f. 3 and 10).—Type: probably lost.

Sphacelaria radicans var. *coactilis* Sauvageau (1901) 36 (= R. 65).—Holotype: *Traill s.n.*, Joppa, Fife, about the high water mark of neap tides, 19/12/1886 (TCD).
Sphacelaria radicans forma *aegagropila* Hylmö (1916) Exsicc. 42 (*nom. nud.*).

Plants forming dense attached carpets (fig. 60) or irregular bushes of ragged appearance (fig. 61), dark brownish olive or dull greenish to olive, turning blackish when dried. The plants are solitary, gregarious, or caespitose, and quite rigid. They are epilithic, or occur on sediment bottoms among halophytes or occasionally they are epiphytic. Sometimes they form loose-and-entangled thread-bundles (fig. 62). Several sparingly branched filaments arise from many small crowded basal discs (fig. 63; 72).

In early stages the basal part is a circular basal disc with marginal growth. The young disc is monostromatic and consists of a number of radiating, branched, coalescent, creeping filaments with apical growth. In later stages the basal disc may become polystromatic by upward growth and subsequent division of the intercalary cells of the coalescent creeping filaments (fig. 64; 65; 402). The polystromatic discs are never more than a few cells thick (fig. 66). Usually several marginal cells of the small basal discs form stolons (fig. 63; 72) which grow into new small discs from which several new erect filaments will arise (fig. 63; 67).

The erect parts of the plants are composed of many axes and few solitary, almost unbranched, long, hypacroblastic laterals of up to the third order (fig. 68). The scattered laterals are irregularly placed, (never pinnate), usually appressed (fig. 69) and they have indeterminate growth. Occasionally some laterals arise by acroheteroblastic branching (fig. 70) or by dichoblastic branching (fig. 72; 73).

There is usually no difference in growth or dimensions between the axes and the mature laterals, but in the proximal part of the laterals the dimensions are usually smaller. Often a few divaricate rhizoids occur (fig. 68; 69; 71). These divaricate rhizoids never form a complete cortication, but by their intricate growth they bind the filaments of the tufts together.

The dimensions of the inferior and superior secondary segments of the erect filaments are equal to each other and they are often as wide as they are long (fig. 70; 74–77). Occasionally some primary segments in a filament are not divided into secondary ones (fig. 78). The secondary segments and primary segments are subdivided by radial, periclinal, and transverse walls into a parenchymatous tissue, without distinct subdivision into medullar and peripheral cells (fig. 79; 80). In almost all cells transverse walls can be formed and there is no constant number of central cells. One or more of the larger cells which extend from the centre to the periphery and which are mainly located in superior secondary segments, can function as branch-initials or pericysts (fig. 73; 75; 81; 82). In living specimens the pericysts have more transparent contents than other cells, but in dried specimens most pericysts become very dark (fig. 75; 83).

In lateral view (2–) 3–6 (–7) longitudinal walls can be observed in secondary segments and the long peripheral cells are subdivided into shorter ones by 1–3 transverse walls (fig. 69–71). Sometimes secondary longitudinal walls occur in these shorter peripheral cells (fig. 69–71, sl). Some peripheral cells form long unbranched divaricate rhizoids, which are at first perpendicular to the erect filaments, but soon start to grow downwards at an oblique angle (fig. 69r; 71r). Fairly long hairs are common on all filaments of sterile specimens (fig. 63; 70; 76; 84). They are geminate or formed in bundles of four (fig. 76; 84). Most hairs

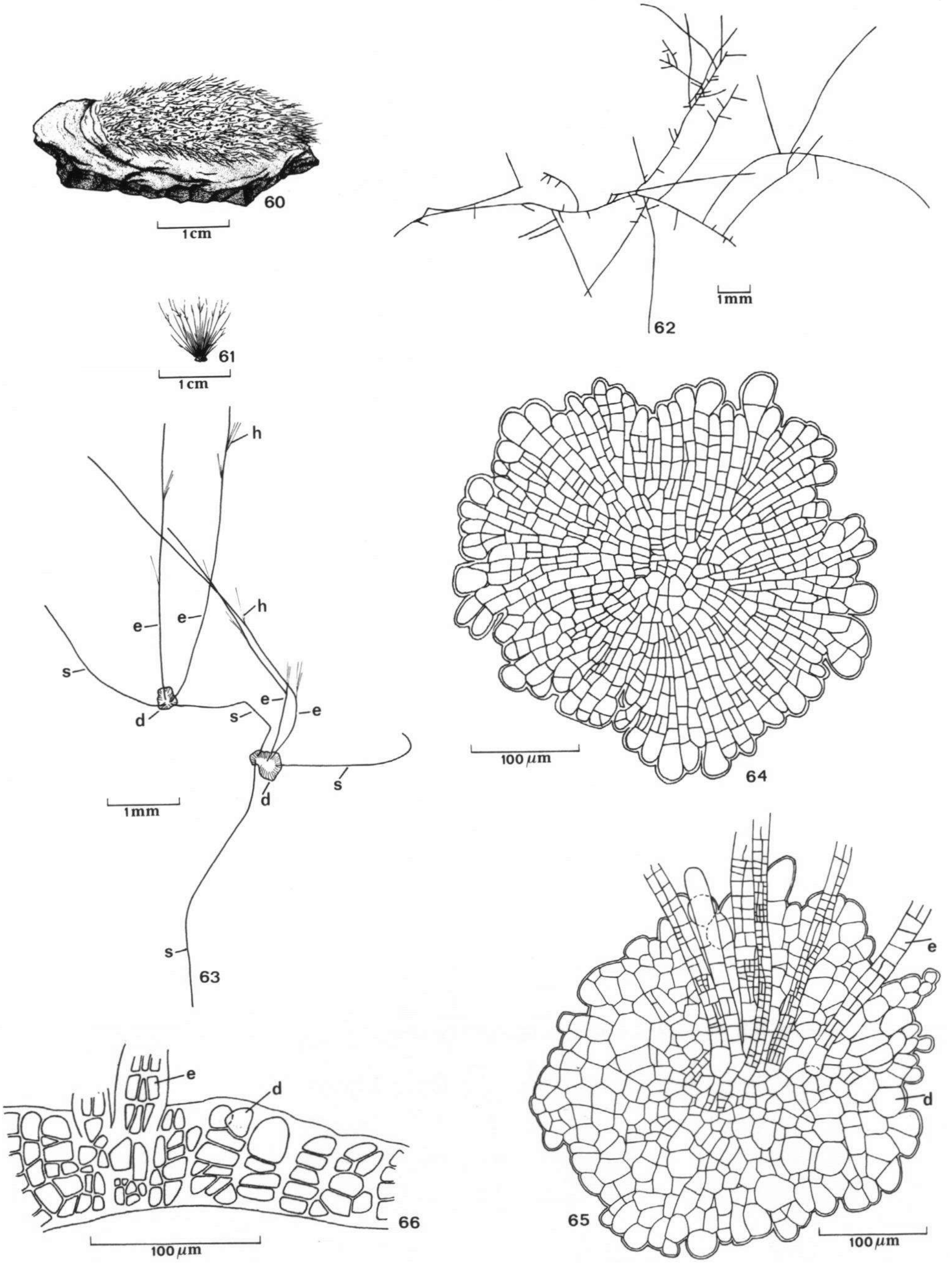


Fig. 60–66. ***Sphacelaria radicans.*** 60–63. Habit; 62. Ecad *libera*; 64, 65. Basal disc of germling from unizoid; 64. Seen from below; 65. Seen from above; 66. Section of basal disc of an adult plant. d. basal disc; e. erect filament; h. hair; s. stolon. 60. Berwick-upon-Tweed, *Fletcher 667* (L, sheet 972.088–208); 61. Cherbourg, *Lenormand* (L, sheet 937.71–623); 62. Putzig (L, sheet 937.71–689); 63. Culture 67-82-4; 64, 65. Culture 67-69; 66. St. Andrews, *Prud'homme van Reine 71-17* (fresh).

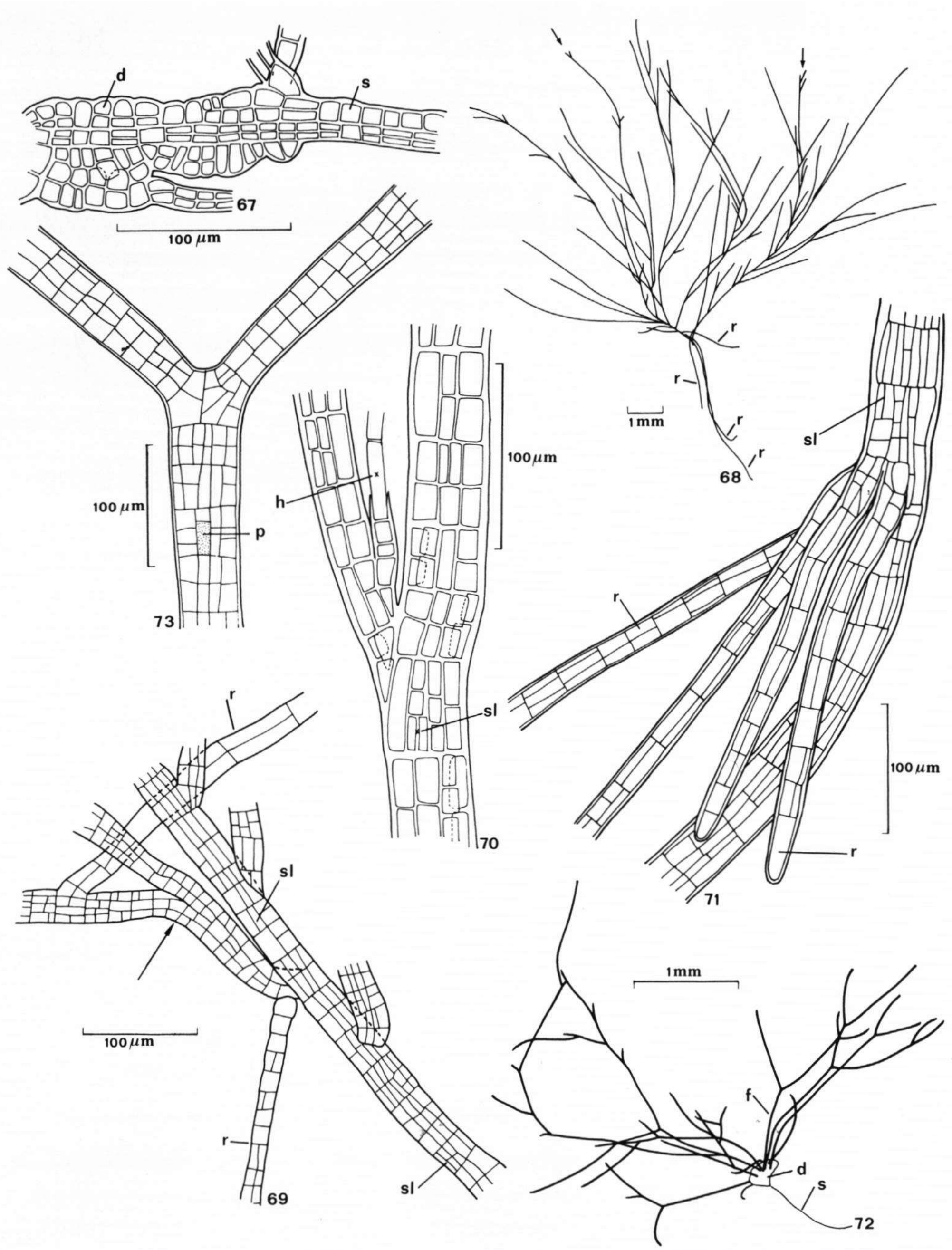


Fig. 67–73. Sphacelaria radicans. 67. Young disc, seen from above; 68, 72. Habit; 68, 69. Hemiblastic branching and filaments replacing damaged apical cell (arrow); 70. Acroheteroblastic branching; 72, 73. Dichoblastic branching. d. basal disc; f. erect filament; h. hair; p. pericyst. 67. Culture 67-59-1; 68. Culture 66-46-1; 69. Culture 67-82-4 (soaked); 70. Culture 67-75-2; 71. Culture 66-4-1; 72, 73. Culture 67-129-2.

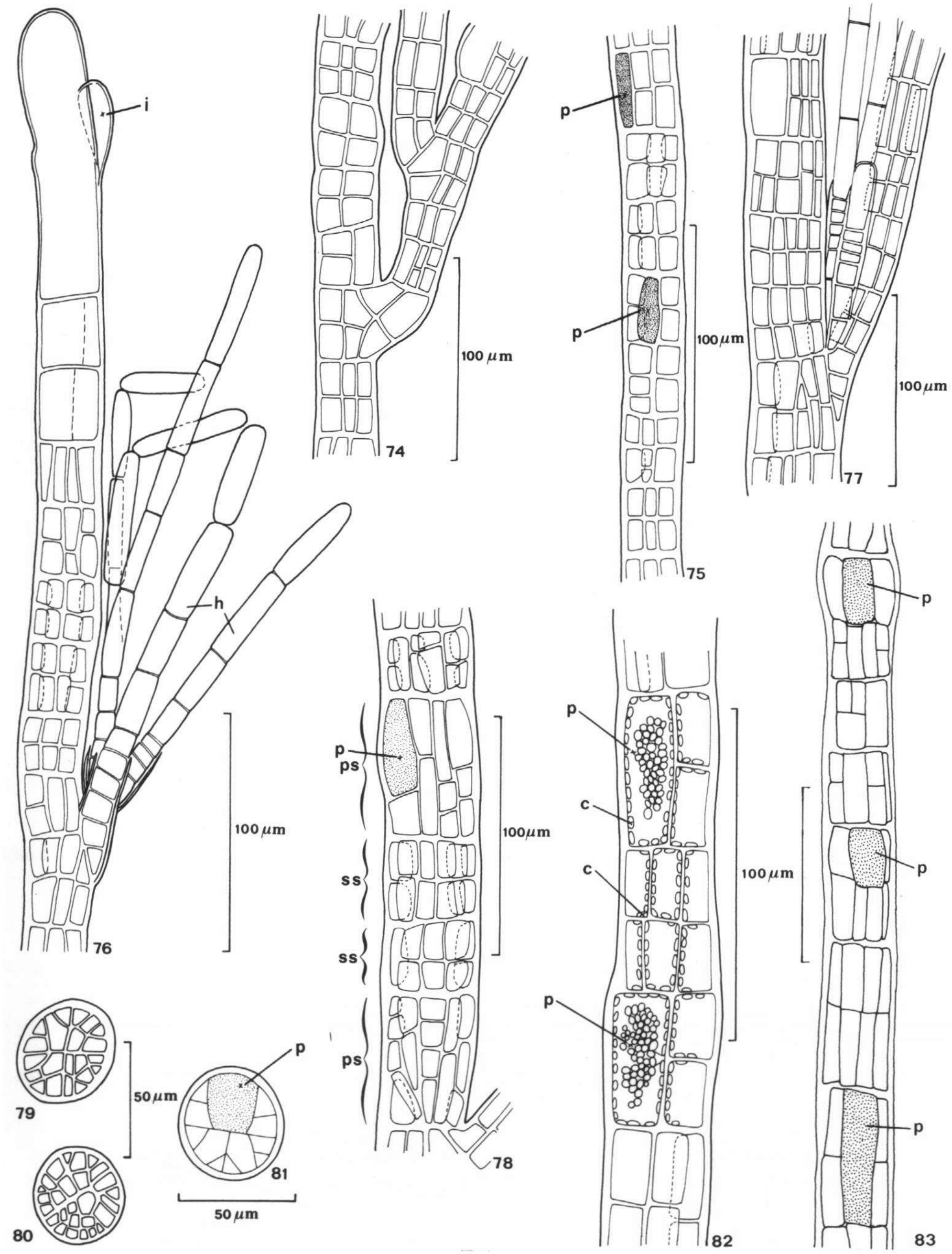


Fig. 74–83. ***Sphacelaria radicans*****,** filaments. 79–81. Cross-sections. c. chloroplast; h. hair; i. lenticular initial cell; p. pericyst; ps. primary segment; ss. secondary segment. 74. Vlissingen *Prud'homme van Reine 71-2-1* (fresh); 75, 76. St. Andrews, *Prud'homme van Reine 71-17* (in formalin); 77. Culture 67-75-2; 78. Culture 66-46-3; 79, 80. Culture 67-9, hand-cut sections; 81. Drøbak, *Prud'homme van Reine 67-75* (permanent microslides); 82. Culture 67-62-3.

are formed by acrohomoblastic branching (fig. 84; 85), but occasionally also by acroheteroblastic branching (fig. 77).

There are no propagules.

The sessile or unicellularly stalked unilocular zoidangia occur singly, in pairs, or in fours on the filaments (fig. 86–91), usually on the proximal parts and sometimes on rhizoids. They are spherical, subspherical, or ovoid when mature, subspherical when young. Unizoids are pear-shaped or somewhat rounded. They have two small chloroplasts and an eye-spot (fig. 92).

Unilocular and plurilocular zoidangia are usually found on separate plants. The plurilocular zoidangia have a stalk with 1–4 segments. They are solitary or arranged in small groups (fig. 93; plate 3a). Plurilocular zoidangia are cylindrical or ellipsoid when mature (fig. 94–96; plate 3a). The plurizoids are pear-shaped and have one curved narrow chloroplast (fig. 97).

Dimensions: Plants up to 2 cm high (usually less) and carpets sometimes covering an area of several m^2. Diam. basal disc 100–400 μm. Stolons 25–50 μm in diam. Rhizoids (10–) 18–25 μm in diam. Angle of ramification 0–20°, in loose-and-entangled specimens 70–90°. Diam. of filaments (19–) 25–60 μm. Height of secondary segments (20–) 30–75 (–85) μm. Hairs diam. 15–20 μm, (with sheath) or 10.5–13 μm (without sheath). Chloroplasts 2–3.5 X 3.5–6 μm in surface view (fig. 98; 99). Pericysts 24–75 X (7–) 9–21 μm. Unilocular zoidangia (40–) 42–65 X (30–) 40–60 μm, stalks 17–21 X 21–23 μm. Unizoids 6–7 μm long. Plurilocular zoidangia 65–115 (–170) X 37–60 (–63) μm, diam. loculi 2.5–6 μm, stalks 21–83 X 11–23 μm. Plurizoids 3.5–4.5 μm long.

Ecad. Ecad *libera.* (fig. 62). The plants are sterile and unattached or loose-and-entangled. Laterals arise perpendicularly or almost so. Pericysts are frequent and usually they each form a lateral.

Distribution. Greenland. Europe: Iceland, Spitzbergen, Norway, Sweden, Finland, Arctic coasts of the U.S.S.R., Poland, Germany, Denmark, The Netherlands, United Kingdom, Eire, French Atlantic coasts.

The species is also known to exist on the Northern American coasts of the Atlantic Ocean and perhaps also in Japan.

European localities have been listed and are given in fig. 109. For an extract of the list of collections and references see below.

GREENLAND. West coast. Christianshaab & Ivigtut: (Jónsson, 1904, p. 41).

ICELAND. Northwest coast. Two collections/references.—Southwest coast. Five collections/references.—North coast. Three references.—East coast. Three references.—South coast. Two references.

SPITZBERGEN. (A. Zinova, 1953, p. 114).

NORWAY. Finmarken. Five collections/references.—Troms. Three collections/references.—Nordland. Three collections.—Tröndelag. Five collections/references.—Möre og Romsdal. Moöya: Bjornsund, (as *Chaetopteris plumosa*), *Gran & Braarud,* 12/8/1931 (O).—Sogn og Fjordane. Solund: Steinsundet, Nora, *Boye*, 2/8/1894 (BG).—Hordaland. More than five collections/references. —Vest-Agder. Two collections.—Vestfold. Four collections/references.—Buskerud. Oslofjord: Tofteholmen, sheltered shadowed localities, 0–0.5 m deep, *Prud'homme van Reine 67–78*, 12/6/1967 (L).—Akershus. Three collections/references.—Ostfold. Two references.

SWEDEN. Bohuslän. More than six collections, amongst which Bahusia: without exact locality, (as *S. cirrosa*), Areschoug, Algae Scand. exs. ser. nov. n. 409 (L, and several other herbaria).—Halland.

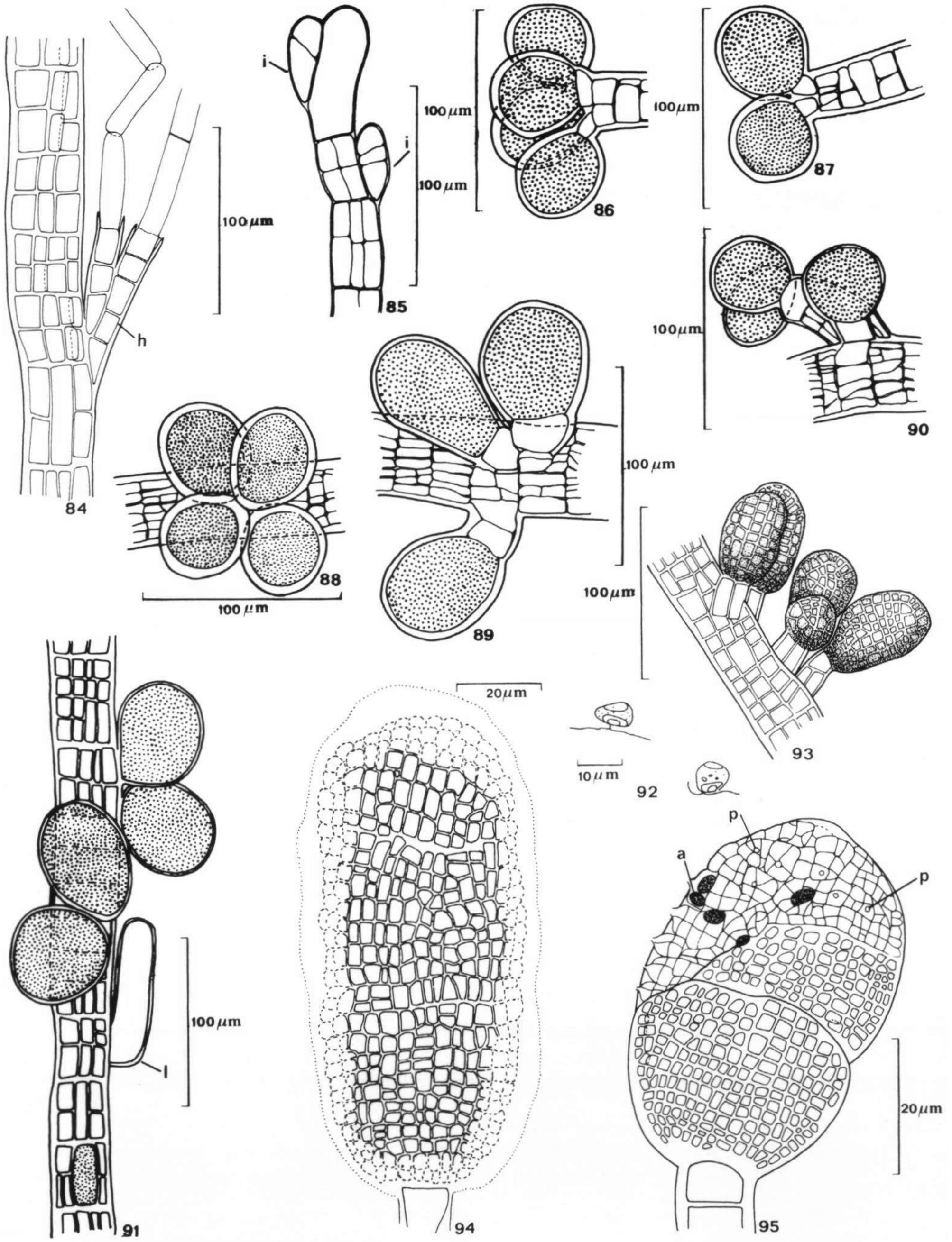


Fig. 84–95. Sphacelaria radicans. 84, 85. Filaments; 86–91. Unilocular zoidangia; 92. Unizoids; 93–95. Plurilocular zoidangia. a. aplanospore (?); h. hair; i. lenticular initial-cell; p. pore. 84. Culture 67-75-2; 85. Culture 66-3-1; 86–90. Holmes, Exsicc. n. 96 (K, soaked); 91–95. St. Andrews, *Prud'homme van Reine 71-17* (fresh).

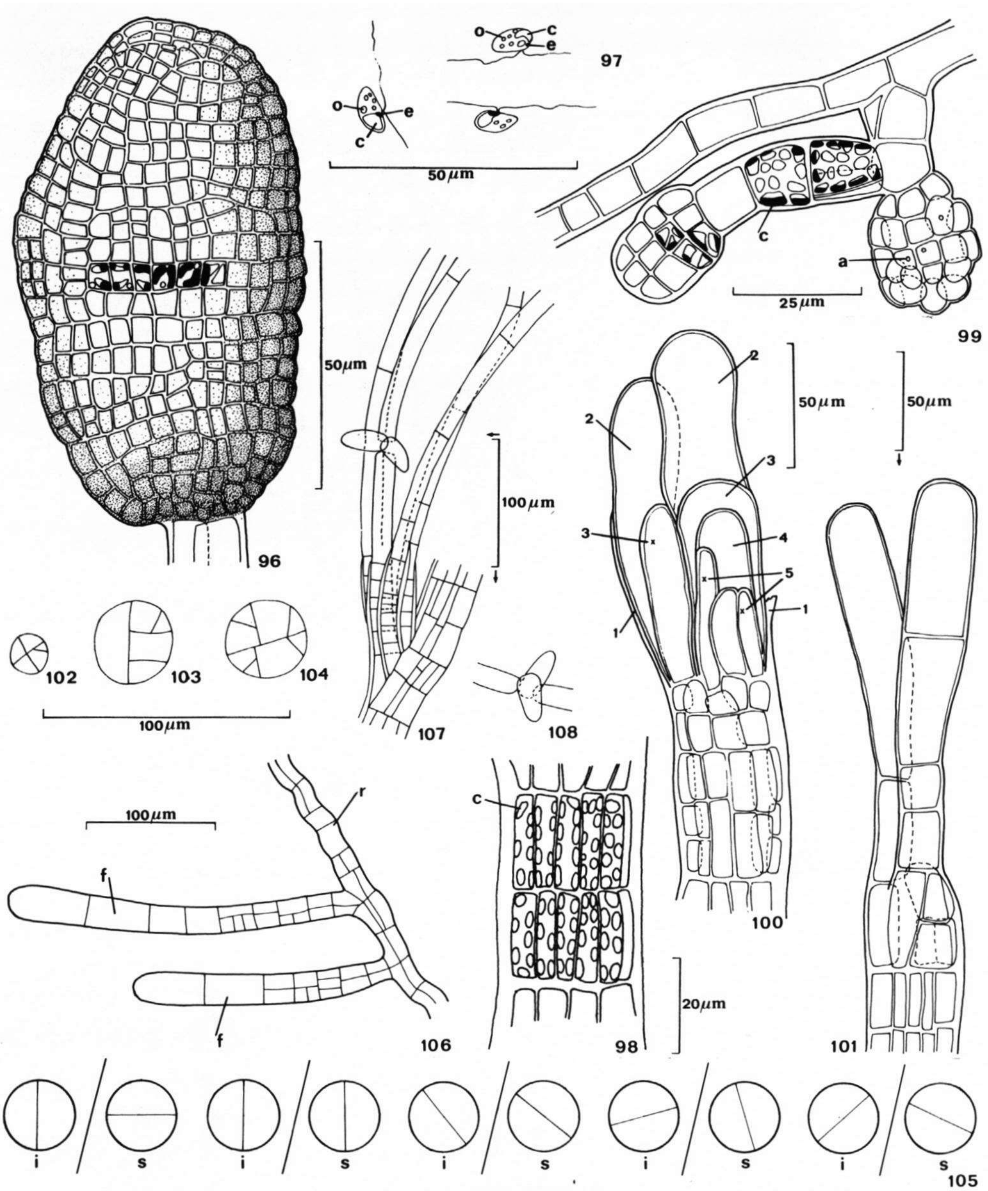


Fig. 96–108. Sphacelaria radicans. 96. Immature plurilocular zoidangium; 97. Plurizoids; 98. Cells of mature filament; 99. Plurilocular zoidangia on a germling; 100, 101. Dead apical cells, replaced by new cells (numbers represent successive generations of apical cells); 102–104. Cross-sections of filaments; 105. Diagram of the sequence of direction of the first longitudinal wall in subsequent secondary segments; 106. Erect filaments arising from a rhizoid; 107, 108. Branched hairs. a. aperture; c. chloroplast; e. eye-pot; f. erect filament; i. inferior secondary segment; o. oil-like drops; r. rhizoid; s. superior secondary segment. 96, 99. Culture 67-59-1; 97. Culture 67-62-6; 98. St. Andrews, *Prud'homme van Reine 71-14* (fresh); 100. Culture 66-46-3; 101. Culture 67-75-2; 102, 104. Culture 67-62-5; 103. Drøbak, *Prud'homme van Reine 67-75* (formalin); 105. Magerösundet, *Kjellman* (UPS); 106. Culture 68-48-1A; 107, 108. Culture 67-52-1.

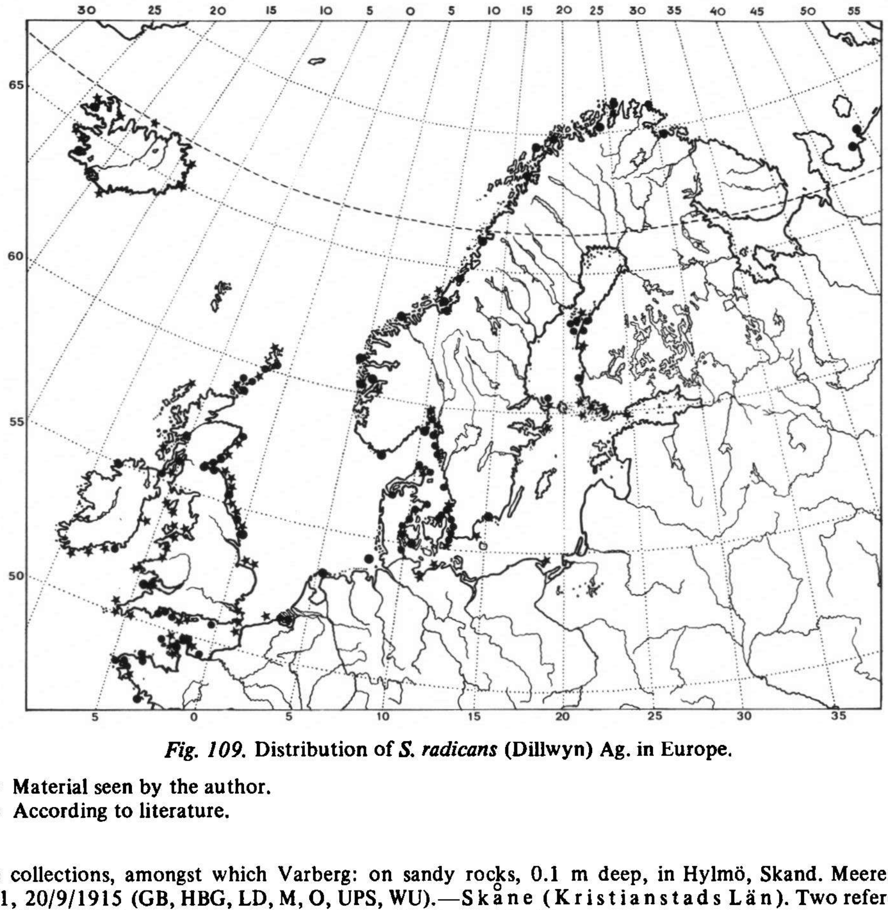


Fig. 109. Distribution of *S. radicans* (Dillwyn) Ag. in Europe.

● = Material seen by the author.
★ = According to literature.

Five collections, amongst which Varberg: on sandy rocks, 0.1 m deep, in Hylmö, Skand. Meeresalgen n. 41, 20/9/1915 (GB, HBG, LD, M, O, UPS, WU).—Skåne (Kristianstads Län). Two references.—Skåne (Malmöhus Län). Twelve collections, of which seven with ecad *libera*. Among these collections: Malmö: Limhamn, (as *S. radicans* forma *aegagropila*), in Hylmö, Skand. Meeresalgen n. 42, 21/6/1913 (HBG, LD, M, MPU, ecad *libera*; in O mixed with *S. arctica*).—Blekinge. Two collections/references of which one collection with ecad *libera*.—Stockholms Län. Three collections/references.

FINLAND. Ostrobottnia media. Munsala: Svärtören Sundet, on old *Potamogeton, Häyrén*, 26/7/1948 (H).—Ostrobottnia australis. Six collections/references of which one collection with ecad *libera*.—Satakunta. Rauma: Northern Archipelago, near Susikari, 4 m deep, *Häyrén*, 13/7/1949 (H, ecad *libera*, partly mixed with *S. arctica* and *Stypocaulon scoparium* forma *scoparioides*).—Regio aboensis. Four references.—Nylandia. Helsinki (Waern, 1952, p. 96).

U.S.S.R. Western Arctic coasts. Five collections/references.

POLAND. Gulf of Gdánsk, off Rewa (Kornas et al., 1960, p. 32).

GERMANY. Baltic coasts. Five collections/references.—Heligoland. More than nine collections, amongst which Nordspitze: Bulnheim in Rabenhorst, Algen Europ. n. 876 (BR, BM, HBG, L, M, O, PC; in W mixed with *S. nana* and *Cladostephus spongiosus*), and without locality: Hylmö in Schiffner: Algae mar. exs. n. 654 (WU).

DENMARK. Skagerrak. Hirthals: mole, *Rosenvinge*, 12/6/1895 (C).—Kattegat. Ten collections/references.—Samsø area. Four collections/references.—Lillebaelt. Two collections.—Sydfynske Øgaard. Aerø: (as *S. cirrhosa*), *Lüders*, 5/1861 (L, UPS, W, WU).—Øresund. Saltholm (Kristiansen, 1978, p. 211).

THE NETHERLANDS. Terschelling. Two collections.—Zuid Beveland. More than six collections.—Walcheren. Westerschelde. Vlissingen: Nolledijk, on stone near M.L.W., *Huwae*, 3/3/1976 (L).

BELGIUM. Oostende: washed up (Chalon, 1905, p. 100).

UNITED KINGDOM. Shetland (including Fair Isle). Six collections/references.—Orkneys. Six collections/references.—Scotland. Ross and Cromarty: Lewis (Norton, 1972, p. 380). Argyll: Two collections/references. Bute: Two collections/references. Aberdeen: Two collections/references. Kincardine: Stonehaven and Angus: Arbroath (Batters, 1902, p. 38). Fife: more than seven collections/references. Midlothian: Four collections/references. East Lothian: Two references. Berwickshire: Two references.—Isle of Man. Three references.—Wales. Anglesey: Two references. Caernarvon: Bangor, (Rees, 1929, p. 252). Merioneth: Ynyslas, River Dovey (Carter, 1933, p. 206). Cardigan: Aberystwyth (Rees, 1929, p. 252). Pembroke: Two references.—England. Without exact locality: in Cocks: Algarum fasc. n. 78 (BM, PC, STA). Cheshire: Two references. Devon: (northern coast): Three collections/references. Northumberland: five collections/references, amongst which: Berwick-upon-Tweed, *Batters*, in Holmes: Algae Brit. rar. exs. n. 96 (BM, BR, KIEL, LIVU, OXF) and (as *S. radicans* var. *olivacea*) in Hauck & Richter: Phycoth. Univ. n. 320 (L, ZA, both mixed with *S. nana*). Durham: Five collections/references. Yorkshire: Four collections. Norfolk: Two references. Cornwall: Six references. Devon: (southern coast): Five collections, amongst which Torbay, Wyatt, Algae Danm. n. 210 (BM, KIEL, L, TCD). Dorset: Four collections/references. Hampshire: Keyhaven (Polderman, 1978, p. 237). Sussex: Two collections. Kent: Two references.—Channel Islands. Alderney (Marquand, 1901, p. 405). Guernsey: Vazon, *Marquand*, 31/10/1894 (NMW). Sark (Dixon, 1961, p. 74). Jersey (Batters, 1902, p. 38).—Northern Ireland. Antrim: Red Bay, Cushendall, *Harvey* (GL, TCD).

EIRE. Donegal: Island of Aran, *Balson*, 8/1852 (GL). Cork: Three collections/references. Dublin: Lambay (Batters, 1907, p. 109). Waterford: Two collections/references.

FRANCE. Atlantic coasts. Pas-de-Calais: Three references. Seine Maritime: Pourville (Tittley & Price, 1978, p. 509). Calvados: Three collections. Manche: Many collections/references, amongst which Cherbourg: in Lenormand: Coll. Hydroph. n. 354 (L), and in Le Jolis: Algues mar. Cherb. n. 161 (BM, CN, DIN, LD, TCD). Finistère: Many collections, amongst which Rade de Brest: Anse de Délec and Baie de Laninon (as *S. olivacea* var. *radicans*), in Crouan: Algues mar. Finist. n. 32 (CONC, L, M, MEL, PC), and Baie de Laninon, in Desmazières: Pl. crypt. France ed. 1, n. 1048 (BM, FI), and ed. 2, n. 348 (BM, L). Morbihan: Three collections, amongst which Belle Ile: in Lloyd: Algues Ouest France n. 292 (CONC, PC).

Specimens distributed or published under this name for localities in Spain, Portugal, Morocco, and the Aegaean Sea proved to be misnamed.

Notes on nomenclature. (1) In Dillwyn's description of *Conferva radicans* (1809, p. 58) two collections have been mentioned: 'On sandy banks among the rocks in Bantry Bay, *Miss Hutchins*' and 'Rocks at Hartlepool, *Mr. Backhouse*'. In the herbarium of the British Museum (Natural History) the only specimen labelled as having been collected by Miss Hutchins had been designated as an isotype by De Haas-Niekerk (1965, p. 158). This specimen must be accepted as the lectotype of *Conferva radicans*. On another sheet of the same herbarium (annotated as *S. radicans*) a label by Miss Hutchins is preserved, but no algal material. The label reads: 'No. 37 grows on hard sandy banks between rocks, it creeps on the sand and fastens itself by roots as it runs along. The fructifications are very numerous, some on short branches, others sitting on the long branches. I would not obtain any regular appearance of joints. The many lines appear to coop the filaments at irregular distances.' These annotations are in perfect accordance with *S. radicans*. Specimens from Hartlepool (syntypes) could not be located, but a specimen in the herbarium at Göttingen (*Tilesius s.n.*, Hartlepool, as *Conferva radicans*) may be related. The drawings of fig. C in Dillwyn's paper were made by Miss Hutchins and W. J. Hooker. The figure in English Botany (Smith & Sowerby, 1810, t. 2138) had been drawn from a sterile specimen collected at Seaton, August 1807 by W. Backhouse. No material is added to the original drawing by Sowerby as preserved in the British Museum (Natural History). The specimens of *Conferva radicans* in the Agardh collection at Lund (Ag. 45551–45552, *ded. Borrer* and Ag. 45557 *misit Hooker*) may be related to the type, but additional data are lacking.

(2) According to De Haas-Niekerk (1965, p. 158) the lectotype of *Conferva olivacea* was

in the herbarium at Kew (now in BM). Other specimens from Papa Westray in the British Museum (Natural History) are isotypes (specimens from Ed. Forster's herbarium, from the herbarium of Batters, and a specimen used to draw the figure 2172 in English Botany) as well as the specimen in the Agardh-herbarium at Lund (Ag. no. 45339).

(3) The combination *Sphacelaria olivacea* (Dillw.) Grev. was published in April 1824 and the combination *Sphacelaria radicans* (Dillw.) C. Ag. after June 1824. So the former combination ought to be retained as the correct name (art. 57.1 Int. Code Bot. Nomencl.). The name *S. olivacea*, however, has been widely and persistently used in different senses (also for taxa not including its type) and has become a long-persistent source of error. I will propose to place this name on the list of nomina rejicienda. The name *S. radicans* has not been used in different senses and is considered the correct name for the taxon.

(4) Hauck (1885) 343 incorporated in his description of *S. radicans* some elements used by Pringsheim (1874) in his description of *S. olivacea*. *S. olivacea sensu* Pringsheim is a mixture of several species.

(5) The descriptions and synonymy of *S. olivacea* by Greville (1824b), J. Agardh (1848), and De Toni (1895) were partly based on *Conferva olivacea* Dillwyn (= *S. radicans*), but also on *S. caespitula* and on *S. nana*.

Notes on morphology. The apical cells of the filaments are usually elongate (fig. 76; 85). They are very vulnerable and often damaged or killed. In these cases new indeterminate filaments will be formed (see fig. 68, arrow; 69, arrows).

Usually the apical cell cuts off primary segments which in their turn divide into two secondary segments. Occasionally, however, not all primary segments become subdivided into secondary ones and in these cases long primary segments can be found in between shorter secondary ones (fig. 78). In these undivided primary segments often a pericyst can be found, which may form a lateral (fig. 78).

The sequence of the development of the longitudinal walls in the secondary segments of *S. radicans* has not been described or figured before. Sauvageau (1901, p. 31 = R. 60) described sections of filaments made from a mixed growth of *S. radicans* and *S. racemosa* from Heligoland. At that moment he did not recognize the filaments of *S. racemosa* as belonging to another species. As a result he observed both the periclinal and the radial pattern of division and he stated that 'la structure des *Sphacelaria*, étudiée en coupe transversale, n'a pas la valeur spécifique qu'on lui attribue depuis Geyler'. His figure 15K gives only transverse sections of *S. racemosa*.

In young secondary segments the primary longitudinal wall is always median. The next longitudinal walls are usually perpendicular to the primary one and in radial direction, but not strictly median (fig. 102–104). Additional longitudinal walls are also radial or sometimes periclinal, resulting in complex structures in which, in transverse section, no distinct subdivision into a medulla and peripheral cells can be observed (fig. 79–81). Almost all long cells of the secondary segments become subdivided by transverse walls (fig. 69–71). Usually one or more central cells in each mature segment extend from the centre of the filament to the periphery (fig. 79; 81). In most superior secondary segments in one (occasionally in two) of these larger cells, transverse cell walls are absent and such cells can function as branch initials. In these initials, commonly called pericysts, the contents of the cells differ from those of adjacent ones. The nucleus is much larger and many tannin-like substances are present. Living pericysts are often more transparent or brighter in colour than other cells, or, in other specimens, the pericysts have a coarse-grained semi-transparent protoplasmatic content (fig. 82). In dried specimens the pericysts become dark-brown (fig. 75; 83). In formaline the pericysts keep their brown colour much longer than the other cells and in preservatives on base of alcohol the contents of the pericysts darken as well. For this reason these special cells are often referred to as 'marked pericysts'. Occasionally a transverse wall can be formed in a young pericyst. In these cases only one of the new cells (fig. 83) or both cells become pericysts. Usually no pericysts are formed in inferior secondary segments. Pericysts may grow into laterals, rhizoids, or zoidangia. The projection of the pericysts (and so also of the laterals) is always perpendicular to the primary longitudinal wall of a superior secondary segment (fig. 81).

The first longitudinal walls in the secondary segments originating from one primary segment are often perpendicular to each other, but smaller angles between these walls occur as well (fig. 105). No relation is observed between the direction of the primary longitudinal walls of subsequent superior secondary segments in a filament (fig. 105).

Laterals are not formed from immature secondary segments as is normal in most other *Sphacelaria* species. In *S. radicans* in most filaments laterals are lacking over a considerable length (often several mm) below the apical cell (fig. 68). Only near the base of the erect filaments do laterals arise. These laterals sprout always from pericysts, so from cells in mature secondary segments. Sauvageau (1903, p. 334 = R. 268) explained that the laterals of *S. radicans* are not comparable with the hemiblastic laterals of most other *Sphacelaria* species, but only with so-called adventitious branches or branches of delayed development as occurring in other genera of *Sphacelariales* (*Halopteris*, *Stypocaulon*). I use the designation 'secondary laterals' in this case. For taxonomical consequences of this type of branching see chapter 'Systematic position' (p. 79).

As described before, almost all laterals arise from pericysts and all pericysts project perpendicularly from the primary longitudinal cell-wall in the superior secondary segment. Moreover, the directions of the primary longitudinal cell-walls in subsequent superior secondary segments seem to be independent of each other. This results in scattered laterals which arise in many directions from the main filaments and which are not pinnate (fig. 68; 69). The angle of branching of a lateral is at first wide, but usually the laterals bend at once and grow often more or less parallel to these main filaments (fig. 69).

Occasionally *S. radicans* can form narrow filaments (20–24 μm diam.) in which only a few longitudinal walls and almost no secondary transverse walls occur. These filaments are especially frequent in cultures in which the culture-medium has not been changed for a long time. If the original normal *S. radicans* filaments are not present any more, the narrow filaments do not differ from *S. nana*. These filaments occur in nature as well. Mr. P. Huwae (pers. comm.) collected them on the salt-marsh of the Dellewal, Terschelling, The Netherlands, where the species grew together with *S. nana*. He also found them in the highest part of the littoral on the slope of a seadike near Sas van Goes, Zeeland, The Netherlands. These specimens could not be distinguished from *S. nana*, and had to be studied in culture. Of 30–40 cultures only 3 grew into *S. radicans*, the other ones appeared to be the genuine *S. nana*.

Rhizoids arise from pericysts. These rhizoids are never appressed or descending along filaments, but they are divaricate, straight or sinuous, and long (fig. 69; 71). They rarely grow as far downward as to reach the substrate. In these cases, they can form a new small basal disc, from which new erect filaments may arise. More often some of the rhizoids form erect filaments without formation of a disc (fig. 106).

Young basal discs are monostromatic. Further development is similar to the process described for *S. mirabilis* (p. 172 and fig. 388), but the upright files of cells often remain short and are not much branched (fig. 66). The margins of the small discs of several specimens often grow over each other. The discs being only 100—400 μm broad, no thick polystromatic crusts are formed. Often stolons form new small discs, from which new erect filaments may arise (fig. 63; 67).

Hairs may occur in large quantities on all filaments but may be lacking as well. In one culture occasional branched hairs have been observed (fig. 107; 108). Their way of branching is reminiscent of the branching of propagules of *Sphacelaria*-species in the subgenus *Propagulifera* and is not comparable to normal branching of filaments in *S. radicans.* All hairs are formed by acroblastic branching. Usually this is acrohomoblastic branching, but occasionally acroheteroblastic branching can be observed. In these cases one of the two or four cells, originating from the lenticular hair-initial (fig. 76; 85) grows into a narrow but normal, erect, coloured filament (fig. 70; 77). This lateral may be short, determinate, and terminated by hairs or long and indeterminate. See also the description and figures by Sauvageau (1909, p. 66–69). That author stated that the lenticular initial-cell can be divided by a curved longitudinal wall, resulting in a small hair-initial and a larger cell which may form a lateral. I have not seen this myself.

Pringsheim (1874, p. 177) described proliferations on the filaments of his *S. olivacea* as 'traubige Brutkörperhaufen'. In his plate 9, figures 10 and 13–17, he depicted these structures for *S. olivacea* var. *caespitosa.* Except for the structure in his f. 13 the figures are in accordance with what Sauvageau (1901, p. 32 = R. 61) described as 'broussins tuberculeux', for *S. radicans*. In *S. caespitula* this curious type of proliferation has not been found again by any of the phycologists who were especially looking for it (i.e. Reinke, 1891, p. 7; Kuckuck, 1894, p. 232; Sauvageau 1901, p. 32 = R. 61) but I found it in a specimen of *S. caespitula* collected near Bergen (*Prud'homme van Reine 67-30*), (fig. 147). Sauvageau (*l.c.*) supposed that Pringsheim found these proliferations in reality on *S. radicans*. When Pringsheim discussed the 'traubige Brutkörperhaufen' he successively compared them to basal discs of germlings, to the zoidangia of *Sorocarpus uvaeformis*, and to the propagules of Bryophytes. These proliferations are, however, caused by a Chytridiaceous fungus parasitizing the pericysts and peripheral cells of the filaments of *S. radicans.* I observed these curious proliferations in specimens of *S. radicans* from Mandal, *Åsen 91-1* (fig. 110). The affected pericysts often form structures which are reminiscent of the nodules formed by zoidangia which failed to release their zoids (compare fig. 110 with fig. 111 & 112). The 'broussins filamenteux', described by Sauvageau (*l.c.*) are young racemes of unilocular zoidangia of *S. racemosa*.

Notes on ecology. The dense carpets and the irregular tufts of *S. radicans* can often be found in sheltered localities in the littoral zone in Iceland, western and southern Norway, southwestern Sweden, the United Kingdom, The Netherlands, and northern and northwestern France. Occasionally it grows in the upper littoral, often together with *S. nana* (see also Van den Hoek, 1958b, p. 193, as *S. olivacea* and Sauvageau, 1901, p. 35–36

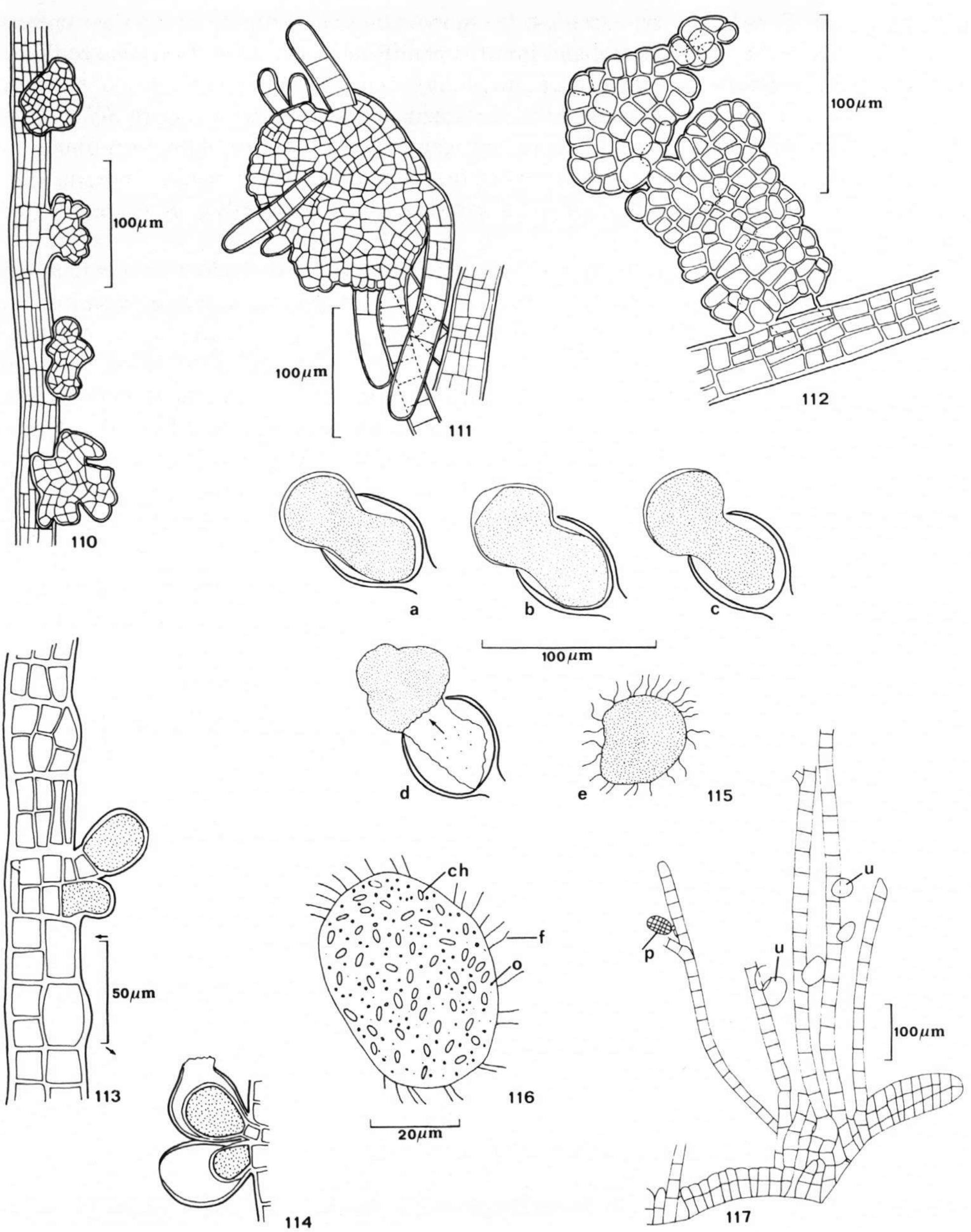


Fig. 110–117. Sphacelaria radicans. 110. Part of a filament with proliferations; 111. Nodule with proliferations; 112. Nodule formed from a plurilocular zoidangium; 113, 114. Geminate unilocular zoidangia, in 114 formed inside remnants of walls of empty zoidangia; 115, 116. Release of unizoids from a unilocular zoidangium. Time: a. 11.43, b. 11.44, c. 11.45, d. 11.46, e. 11.47. In 115, e and in 116 unizoids still enclosed in common mucilage-envelope. 117. Mixed stand of filaments with unilocular zoidangia and filaments with plurilocular zoidangia. ch. chloroplast; f. flagella; o. oil-like drop; p. plurilocular zoidangium; u. unilocular zoidangium. 110. Mandal, Åsen 91-1 (formalin); 111. Culture 67-62-6; 112. Culture 66-3-1; 113–115. Vlissingen, *Prud'homme van Reine 71-2-1* (fresh); 116, 117. St. Andrews, *Prud'homme van Reine 71-17* (fresh).

= R. 64–65, as *S. radicans* var. *coactilis*). In Saint Andrews in and near Piper's Cave on vertical rock-walls in the upper littoral and lower supralittoral a dense felt of *S. nana* could be observed in February 1971. Below this a dark-brown and thicker felty carpet of *S. radicans* occurred, with its upper margin near LWN. In a narrow transitional zone both *Sphacelaria* species grew intermingled. Often the tufts and carpets of *S. radicans* have been found on sandy or even muddy rocks. On these coasts they function as sand-binding algae, usually together with *Rhodochorton floridulum*, *S. rigidula*, and *Cladostephus spongiosus* forma *spongiosus*.

Sphacelaria radicans can also grow in shaded littoral pools. In St. Andrews it was found in pools together with *S. plumigera* and *S. mirabilis* at one locality, and with *S. racemosa* on two other localities. In Heligoland *S. racemosa* and *S. radicans* also occurred in mixed populations.

S. radicans has also been found in salt-marshes often near fresh-water streams in The Netherlands (Terschelling), the United Kingdom (St. Andrews, Ynyslas, Norfolk, Dorset, Hampshire), Eire (Loch Ine), and France (Térénez, Penzé), sometimes together with *S. nana* and often on the highest parts of the marshes. Occasionally a *S. nana*-like growthform of *S. radicans* has been found (see section: 'Notes on morphology'). A similar growth-form, but with marked pericysts, has been found on the Shetlands by Dr. D. E. G. Irvine. Apart from being a common inhabitant of the littoral zone, *S. radicans* can also be found in the sublittoral. It has been noted at depths down to 15 m, growing on rocks, wood, shells, and large brown algae in Iceland, western Norway, southwestern Sweden, the Baltic, Heligoland, Denmark, the Shetlands, and western France. In the Baltic it is confined to the sublittoral. *Sphacelaria radicans* is a marine species which can penetrate into brackish areas. In the polluted river Tyne (Durham, England) it has been found 15 km upstream in the estuary (Edwards, 1972, p. 58). Jorde & Klavestad (1960, p. 100) recorded it in the innermost branches of the Hardangerfjord. A particularly dense vegetation of *S. radicans* (presumably mixed with some *S. arctica*) was found by them in the littoral of a locality near the head of the Sørfjord. According to Alstadsaeter (1954) this part of the fjord is poor in algae and polluted by industrial waste. The salinity in surface waters decreases there to values below 5‰, due to the discharge of water from melting glaciers. In winter, when the zoidangia can be found, salinity is much higher in these localities. Waern (1952, p. 96) described the habitats where he found attached and fertile *S. radicans* in the Oregrund Archipelago in the Baltic. Salinity in this area is always around 5‰, both at the surface and around 10 m depth. *S. radicans* has also been collected near Munsala (Finland), growing on old *Potamogeton* in an area where salinity of the surface water is below 4‰. It is not clear whether in Munsala *S. radicans* is attached or loose-and-entangled. In many other collections from the Finnish part of the Baltic it is entangled as ecad *libera* among *S. arctica* and *Stypocaulon scoparium* forma *scoparioides*. *Sphacelaria radicans* can be considered as a polyhalobe pleioeuryhaline species, as proposed by Von Wachenfeldt (1975, p. 218).

Form range and cultures. In *S. radicans* there is a lot of morphological variation. The dimensions of tufts and carpets, the number of laterals and rhizoids, and their way of branching, the number of stolons and pericysts, and the occurrence of hairs show often large variations. *S. radicans* can be found as single, often *S. nana*-like, unattached, narrow filaments in the mud of the salt-marshes as well as in 0.5–3 cm thick, dark-brown, felty carpets of several m^2 diameter on sandy rocks. When growing in the upper part of the littoral the filaments are often more compact and have smaller dimensions than specimens growing lower on the shore. These upper-littoral growth-forms have been described as *S. radicans* var. *coactilis* by Sauvageau (1901, p. 36 = R. 65). There is no reason to maintain the separate variety. See also Van den Hoek (1958b, p. 193).

In winter most apical cells die off and the erect filaments become truncated at the same height, as if cut by a knife. In early spring the few pericysts that did not form zoidangia can grow into secondary laterals of the second generation.

On very sheltered localities, and in cultures, filaments are not truncated. If their habitat is not much shaded these filaments may form hairs (fig. 63). In several cultures together with these hairs primary laterals can also be formed by acroheteroblastic branching (fig. 70; 77). (see section: 'Notes on morphology'). Occasionally all or most pericysts form laterals, resulting in densely branched plants. In unattached plants (ecad *libera*), as occurring in the Baltic, the laterals do not bend but become perpendicular to the main filament, resulting in a very peculiar habit (fig. 62).

The number of pericysts is quite variable. In some filaments all superior secondary segments have one (sometimes even more than one) pericyst (fig. 75; 83). In other filaments pericysts may be very rare or occasionally lacking (fig. 74).

Cultures have been isolated from material collected on the coasts of Norway (Espegrend, Øystese, Tjøme, Drøbak), The Netherlands (Kattendijke, Sas van Goes), and France (Roscoff, Térénez). Some of these cultures and their subcultures have been maintained during more than 10 years. For a synopsis of the conditions in the culture rooms see table II. *S. radicans* grew well in culture at 4°C and 12°C, but at the higher light-intensities used (2500–3000 Lx) often many apical cells died off (fig. 100) and other cells in these filaments too. In some of these cultures many dead filaments and only a few small living laterals occurred. Usually several pericysts stayed for a long time alive in dying filaments. All plants cultured at 20°C died within a few months.

Growth at 12°C was faster than at 4°C, but at 12°C fewer laterals were formed. Hairs and acroheteroblastic branching were frequent in cultures grown at 4°C at relatively high light-intensities (see figs. 70; 77). Hairs were also found in cultures grown at 4°C at low light-intensities (see fig. 84), and 12°C high light-intensities but not at low light-intensities at 12°C. Acroheteroblastic branching has not been observed in any of these last-mentioned cultures. Some cell-walls occurring in young hair-initials suggested the possibility of formation of laterals, but I did not observe developing laterals. Apart from the occurrence of basal discs and stolons in the attached specimens, there were no morphological differences between specimens growing attached or unattached in culture.

Morphological differences between plants grown in different culture-media were conspicuous and similar to those described for *S. racemosa*. Often nodules or clumps of cells were formed, from which many narrow filaments proliferated (fig. 111). These nodules were sometimes formed as proliferations of filaments, but often they were old unilocular or plurilocular zoidangia. In culture often no release of zoids took place and the zoidangia grew into vegetative nodules (fig. 112). The occurrence of *S. nana*-like growth-forms is reported in the section: 'Notes on morphology' (p. 73).

Secondary attachment of fragmented filaments in subcultures was not common. Occasionally these fragments functioned as stolons and formed small basal discs—but usually unattached sparsely branched plants were formed. Often rhizoids arose from these plants (fig.

69), but secondary attachment in culture by rhizoids was not observed. In most cases plants with basal discs developed from germlings (fig. 63–65). Presumably the same applies for attached and loose-and-entangled specimens occurring in the Baltic.

Reproduction and life-history. Unilocular zoidangia are well known, but plurilocular zoidangia have only once been observed and figured before (Kuckuck, 1894, f. 4 H). In the winter of 1971 I observed many specimens with plurilocular zoidangia near St. Andrews (Fife, Scotland) (fig. 93–95) and in the same period Dr. R. L. Fletcher collected specimens of *S. radicans* with plurilocular zoidangia near Elie (Fife, Scotland) and near Berwick-upon-Tweed (Northumberland, England).

In cultures from The Netherlands, Norway, and France, grown at 4°C low light-intensity and short-day conditions, plurilocular zoidangia were not uncommon (fig. 96; 99). The loculi of these plurilocular zoidangia were 3.5–4 × 4.5–6 μm, and they were often arranged in groups of four. At maturity the plurizoids were separately released through small pores in the wall of the plurilocular zoidangium (fig. 95; 99). Often all four plurizoids of a peripheral group escaped through the same pore (fig. 95). After that the four plurizoids of the inner loculi pressed themselves separately through a common aperture into the cavity of the peripheral group and after that they were released through the open pore. This proceeded until all plurizoids were released of a file of groups of four loculi running from the centre of the plurilocular zoidangium to its periphery. Usually several or all files were releasing their contents within the same period of 10–30 minutes. In empty plurilocular zoidangia the very thin walls between the loculi in the groups of four usually disappeared.

Occasionally more than one pore was formed for each group of loculi or not all loculi were arranged in fours (fig. 99). The zoids swam quite slowly with their acute ends forward and the obtuse end behind (fig. 97). The long mobile flagella stuck in front, and the stiffer short flagella was dragged behind. Plurizoids from plurilocular zoidangia from the same plant did not clump or copulate. I did not succeed in obtaining swarming of plurizoids from different plants at the same moment, so no copulation-experiments with plurizoids of different specimens could be carried out. The plurilocular zoidangia were solitary and the segments of the few-celled narrow stalks were sometimes subdivided by a longitudinal wall (fig. 93, plate 3a). Usually only one zoidangium was formed on a stalk, but occasionally a lateral zoidangium sprouted from the same stalk (fig. 99). Geminate plurilocular zoidangia, as figured by Kuckuck (*l.c.*), have not been observed by me.

The sessile geminate unilocular zoidangia have already been mentioned and figured by Dillwyn (1808, 57, t. C). Usually they arise in pairs from a pericyst and often both zoidangia arising from one pericyst reach maturity at the same time (fig. 91). In other specimens, however, in each pair one of the unilocular zoidangia reaches maturity earlier than the other one (fig. 113). In these cases mostly the superior zoidangia have a faster development than the inferior ones. In addition to the sessile geminate unilocular zoidangia other possibilities occur, like unicellular stalks; groups of 2–4 unilocular zoidangia on top of short laterals; or solitary zoidangia in which only one zoidangium of a pair is formed (fig. 86–90). Often new unilocular zoidangia are formed inside the remaining walls of empty ones (fig. 114). Kuckuck (1894, f. 4J) figures even 2–3 unilocular zoidangia formed inside such a remaining wall.

At maturity the contents of the unilocular zoidangia escape through an apical aperture.

The unizoids are enclosed in a common mucilage-envelope (fig. 115e; 116) and their release takes several minutes when observed under the microscope (fig. 115). An elastic membrane can be observed around the protruding mass of unizoids in early stages of the release. Suddenly this membrane seems to burst and the whole mass of unizoids escapes from the unilocular zoidangium. Within 10—40 seconds after this the unizoids separate from each other. They move faster than plurizoids and no sign of clumping or copulation has been observed. Their form is very similar to that of plurizoids, but two small chloroplasts occur in the obtuse end of a unizoid (fig. 92). In culture unizoids often attached within 20 minutes after release. Embryospore formation has not been observed at all. In culture very often the release of zoids failed both from unilocular and plurilocular zoidangia. In these cases the zoidangia grew into nodules or cell-balls, from which narrow filaments arose (fig. 111). It is not clear whether in these cases the circumscription 'viviparous aplanospores' can be used, or if this phenomenon can be described as vegetative development of zoidangia (see also the section: 'Form range and culture').

Unilocular and plurilocular zoidangia were always formed on separate plants in culture. In nature it is not always possible to tell whether filaments which grow together belong to one specimen or not. Mixed stands of filaments with unilocular zoidangia and others with plurilocular zoidangia occurred quite frequently in St. Andrews (Fife, Scotland) in February 1971 (fig. 117).

Kuckuck's figure 4H and his description show that he found unilocular and plurilocular zoidangia on the same filament. Both unilocular and plurilocular zoidangia are formed in winter (December–March), but occasional unilocular zoidangia have been found in warmer months as well.

Germlings of both unizoids and plurizoids form small basal discs from which narrow erect filaments and stolons arise (fig. 63–65). Plants grown from plurizoids have not yet been fertile. It is not known whether there had been fusion of plurizoids before attachment and germination.

The available data do not permit any conclusion with regard to the life-history model which could be applied to *S. radicans.* The data are, however, not incompatible with the image of an isomorphic diplo-haplontic life-history with plurilocular iso-gametangia and unilocular zoidangia and perhaps also plurilocular asexual zoidangia.

Systematic position. After inclusion into the genus *Sphacelaria* in 1824, *S. radicans* has never been transferred to another genus. In his discussion of the branching systems of *Sphacelariales* (as Sphacélariacées) Sauvageau (1903, p. 334 = R. 268) suggested *S. radicans* and related species (he cited *S. olivacea* and *S. caespitula*) belong to a separate group, the subgroup 'Acladées' of the 'Sphacélariacées hemiblastées'. He based this suggestion mainly on the forming of the secondary laterals (which were the only ones known to him at that moment) always arising from pericysts. He had not observed the acroheteroblastic laterals, but in a later publication (Sauvageau, 1909, p. 67, f. 11) he described and figured this special type of branching. According to his observations the insertion of the hairs suggests an intermediate position between hemiblastic and genuine acroheteroblastic branching.

Consequently Sauvageau suggested an intermediate position of *Sphacelaria radicans* and related species between the Hemiblastées (*Sphacelaria* and related genera) and the

TABLE VI. Comparison between S. arctica, S. racemosa, and S. radicans

	S. arctica	S. racemosa	S. radicans
habitat	mainly sublittoral	littoral	mainly littoral
tufts	broom-like or broadly fusiform	penicillate or cushion-like	small cushions or extensive mats
height plants in cm	1–8(–10)	0.5–2	0.5–2
branching	regularly or irregularly pinnate	irregular, not pinnate	irregular, not pinnate
laterals	often frequent	scarce	few
diam. filaments in µm	(35–)40–65(–75)	(36–)40–55(–61)	(26–)30–60
length-width ratio usually	> 1	< 1	⩽ 1
medulla	1–4 cells	1(–2) cells	4 cells
central protoplast of medullar cells	conspicuous in distal parts only	conspicuous	inconspicuous
marked pericysts	absent	absent	in superior secondary segments
rhizoids	often frequent, corticicating, spreading over the basal disc	scarce, never corticicating, rarely reaching the substrate	scarce or frequent, divaricate, rarely reaching the substrate
basal disc	extensive	several small discs	several small discs
unilocular zoidangia:			
arrangement	in loose, elongate racemes (or solitary)	in compact, globular racemes	sessile, often geminate
form	ovoid	broadly ovoid	often globose
dimensions in µm	(40–)45–60(–75) x (37–)40–55(–62)	(48–)54–75(–80) x (40–)45–70(–75)	(40–)42–60(–66) x (30–)40–60

Holoblastées (*Halopteris* and *Stypocaulon*). Finally Sauvageau (1914, p. 606) suggested that the special formation of laterals can be used to characterize a new group of 'Sphacélariacées Opséblastées', in which *S. radicans* and related species ought to be classified in a new genus. He did not, however, suggest a name for this new genus. In the present paper *S. radicans* is treated as a species of the subgenus *Sphacelaria.*

For comparison between *S. radicans*, *S. racemosa*, and *S. arctica* see table VI and for comparison between *S. plumigera*, *S. caespitula*, *S. radicans*, and *S. mirabilis* see table VII. *S. nana*-like growth-forms often do not differ from the species of that name, so only culturing of these sterile filaments can give certainty about their identity. For comparison between *S. radicans*, *S. nana*, and other *Sphacelaria* species with narrow filaments see table X.

S. radicans has often been found mixed with *Cladostephus spongiosus*, *S. plumigera*, and/or *S. racemosa.* It differs from all these species in having marked pericysts, and in the absence of large medullar cells in *S. radicans.*

3. Sphacelaria caespitula Lyngbye—Fig. 118–151

Sphacelaria caespitula Lyngbye (1819) 105, t. 32A, f. 2 (*p.p.*, excl. specimen from Svinoër); C. Agardh (1824) 164, (1828) 32; J. Agardh (1848) 30; Batters (1889) 59, t. IX, f. 5–8; Reinke (1891) 13, t. 4, f. 1–4; De Toni (1895) 506; Newton (1931) 190; Kylin (1947) 26, f. 24A; Lund (1950) 12, f. 1; Irvine (1956) 37; Prud'homme van Reine (1974) 174; Russell & Fletcher (1975) 766; Kornmann & Sahling (1977) p. 156, f. 84; Prud'homme van Reine (1978) 303.—Type: *Lyngbye s.n.* Naes, Österö, Faeroes, *ad stipitem Fuci digitali inter Conferva Rothii*, 29/7/1817 (C, lecto; LD). See notes on nomenclature 1.

Sphacelaria olivacea Greville (1824b) 314 (*p.p., excl. syn. Conferva olivacea*); Pringsheim (1874) 165 (*p.p.*: t XI, f. 2–5); Reinke (1890a) 206 (*p.p.*: *non* f. 1), (1891) 6 (*p.p.*), (1892) 66 (*p.p.*: *non* t. 46); Kuckuck (1894) 232, f. 5 (excl. f. 6); Sauvageau (1900) 220 (= R. 8), (1901) 60 (= R. 76), f. 17; Jónsson (1903) 160; Kylin (1907) 63; Kuckuck (1912) 178, t. 19, f. 4.– *Sphacelaria olivacea* var. *caespitosa* Pringsheim (1874) 166 (*p.p.*: t. IX & t. X, f. 2, 4, 8, 9).—No type. See notes on nomenclature 2.

Sphaceloderma helgolandicum Kuckuck (1894) 232, f. 7; De Toni (1895) 498; Kuckuck (1899) 375.—*Sphacelaria helgolandica* Waern (1945) 399.—Type: Probably lost.

Plants growing in low, brush-like bushes (fig. 118), often forming confluent mats, dark brownish olive or dull greenish, often turning green when dried and solitary, gregarious, or caespitose. They are quite rigid and epilithic or epiphytic, in the latter case mostly on stipes of *Laminaria hyperborea*. Many sparingly branched filaments arise from a thick polystromatic basal crust (fig. 119; 120).

In early stages the basal part is a circular basal disc with marginal growth. The young disc is monostromatic and consists of a number of radiating, branched, coalescent, creeping filaments with apical growth. Upward growth and subsequent division of the intercalary cells of the coalescent creeping filaments results in the formation of a polystromatic disc (fig. 121; 122). Usually several discs grow over one another, forming a thick crust (fig. 120; 123; 124). Stolons are short and of irregular occurrence (fig. 122).

The erect parts of the plants are composed of many main axes and scattered, solitary, unbranched or almost unbranched, meriblastic laterals of up to the fourth order (fig. 119). The laterals are irregularly placed (never pinnate, but sometimes slightly secund), often somewhat appressed and they have indeterminate growth.

There is usually no difference in growth or dimensions between the axes and the mature laterals, but in the proximal part of the laterals the dimensions are usually smaller.

The dimensions of the inferior and superior secondary segments of the erect filaments are usually equal to each other. It is difficult, however, to determine the dimensions of the secondary segments in most mature filaments (fig. 130; 135). Usually these secondary segments are longer than they are wide (fig. 125; 126). The secondary segments are subdivided by radial and transverse walls into a parenchymatous tissue, without a strict subdivision into a medulla and peripheral cells (fig. 127; 128). In almost all cells transverse walls are formed (fig. 125; 129; 130; 139). One of the larger cells in a superior secondary segment which extends from the centre of the filament to the periphery can function as branch-initial or pericyst (fig. 125; 129). Pericysts in *S. caespitula* are often inconspicuous (fig. 130), and they are frequently shorter than the superior secondary segments. In these cases the pericysts are located in the superior part of these segments (fig. 129).

In lateral view 1–4 (–5) longitudinal walls can be observed in secondary segments and the narrow peripheral cells are subdivided into shorter ones by 1–4 (–5) transverse walls. Sometimes secondary longitudinal walls occur in these shorter peripheral cells (fig. 129). Hairs and rhizoids are lacking.

There are no propagules.

The solitary unilocular zoidangia are usually formed on 3–5-celled stalks on the proximal parts of the mature filaments. They are spherical or subspherical when mature, ellipsoid or ovoid when young (fig. 131–133). Occasionally sessile unilocular zoidangia can be found on the basal crusts (fig. 123). Unizoids are ovoid or subspherical (fig. 134). They have 1–2 chloroplasts and an eye-spot.

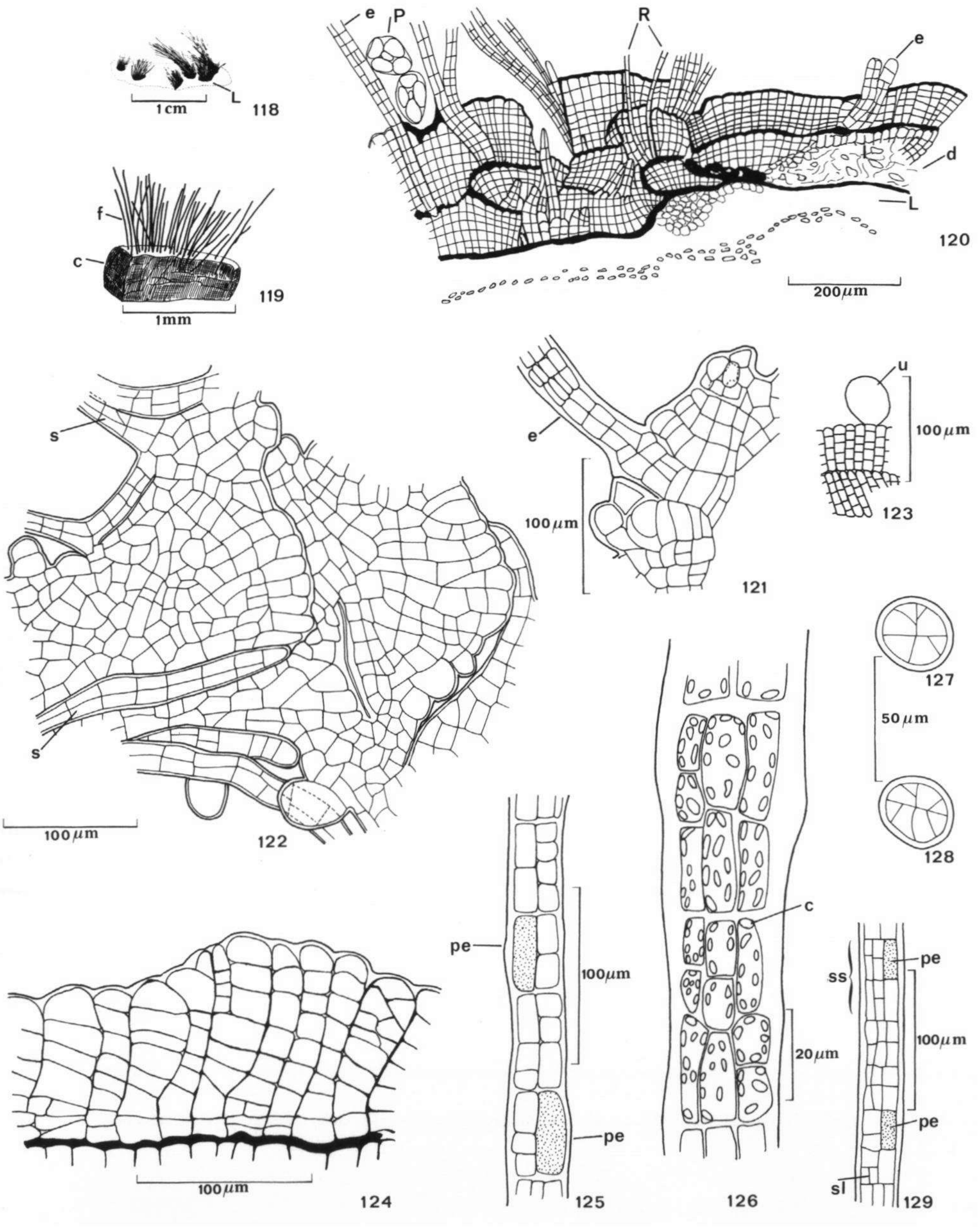


Fig. 118–129. Sphacelaria caespitula. 118. Habit; 119. Detail of habit and basal crust; 120–124. Basal parts, sections in 120, 121, 123, & 124, in 122 seen from below; 125, 126, & 129. Parts of erect filaments; 127, 128. Cross-sections of erect filaments. c. chloroplast; d. dead part of basal crust; e. erect filament; L. *Laminaria hyperborea*; P. *Polysiphonia spec.*; pe. pericyst; R. *Rhodochorton spec.*; s. stolon; sl. secondary longitudinal wall; ss. secondary segment; u. unilocular zoidangium. 118. Börnestangen, Espegrend, *Prud'homme van Reine 67-27* (formalin); 119. Stångeholmegrundet, Kristenberg, *Prud'homme van Reine 67-19* (formalin); 120, 124, 126–128. St. Andrews, *Prud'homme van Reine 71-6* (mainly fresh); 121, 122. Tyskerens Rev, *Lund* (C, microslide); 123. Heligoland (HELG, microslide); 125. Svinoer, *Lyngbye* (KIEL, soaked); 129. Faeroes, *Lyngbye* (C, microslide).

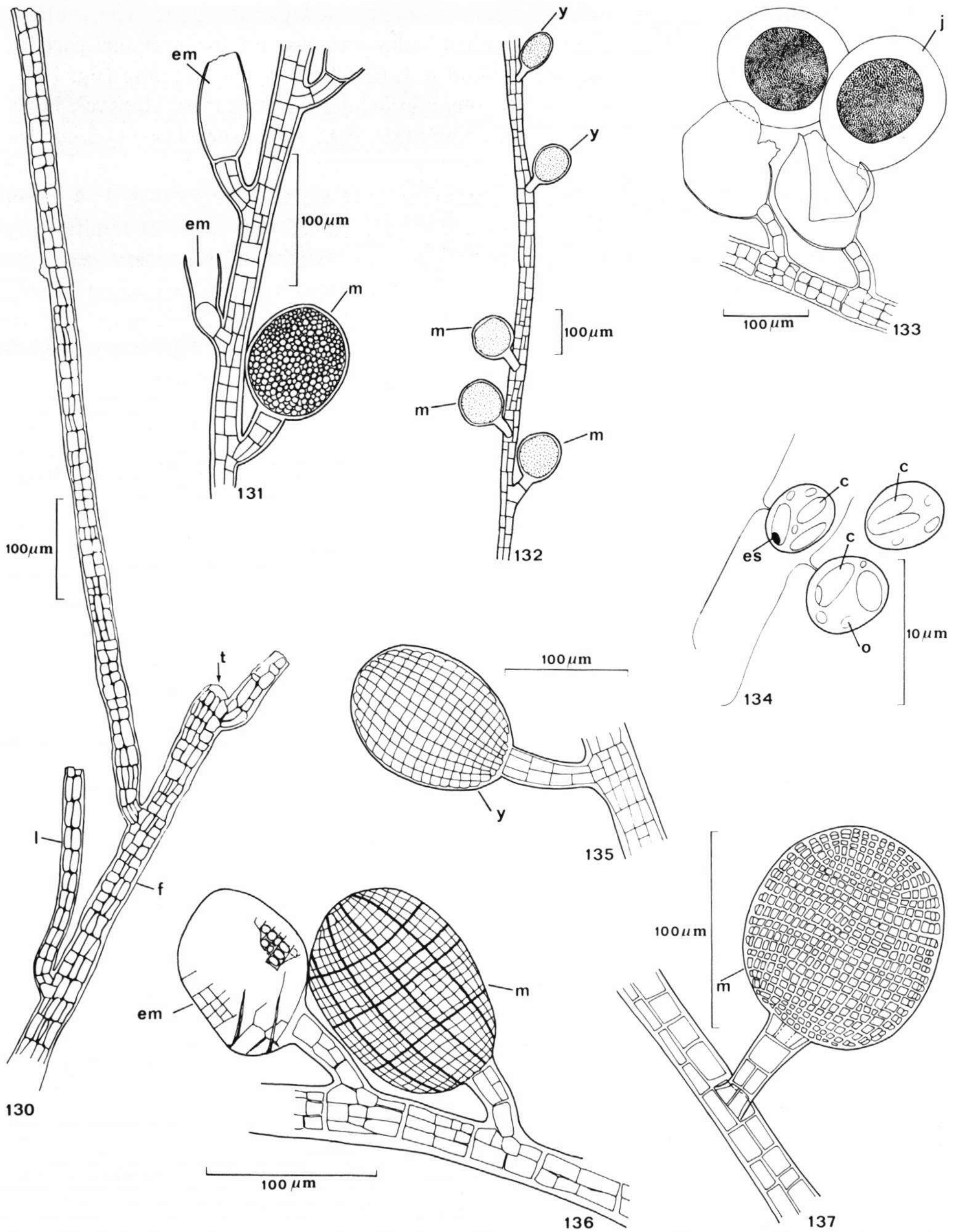


Fig. 130–137. Sphacelaria caespitula. 130. Part of a truncated erect filament; 131–133. Unilocular zoidangia, in 133 dehisced by pressure of a cover slip; 134. Unizoids; 135–137. Plurilocular zoidangia. c. chloroplast; em. remnants of empty zoidangia; es. eye-spot; j. jelly-like substance; l. lateral; m. mature; o. oil-like drop; t. truncature; y. young. 130. Svinoer, *Lyngbye* (KIEL, soaked); 131. Tyskerens Rev, *Lund* (C, microslide); 132, 133, & 136. St. Andrews, *Prud'homme van Reine 71-6* (fresh); 134. Culture 67-47-1; 135. Heligoland (HELG, microslide); 137. Culture 68-48-6.

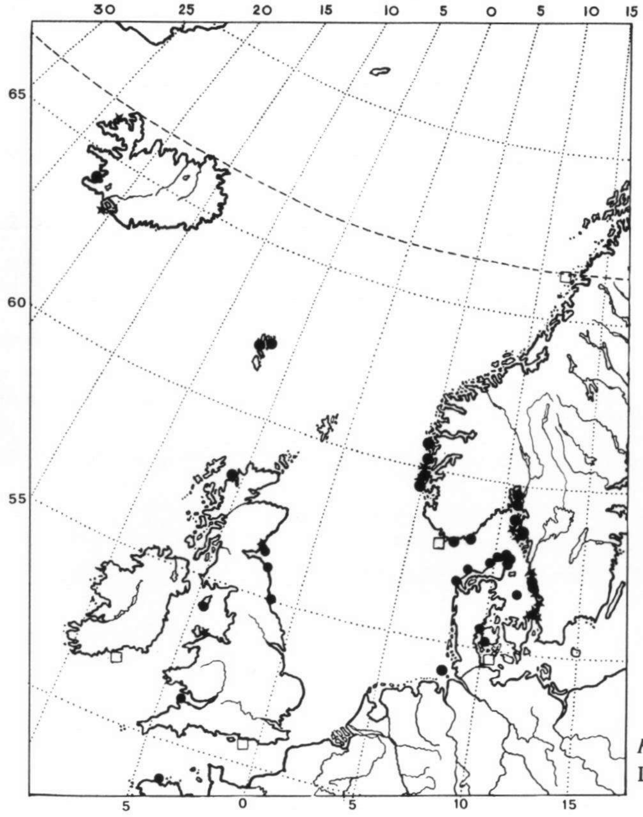
Unilocular and plurilocular zoidangia occur probably on separate plants. The solitary, plurilocular zoidangia are formed on 2–4-celled stalks and also on the proximal parts of mature filaments. They are subspherical, cylindrical, or ellipsoid when mature (fig. 135–137) occasionally medially constricted. Young plurilocular zoidangia are ellipsoid. Plurizoids are ovoid or spherical according to Kuckuck (1912, p. 179). They have 1–2 chloroplasts.

Dimensions: Plants up to 2 cm high (usually less) and mats not more than 3–4 cm in diameter. Diam. basal crusts 2–3 mm. Diam. of stolons 20–25 µm. Angle of ramification 10–45°. Diam. of filaments (13–) 18–30 (–35) µm. Height of secondary segments 45–60 µm. Chloroplasts 1–4 X 1–3 µm in surface view (fig. 126). Pericysts 30–50 X 10–17 µm. Unilocular zoidangia, 80–110 X 60–100 µm, stalks 40–50 X 12–23 µm. Unizoids 4.5 X 6.5–9 µm according to Kuckuck. Plurilocular zoidangia 75–125 (–160) X (40–) 60–95 (–130) µm, diam. loculi 3–5 µm, stalks 30–40 X 11–20 µm. Plurizoids 4.5 X 6.5 –9 µm according to Kuckuck.

Distribution. Europe: Iceland, Faeroes, Norway, Sweden, Denmark, Germany (Heligoland), United Kingdom, French Atlantic coast.

The species has also been mentioned from one locality in Eire and one locality in the Baltic. It has not been found outside Europe.

European localities have been listed and are given in fig. 138. For an extract of the list of collections and references see next page.



● = Material seen by author.
★ = According to literature.
□ = Doubtful locality.

Fig. 138. Distribution of *S. caespitula* Lyngbye.

ICELAND. **Northwest coast.** Dyrafjördur (as *S. olivacea*, Jónsson, 1903, p. 160).—**Southwest coast.** Two collections/references.—**South coast.** Vestmannaeyjar (Jónsson, *l.c.*).

FAEROES. Two collections.

NORWAY. **Nordland.** (? Kjellman, 1890, p. 69).—**Hordaland.** More than six collections/references.—**Rogaland.** Haugesund: Kvalöy (as *S. olivacea*), *Norum*, 6/6/1897 (BG).—**Vest-Agder.** Two collections.—**Aust-Agder.** Høvåg: *Rueness*, 17/7/1965 (L).—**Akershus.** Two collections/references.—**Ostfold.** Rauergrundet, on *Laminaria hyperborea*, *Rueness*, 6/5/1969 (L).

SWEDEN. **Bohuslän.** More than seven collections/references.—**Halland.** Five collections/references.—**Skåne. (Malmöhus Län).** Two references.

GERMANY. **Baltic coasts.** Kiel: *Reinbold* (MEL, locality correct ?).—**Heligoland.** More than three collections.

DENMARK. **North Sea.** Near Lodbjerg Lighthouse: 27 m deep, *Rosenvinge 9729*, 2/10/1922 (C).—**Skagerrak.** Six collections.—**Kattegat.** More than five collections.—**Lillebaelt.** Faenø Kalv: 13 m deep, on stones, *Rosenvinge 1385*, 29/6/1891 (C).—**Sydfynske Øgaard.** Hornenaes: 8 m deep, on *Mytilus*, *Rosenvinge 2109*, 21/9/1891 (C, mixed with *S. cirrosa*).—**Øresund.** Hornbaek Bay (Von Wachenfeldt, 1975, p. 216).

UNITED KINGDOM. **Scotland.** Ross & Cromarty: Taner Mhor, Summer Islands, sublittoral, *Farnham*, 10/6/1972 (PORT). Fife: Two collections/references.—**Isle of Man.** Without exact locality, sublittoral, *Irvine* (priv. coll.).—**Wales.** Caernarvon: Bangor (Batters, 1902, p. 39).—**England.** Devon: Ilfracombe, Hele, (as *S. radicans*), *George*, 26/5/1892 (BM). Northumberland: Two collections, amongst which Berwick-upon-Tweed, *Batters*, in Holmes, Algae Brit. rar. exs. n. 48 (BM, BR, KIEL, LIVU, OXF). Durham: South Shield, Lizard Point (as *S. radicans*), *Edwards*, 20/2/1971 (L). Sussex: Bognor, 4/1887, *Batters 10333* (BM, locality correct ?).

EIRE. ?Waterford: Helvick Point (Scannell, 1969, p. 196).

FRANCE. **Atlantic coasts.** Finistère: Three collections.

Specimens distributed or published under this name for other localities in France (Calvados, Cherbourg, Rade de Brest) and outside Europe proved to be misnamed.

Notes on nomenclature. (1) In the herbarium at Copenhagen three collections of *S. caespitula* can be found. In all cases these are mixtures of two different collections: fragments of stipes of a *Laminaria*, on which *S. caespitula* is growing (from Naes, Osterö, Faeroes) and fragments of phylloids of *Laminaria saccharina* on which tufts of a small red alga can be found (from Svinoer, Norway). Lyngbye (1819, p. 105, t. 32A) mentioned both collections in his description of *S. caespitula*. In his plate 32A f. 1 and 3 represent the red alga can be found (from Svinoer, Norway), Lyngbye (1819, p. 105, t. 32A) mentioned both locality (ex herb. Hofman Bang), the second gives Svinoer as the locality and the third reads: '*Cum Delin.* d. 21 Maij 1818. *Sphacelaria caespitula—Sphacelaria minuta* var. *pusilla* (deleted)—*Conferva Rothii* var. *nigra?* (deleted)—d. 29 julij 1817 *ad littus Naes ad stipitem Fuci digitali inter Conf. Rothii*'. The specimens in this third collection of *S. caespitula* as found on the fragments of the stipes of the *Fucus digitalis* (probably *Laminaria hyperborea*), are selected as lectotypes. They are mostly sterile, but a few emptied zoidangia occur.

(2) The description and synonymy of *S. olivacea* by Greville is partly based on *S. caespitula*, but partly also on *S. radicans* and *S. nana* respectively. The description and synonymy of *S. olivacea* by Reinke is also partly based on *S. caespitula*, but mainly on *S. arctica*.

Notes on morphology. The apical cells of the filaments are usually elongate (fig. 139a). They are very vulnerable and often damaged or killed. In these cases usually a lateral is formed from a cell of one of the superior secondary segments just below the dead apical cell (fig. 140). This lateral grows in the same direction as the original main axis. Occasionally two new filaments can be formed from the subapical segment (fig. 141). The filaments themselves are also very vulnerable and in nature they are usually truncated in winter (fig.

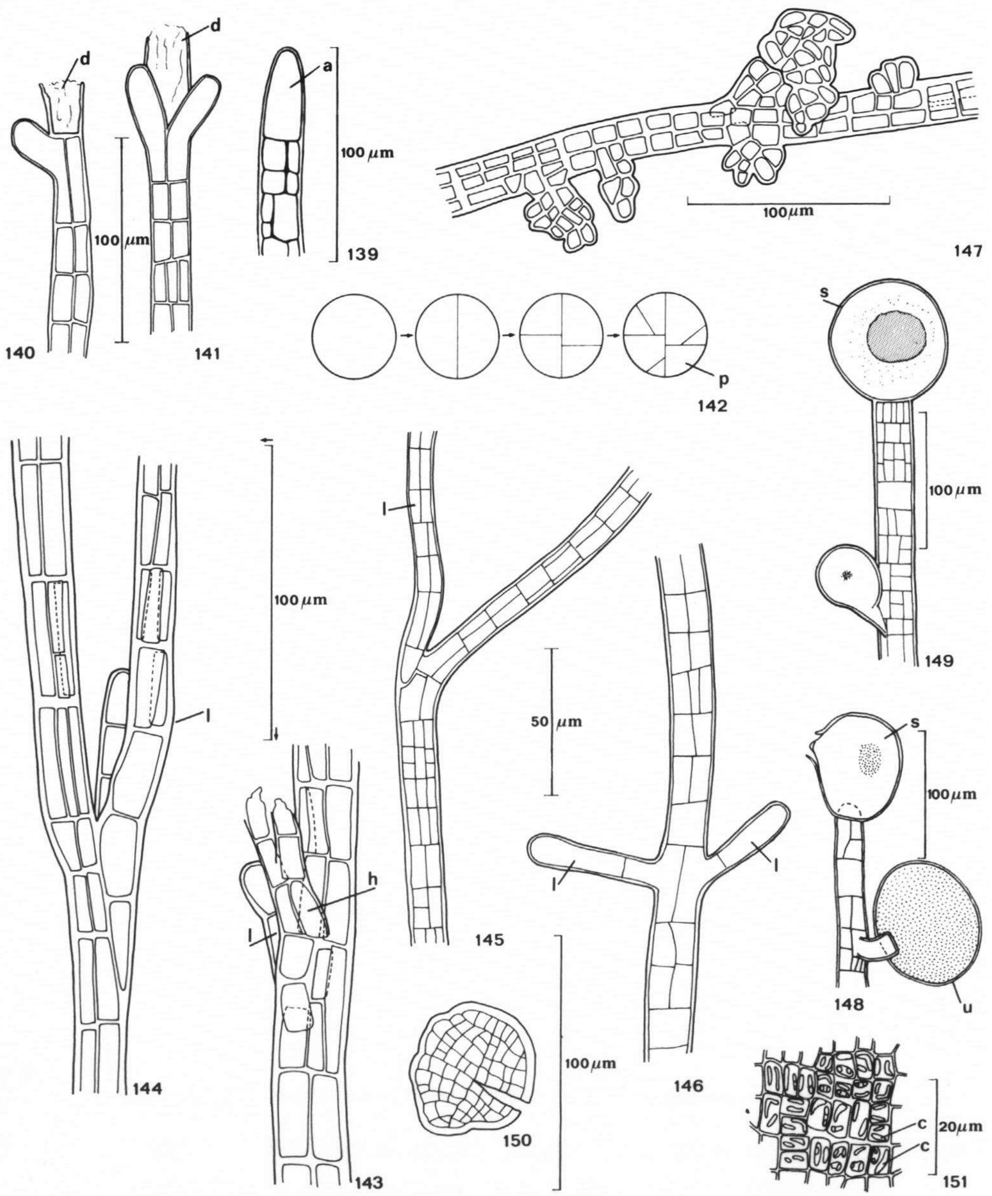


Fig. 139–151. Sphacelaria caespitula. 139. Part of a lateral; 140, 141. Formation of erect filaments replacing a dead apical cell; 142. Sequence of longitudinal walls in superior secondary segments (diagram); 143, 145. Acroheteroblastic branching; 144. Acrohomoblastic branching; 146. Aberrant branching; 147. Proliferations; 148, 149. Subspherical structures probably caused by Chytridiaceous fungi (in 148 also a unilocular zoidangium); 150. Cross-section of a plurilocular zoidangium. a. apical cell; c. chloroplast; d. dead apical cell; h. hairs; l. lateral; p. pericyst; s. subspherical structure; u. unilocular zoidangium. 139. Svinoer, *Lyngbye* (KIEL, soaked); 140, 141. Culture 67–18; 143, 144. Faenø Kalv, *Rosenvinge 1385* (C, soaked); 145, 146. Culture 67-47-1; 147. Skjerholmen, Espegrend, *Prud'homme van Reine 67-30* (formalin); 148. Heligoland (HELG, microslide); 149. Tyskerens Rev, *Lund* (C, microslide); 150, 151. St. Andrews, *Prud'homme van Reine 71-6* (fresh).

130t). From the short truncated erect filaments one to several laterals arise next spring (fig. 130l). These laterals function as the new main filaments.

Sauvageau (1901, p. 57, f. 17 = R. 72) figured cross-sections of filaments of *S. caespitula* (as *S. olivacea*), but he did not mention these sections in the text. His figures agree with my figures 127, 128, and 142. The primary longitudinal wall is always median. The next longitudinal walls are perpendicular to the primary one and in radial direction, but not always strictly median. Additional longitudinal walls are radial and not perpendicular. The total number of longitudinal walls is always quite small and there is no subdivision into a medulla and small peripheral cells. In superior secondary segments often one of the first four cells formed by the perpendicular longitudinal walls will not be divided further, and becomes a pericyst (fig. 142p). Almost all long cells of the secondary segments become subdivided by transverse walls (fig. 129; 130; 139). In young filaments the pericysts are not subdivided by these transverse walls (fig. 125), but in older filaments the pericysts are subdivided as well. Usually the superior part of the original pericyst still functions as a pericyst (fig. 129). In other filaments, however, no marked pericysts can be located (fig. 130). In most living filaments the pericysts can only be distinguished by their dimensions, but sometimes they are somewhat lighter brown in colour and have a small central clump of semi-transparent coarse-grained protoplasma. In dried specimens the pericysts often become olivaceous and somewhat darker in colour than the surrounding cells, but the contrast is not as marked as in *S. radicans*. Pericysts may grow into laterals or into zoidangia. The bases of the laterals are not as broad as the whole length of secondary segments, so laterals are formed by meriblastic branching. Occasionally pericysts formed two small proliferations in culture.

As in *S. radicans* the laterals are not formed from immature secondary segments, but they sprout from pericysts, and so they are secondary laterals. The angle of branching of a lateral is at first wide, but usually the laterals bend and grow at a small angle or even parallel to the main filaments (fig. 130).

In specimens from Denmark (Faenø Kalv, *Rosenvinge 1385* and Hornenaes, *Rosenvinge 2109*) acroheteroblastic branching has been observed. The first specimen had already been discussed by Sauvageau (1902, p. 400 = R. 212 and 1909, p. 69). In 1902 he mentioned the specimen as *S. olivacea* Pringsheim (= *S. caespitula*) but in 1909 he was less sure, and speculated about it being an undescribed species. In accordance with a remark of Lund (1950, p. 16), the annotations by Sauvageau on both specimens are still present in the Copenhagen herbarium. I found some remnants of hairs on the specimen from Faenø Kalv and from the basal cells of these old hairs narrow laterals arise (fig. 143). Apart from these remnants the occurrence of hairs has not been mentioned or observed in *S. caespitula*. In the Faenø Kalv-specimen I observed once branching without indication of incidence of hairs, so this branching was acrohomoblastic (fig. 144). Acrohomoblastic branching occurred also in one of my cultures (fig. 145). In this culture also other aberrant forms of branching occurred (fig. 146).

Sauvageau (1909, p. 69) observed some long, divaricate rhizoids in a specimen from Heligoland, and Lund (1950, p. 15) observed two short rhizoids. According to Reinke (1891, p. 14 & t. 4, f. 1) *S. caespitula* forms rhizoids (einzelne Zellstränge) which grow deep into the tissue of *Laminaria*. I have not observed rhizoids in *S. caespitula* and in most cases the basal crusts are epiphytic and do not penetrate into the tissue of *Laminaria hyperborea*. Occasionally, however, some polystromatic lobes of the basal crust of *S. caespitula* were found between the cells of the stipes of the *Laminaria*. Some stolons have been found in culture (fig. 122), but they were always small and never formed new discs.

Young basal discs are monostromatic, but soon they become polystromatic. This development is similar to the process described for *S. mirabilis* (p. 172 and fig. 388), but the upright files of cells are almost unbranched and therefore the apical cells are not narrower than the cells below it (fig. 120; 121; 123; 124). Meristematic activity of the inferior cells of the discs has not been observed. The discs of neighbouring germlings may overlap each other and form the polystromatic crust. In my cultures, however, the basal discs of neighbouring germlings never grew together. More often the lobes of the disc overgrow one another and form together the polystromatic crust. Stiff mucilaginous layers of varying thickness are generally interposed between the polystromatic discs forming the crust. Quite often also specimens of other algae can be found between the superposed discs.

Pringsheim (1874, p. 177 & t. 9, f. 10; 13–17) described and depicted proliferations on the filaments of his *S. olivacea* var. *caespitosa* as 'traubige Brutkörperhaufen'. This curious type of proliferation had not been found again by Reinke, Kuckuck, and Sauvageau, who all carefully searched for it. I found these proliferations in a specimen growing on the stipes of *Laminaria hyperborea* near Bergen, Norway. The curious proliferations (fig. 147) arose without order from the normal peripheral cells of the filaments. It was probably caused by a Chytridiaceous fungus parasitizing these cells. Another case of probable fungal infection will be discussed later (in 'Reproduction and life-history').

Notes on ecology. *Sphacelaria caespitula* is a sublittoral, permanently submerged species. In Oslofjord, where the tides are insignificant, the species grows between 0.5 and 16 m depth (Sundene, 1953, p. 157), but in other localities it has always been found in deep water. It often grows together with *S. plumosa* on substrates like rocks, stones, gravel, shells, and large algae. It is a common epiphyte of the stipes of *Laminaria hyperborea* in Norway, Southwestern Sweden, and Denmark, and it has also been found on this large alga in Iceland, on the Faeroes, and in Scotland. Sundene (*l.c.*) mentioned growth on *Laminaria digitata* in Oslofjord. Batters found it, according to a label in the British Museum, in 1883 on *Sacchoriza polyschides* and Reinke (1891, p. 13) also mentioned that alga as its host. *Sphacelaria caespitula* is a small alga and it has probably often been overlooked. It never forms large patches on rocks or stones and the confluent mats, as occurring on the stipes of *Laminaria hyperborea*, are often inconspicuous.

When growing on stipes of *Laminaria hyperborea*, the basal crusts of *S. caespitula* are usually strictly epiphytic. Occasionally the crusts penetrate in between the tissue of the *Laminaria* or of the *Sacchoriza*-stipe. It is not yet clear whether this penetration is of parasitic nature, as Reinke (1891, p. 14 & t. 4, f. 1) asserted, or if it is merely occupying available space. The surface of the stipes of *Laminaria hyperborea* is quite rough and irregular. Thus there are many ridges and pits and in the latter the basal crusts of *S. caespitula* may find unoccupied space to grow. A real parasitic approach, with decay of tissue cells of the *Laminaria* or the *Sacchoriza* stipes, has not been observed.

Sphacelaria caespitula is a strictly marine species, which does not penetrate far into brackish waters. In the Oslofjord it has been found in localities where in summer salinity may become as low as 11.1‰, but usually salinity in this region is much higher. Von Wachenfeldt (1975) who carefully studied the geographic distribution of marine algae of the Øresund in relation to salinity found *S. caespitula* only in deep water, where salinity was always high (> 33‰). He (*l.c.*, p. 216–217) calls *S. caespitula* a polyhalobe oligo-euryhaline species, i.e. a species with a tolerance to changes in salinity between 35 and 30‰ only.

The specimens found in more brackish water in Denmark (Lillebaelt and Sydfynske Øgaard) have an aberrant growthform with acroheteroblastic branching. The specimen in the Melbourne herbarium, annotated as having been found near Kiel by Reinbold, may be mislabelled and has perhaps been found in Heligoland.

Form range and cultures. In *S. caespitula* there is little morphological variation. The habit of the plants varies with the season: new erect filaments sprout from the truncated old ones in early spring and in summer or early autumn they become truncated again. In nature the dimensions of the basal crusts or the diameter of the erect filaments do not vary considerably.

Cultures have been isolated from material collected on the coasts of southwest Sweden (Kristineberg), southwest Norway (Bergen-Espegrend), southeast Norway (Oslofjord-Rauergrundet), and west France (Brittany–Roscoff). Most cultures have been maintained during ten years, during which many subcultures have been made.

Sphacelaria caespitula grew well in culture at 4°C or 12°C and at all light-regimes used. Fragments of filaments never formed basal crusts again, but often large branched plants (till 6 cm high) were formed. Basal discs were formed by germlings from unilocular or plurilocular zoidangia. In culture they usually soon became polystromatic, but thick basal crusts were only occasionally formed. In one culture (67-47-1), when grown at 12°C and low light-intensities (175–700 Lx) acrohomoblastic branching (fig. 145; 146) and other aberrant types of branching (fig. 145; 146) occurred. In later subcultures from the same number only normal meriblastic branching could be found; just as in all other cultures of *S. caespitula.*

No spontaneous fragmentation was observed. Even in glass-dishes with large plants no new small plants turned up, except after sporulation. Stolons, rhizoids, and hairs did not occur in my cultures.

Reproduction and life-history. Unilocular and plurilocular zoidangia have often been described, but propagules or other vegetative reproduction have never been observed. If fragmentation should take place, the fragments would probably not adhere, as is evident from the results of culture-experiments.

Zoidangia did only occasionally occur in my cultures. I found them for the first time after nine years of culture. Germlings of both unizoids and plurizoids grew well, but they have never formed zoidangia so far. Pringsheim (1874, p. 168, t. IX, f. 1a; 3; t. XI, f. 4a) described supposedly dehisced unilocular zoidangia. He also described the plurilocular zoidangia of his *S. olivacea* var. *caespitosa* (*l.c.* t. IX, f. 1b; 2b; t. XI, f. 4b). In his figures 1 and 4 Pringsheim figured apart from empty unilocular zoidangia also filled ones. Sauvageau (1901, p. 59 = R. 75) found that the walls of the loculi of the plurilocular zoidangia are not persistent, and that the dehiscence may be apical as in unilocular zoidangia. In that case it is almost impossible to discriminate between very young or emptied unilocular zoidangia and plurilocular ones. For these reasons Lund (1950, p. 15, f. 1B) did not try to discriminate his figured emptied zoidangia.

Pringsheim (*l.c.*) found his unilocular and plurilocular zoidangia on the same plant, as is clear from his figures. He found, however, only very young or emptied unilocular zoidangia, and, as discussed above, these are very similar to very young or emptied plurilocular zoidangia. So the observations by Kuckuck (1894, p. 232), who found the two different zoidangia always on different plants, seem to be correct. Sauvageau (1901, p. 56 = R. 71), however, found unilocular zoidangia and plurilocular ones on the same plant again, but in these cases he always found stalked plurilocular zoidangia on the erect filaments and sessile sori of unilocular zoidangia on the basal crusts.

Kuckuck (1894, p. 232, f. 5A) figured the unilocular zoidangia he found of his '*S. olivacea* Pringsh.'. These are ovoid and stalked. A description by Sauvageau (*l.c.* p. 58, = R. 74) corresponds very well with Kuckuck's figures. Kuckuck's f. 6 has nothing to do with *S. caespitula* (it is probably *S. nana*) and in f. 7 he figured a new species which was, according to Kuckuck, the only species of the new genus *Sphaceloderma*. On a thick basal crust (not unlike the basal crust of *S. olivacea* Pringsheim *sensu* Kuckuck) sori of sessile unilocular zoidangia were detected, and erect filaments were absent. These sessile unilocular zoidangia are figured in Kuckuck's f. 7. Sauvageau (*l.c.* p. 55 = R. 71) found these sessile unilocular zoidangia also on the basal crust of *S. olivacea*, and so he combined both taxa into one.

Pringsheim did already know that apical cells of *Sphacelaria* species may be parasitized by Chytridiaceous fungi. In his t. VIII, f. 15 he figured a similar case for *S. tribuloides* and in t. IX, f. 7 for *S. olivacea* var. *caespitosa*. He also described and figured (t. IX, f. 9; t. X, f. 5–7) structures of which he was less sure. He did not know whether they were caused by Chytridiaceous fungi or whether they were true fructifications. Similar structures can often be found in *S. caespitula* and in some cases it is difficult to discriminate between these structures and true unilocular zoidangia. Most likely these subspherical structures are caused by Chytridiaceous fungi, perhaps by another species than the one that causes the curious proliferations described as 'traubige Brutkörperhaufen'. I found the subspherical structures, amongst others, in material from Heligoland (fig. 148), Kristineberg and Denmark (fig. 149). In the same material from Heligoland where I found these structures (as well as true unilocular zoidangia) I also found a structure similar to the sessile unilocular zoidangia described by Sauvageau (see fig. 123). The figures by Kuckuck (*l.c.* f. 7) and Sauvageau (*l.c.* f. 17, D, E) do not exclude the possibility that their sessile unilocular zoidangia are also structures caused by Chytridiaceous fungi. If this supposition is correct the (always stalked) unilocular zoidangia and the plurilocular zoidangia are still to be found on different plants. This is in accordance with my results, both with regard to specimens from nature and from specimens in culture.

Kornmann & Sahling (1977, p. 156, f. 84G) mentioned and figured the thick wall of the unilocular zoidangia as a specific character. Similar unilocular zoidangia have been found by the present author on several occasions (fig. 131–133; 148). The unilocular zoidangia figured by Kuckuck (1894, p. 232, f. 5A) are probably immature. Nevertheless the same author (Kuckuck 1912, p. 179) mentioned dehiscence of unilocular zoidangia and he described and figured (t. VIII, f. 4B) the unizoids. According to him they are exactly like the plurizoids. I observed only once the dehiscence of a unilocular zoidangium (from culture 67-47-1). A very narrow semi-terminal pore was formed through which the zoids escaped one by one. After a few seconds they unfolded their flagella and started to move slowly.

Sauvageau (1900, p. 220 = R. 8, and 1901, p. 59 = R. 74) and Kuckuck (1894, p. 232, 1912, p. 180) discussed the different forms of the plurilocular zoidangia in *S. caespitula*. Lund (1950, p. 16) discussed the occurrence of remnants of the walls of the loculi in emptied plurilocular zoidangia. According to Sauvageau the walls between the loculi are only peripheral, and do not traverse the central part of the zoidangium. For that reason no or almost no remains of the walls of these loculi should be present in emptied plurilocular zoidangia. Lund, however, described plurilocular zoidangia in which these walls of loculi were more persistent. As shown in my fig. 150 the walls of the loculi do (at least sometimes) traverse the central part of a plurilocular zoidangium. Persistence and non-persistence of walls of loculi can be sometimes found in parts of the same zoidangium (fig. 136).

As described before, the plurizoids escape together through an apical aperture. In a figure published by Kornmann & Sahling (1977, f. 84D) the apical aperture can be observed, but some small pores of loculi seem to be present as well. The ellipsoid or cylindrical plurilocular zoidangia have often been found in nature (fig. 135; 136), but the subspherical ones I have only seen in my culture 68-48-6 (fig. 137). Kuckuck (1912, p. 179) observed, described, and figured (*l.c.* t. VIII, f. 4A) the plurizoids. He stated that no fusion of plurizoids took place, even when he brought together plurizoids from different zoidangia. As in his description of the unizoids he stated that the plurizoids usually contain one chloroplast and only occasionally two. I have not seen mature plurizoids, but in the loculi of an almost mature plurilocular zoidangium I observed always two chloroplasts in each loculus (fig. 151).

Kuckuck (1912, p. 179, t. VIII, f. 4C) also tried to study the germlings of the plurizoids. His figure gives a three-celled filament, found four weeks after dehiscence of the plurilocular zoidangia and grown from an unfused zoid. In my cultures I often observed germlings of both unizoids and plurizoids but usually only the older stages. In all cases a basal disc was formed, from which at first few, but later many erect filaments arose.

The available data do not permit any conclusion with regard to the life-history model which could be applied to *S. caespitula*.

Systematic position. *Sphacelaria caespitula* is one of the two species in *Sphacelaria* which still have the same name as when published by Lyngbye in 1819. In his discussion of the branching systems of the *Sphacelariales* Sauvageau (1903, p. 334 = R. 268) suggested *S. olivacea* Pringsheim and *S. caespitula*, together with *S. radicans*, may belong to the subgroup 'Acladées' of the 'Sphacélariacées hemiblastées'. For further discussion about this group see *S. radicans* (p. 79).

The radial pattern of longitudinal walls, as seen in cross-sections, separates *S. caespitula* (and *S. radicans*) from all other *Sphacelaria*-species with frequently occurring transverse walls in the secondary segments of their erect filaments. The narrow filaments of *S. caespitula* have sometimes been mistaken for *S. rigidula* or *S. nana*. Sauvageau (1901, p. 394 = R. 150) stated that possibly even Lyngbye confused *S. caespitula* and *S. furcigera* (= *S. rigidula*). Usually the number of transverse walls in *S. caespitula* suffices to separate these species.

Lund (1950, p. 12) united *S. olivacea* Pringsheim emend Sauvageau and *S. caespitula* under the last-mentioned name. Sauvageau (1901, p. 56 = R. 71) united *Sphaceloderma helgolandicum* Kuckuck and *S. olivacea* Pringsheim emend Sauvageau, as described above.

TABLE VII. Comparison between S. mirabilis, S. plumigera, S. caespitula, and S. radicans

	S. mirabilis	S. plumigera	S. caespitula	S. radicans
number of superposed discs in basal crust	several	one or two	several	one or two
rhizoids	absent	corticating	absent	divaricate
dimensions apical cells in upper layer of discs				
diameter	2–15	13–16.5	10–23	7–23
height	5–17	10–16.5	10–20	12–19
germlings	discoid or filamentous	irregularly discoid	discoid	discoid
hairs on germlings	absent	present	absent	sometimes present
diam. of cells	often < 5	10–20	10–20	(7–)10–15(–18)
unilocular zoidangia	stalked, spherical, elliptical, or obovoid, in sori on basal disc	stalked, sperical or ovoid, in groups on ultimate or penultimate det. laterals	stalked (occasionally sessile?), spherical or subspherical, solitary on proximal parts of erect filaments	sessile, occasionally stalked, spherical or ovoid, usually geminate, all over the filaments
length	44–60	(30–)45–70(–85)	80–110	(40–)42–65
width	40–52	(25–)40–60(–65)	60–110	(30–)40–60
plurilocular zoidangia	long-cylindrical or conical, solitary, or in small groups on basal disc or stolons	cylindrical, ellipsoid, or obovoid, in groups on ultimate or penultimate det. laterals	subspherical, cylindrical, or ellipsoid, solitary on proximal parts of erect filaments	cylindrical or ellipsoid, solitary, or in small groups all over the filaments
length	40–65	45–80	75–125(–160)	65–115(–170)
width	20–30	30–40	(40–)60–95(–130)	37–60(–63)
diameter loculi	6–7	5–7	3–5	2.5–6
diameter filaments	15–25	(10–)75–100	(13–)18–30(–35)	(19–)25–60
number of longitudinal walls	0–1(–2)	7–10	1–4(–5)	(2–)3–6(–7)
marked pericysts	absent	absent	often present	present
branching	very scarce, irregular	pinnate	usually scarce, irregular, not pinnate	usually scarce, irregular, never pinnate

dimensions in µm

For comparison between *S. plumigera*, *S. radicans*, *S. caespitula*, and *S. mirabilis* see table VII. *Sphacelaria caespitula* has often been found mixed with *S. plumosa*. The filaments of the latter are always much thicker than the filaments of *S. caespitula*. For comparison between *S. caespitula* and other *Sphacelaria* species with narrow filaments see table X.

Sauvageau (1902, p. 400 = R. 212) mentioned acroheteroblastic branching in specimens of *S. caespitula* (as *S. olivacea*) from Denmark. Later (1909, p. 69) he was less sure and supposed that it might be a separate (yet undescribed) species. I have also observed acroblastic branching of *S. caespitula* in my culture 67-47-1, but in this case it was acrohomoblastic branching. In the related species *S. radicans* acroheteroblastic branching has been observed quite often, without giving rise to the speculation that these acroheteroblastic specimens should belong to a separate species. In *S. caespitula*, however, hairs have not been observed on any other occasion. The Danish specimens, occurring near the border of their geographic area and probably in more brackish water than where the other specimens grew, are probably somewhat aberrant specimens of *S. caespitula*.

4. **Sphacelaria nana** Naegeli *ex* Kützing—**Fig. 152–211, plate 3b, 4**

Sphacelaria nana Kützing (1855) 26, t. 87, f. 1.—Type: *Naegeli 214*, Torquay (L, sh. 937.71-710, lecto; HBG, M, W).—See also notes on nomenclature 1.

Sphacelaria olivacea Greville (1824b) 314 (*p.p., excl. typo*); J. Agardh (1848) 30 (*p.p.*); Traill (1887) p. 77, t. II, f. 2 (*excl. syn.*); Holmes (1887) 80 (*excl. syn.*); De Toni (1895) 500 (*p.p.*); Sauvageau (1901) 61 (= R. 76); Newton (1931) 189; Kylin (1947) 27.—*Sphacelaria radicans* forma *olivacea* Batters (1889) 60.—*Sphacelaria radicans* var. *olivacea* Traill (1890) 282.—*Sphacelaria britannica* Sauvageau (1901) 53 (= R. 69), f. 16; Børgesen (1902) 432; Jónsson (1903) 159, f. 16; (1904) 41; Hamel (1938) 251; Waern (1945) 402, t. II; Lund (1950) 22, f. 3; Waern (1952) 95; Irvine (1956) 26; Van den Hoek (1958b) 188, f. 1a–c; Jorde & Klavestad (1960) 95, f. 5; De Haas-Niekerk (1965) 152, f. 34–43; Jaasund (1965) 69; Blackler & Jackson (1966) 85; Prud'homme van Reine (1974) 174; Russell & Fletcher (1975) 766; Prud'homme van Reine (1978) p. 303.—Type: *Sphacelaria radicans* var. *olivacea, Batters* in Hauck & Richter, Phycoth. Univ. n. 320, Berwick-upon-Tweed, January 1888 (PC, lecto; isotype-duplicates in many other herbaria).—See also notes on nomenclature 2.

Sphacelaria olivacea auct. non (Dillw.) Grev.: Kuckuck (1894) 232, f. 6.—*Sphacelaria furcigera* var. *saxatilis* Kuckuck (1897) 373, f. 1, excl. K, N, O (*p.p.* only 'Rasen'); Newton (1931) 189 (*p.p.*); Waern (1945) 401 (*p.p.*).—*Sphacelaria saxatilis* Sauvageau (1900) 217 (= R. 5), (1901) 53 (= R. 69), (1909) 71; Kylin (1947) 28; Lund (1950) 27, f. 4; Sundene (1953) 158; Irvine (1956) 27; De Haas-Niekerk (1965) 152; Jaasund (1965) 70; Prud'homme van Reine (1978) 303.—Type: *Kuckuck s.n.*, Helgoland, Westspitze, 28/1/1896 (PC, lecto; isotypes in BM, BR, C, HELG, L, M, PC).—See also notes on nomenclature 3.

Plants forming low felty mats (fig. 152) or small felty patches (fig. 153), dark brown to olive, turning greenish when dried. The plants are gregarious or caespitose, and quite flaccid. They are epilithic or occur on sediment bottoms among halophytes, or occasionally they are epiphytic (fig. 153). Many unbranched or sparingly branched erect filaments arise from the creeping basal parts of the plants (fig. 154–156).

In early stages the basal part is a circular basal disc with marginal growth. The young disc is monostromatic and consists of a number of radiating, branched, coalescent, creeping filaments with apical growth (fig. 157–159). In later stages the basal disc may become polystromatic by upward growth and subsequent division of the intercalary cells of the coalescent creeping filaments or by formation of new monostromatic discs by the basal parts of erect filaments (fig. 160). The polystromatic discs are usually only a few cells thick, but

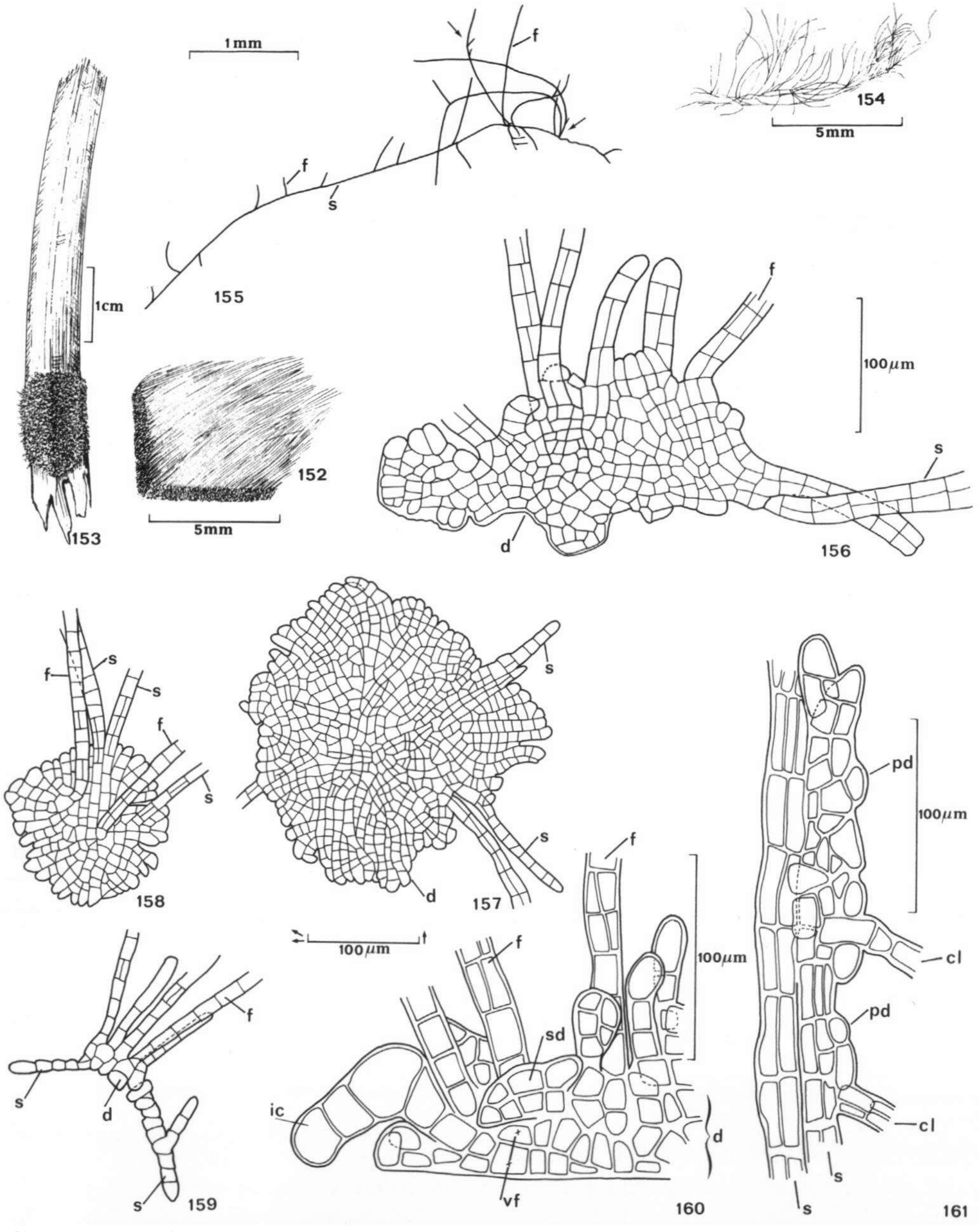


Fig. 152–161. Sphacelaria nana. 152, 153. Habit (152. Mat on rocks; 153. Epiphytic on *Scirpus maritimus*); 154, 155. Details of habit; 156, 160. Sections; 157–159. Germlings of unizoids (157. From below; 158. From above; 159. Lateral view); 161. Two linked stolons. cl. creeping lateral; d. basal disc; f. erect filament; ic. irregular clump of cells; pd. disc formed by proliferation of stolons; s. stolon; sd. superposed basal disc; vf. vertical file of cells. 152. Berwick-upon-Tweed, *Batters* (L, soaked); 153. Terschelling, *Prud'homme van Reine 1947* (formalin); 154. Roscoff, mole, *Prud'homme van Reine 428* (L, soaked); 155. Culture 72-13; 156. Saltholm, *Lund* (C, microslide); 157. Culture 67-64-4; 158, 159, 161. Culture 66-3-5; 160. Culture 67-34-3.

sometimes they become much thicker or form small irregular clumps of cells (fig. 160). Usually many stolons are formed, in some cases directly from the germinating zoids and without formation of a disc. From the long creeping stolons many unbranched, erect, flexuous, flaccid laterals arise perpendicularly (fig. 155). Not all laterals of stolons are perpendicular; new stolons arise as laterals from the older ones, and their angle of branching is quite sharp (fig. 161; 162). Often the stolons form one or several small discs (fig. 163). Sometimes several (2–8) stolons link together and grow alongside each other. Occasionally many cells of stolons proliferate and form long and narrow attachment discs, which may become quite extensive when the majority of the linked stolons and their creeping laterals form these proliferations (fig. 161; 162).

Occasionally scattered, solitary, usually unbranched, hypacroblastic laterals arise from the older parts of the erect filaments. These laterals of the second order are irregularly placed (never pinnate), usually appressed or sharply divaricate and they have indeterminate growth (fig. 155, arrow; 162).

There is no difference in growth or dimensions between the erect filaments and their laterals. The laterals in the proximal parts of the erect filaments often grow into rhizoids (fig. 165) or into stolons. The rhizoids never corticate the erect filaments, but by their intricate growth they bind the erect filaments together (fig. 166). Usually the diameter of stolons is larger than that of erect filaments, while the diameter of the more twisted rhizoids is usually smaller (fig. 162).

The dimensions of the inferior and superior secondary segments of erect filaments are quite variable. Usually segments in sterile parts of erect filaments are longer than they are wide (fig. 156; 164; 165), and in fertile parts of erect filaments they are often much shorter than they are wide (fig. 164). The diameter of the erect filaments is often quite irregular and local swellings occur (fig. 167; 168). Occasionally the superior secondary segments are shorter and wider than the adjacent inferior secondary segments (fig. 168). Secondary segments are usually subdivided by radial walls (fig. 169–172) and occasionally secondary transverse walls also occur (fig. 164). There are no medullar cells, all cells of the filaments are peripheral cells. Branch initials cannot be distinguished from other cells by dimensions, colour, or marked difference in contents.

In lateral view 0–2 (–4) longitudinal walls can be observed in secondary segments (fig. 164; 165). Solitary hairs are very rare; they have been found on germlings of unizoids in culture (fig. 173; 174).

There are no propagules but fragments of all filaments can grow into new attached plants again.

The stalked unilocular zoidangia are solitary (fig. 166), geminate (fig. 175), or occur in small groups (fig. 176; 177; 179; plate 3b) on the proximal parts of erect filaments and their laterals (fig. 164; 175; 177) and often also on the stolons (plate 3b) and on the basal discs. The stalks are often short and unicellular (fig. 175) or formed by 2–5 segments (fig. 164; 177; 179), but longer and multi-cellular stalks occur as well (fig. 179). The monosiphonous stalks become polysiphonous when longitudinal walls are formed in their cells (fig. 164; 175; 177; 179). Usually only one unilocular zoidangium is formed on each stalk (fig. 164; 175; 177), but after discharge of the zoids the upper stalk-cell may grow out and form a new unilocular zoidangium, often partly inside the remnants of the wall of the empty unilocular zoidangium (fig. 178). Occasionally dichasium-like branching of stalks of uni-

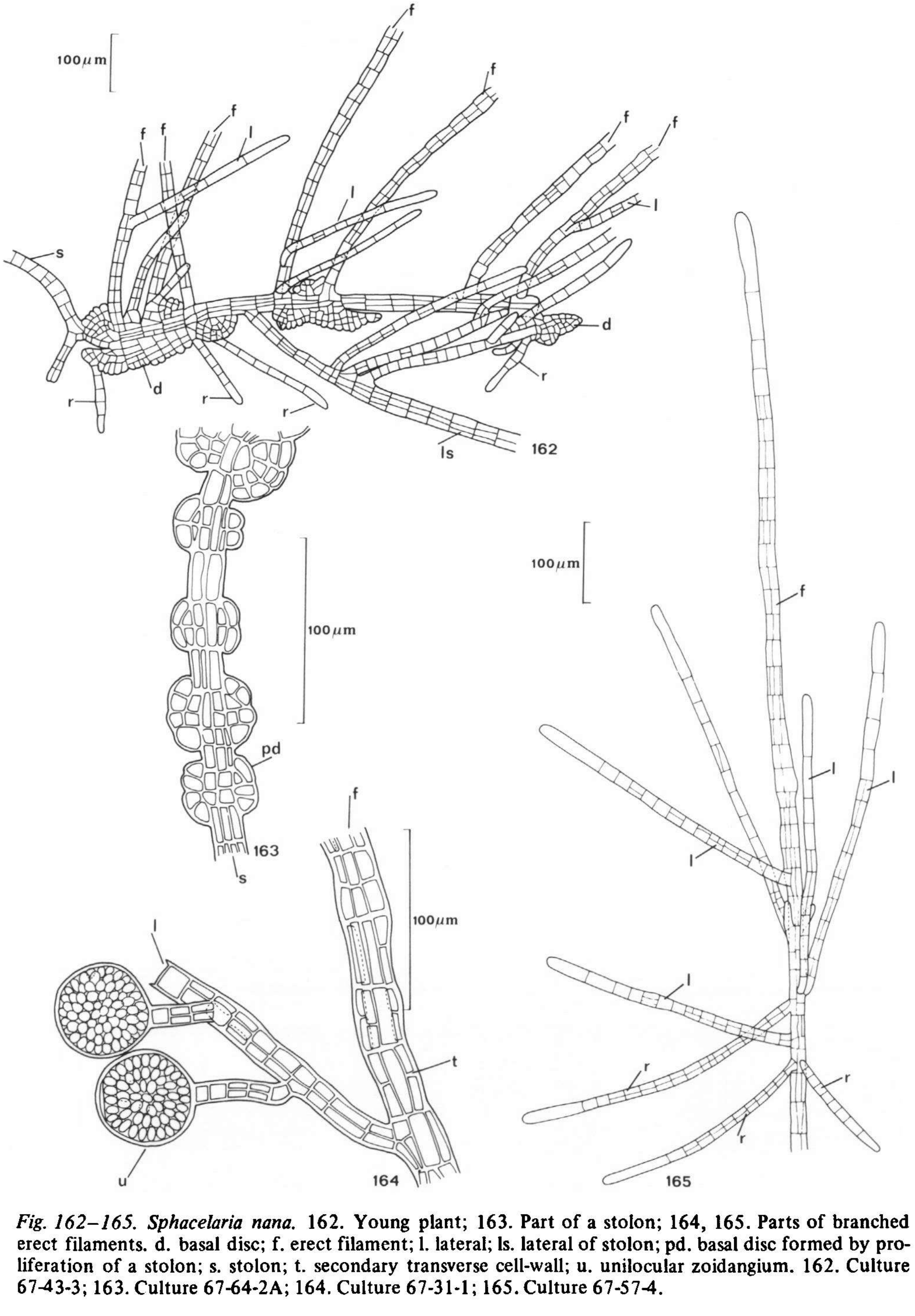


Fig. 162–165. Sphacelaria nana. 162. Young plant; 163. Part of a stolon; 164, 165. Parts of branched erect filaments. d. basal disc; f. erect filament; l. lateral; ls. lateral of stolon; pd. basal disc formed by proliferation of a stolon; s. stolon; t. secondary transverse cell-wall; u. unilocular zoidangium. 162. Culture 67-43-3; 163. Culture 67-64-2A; 164. Culture 67-31-1; 165. Culture 67-57-4.

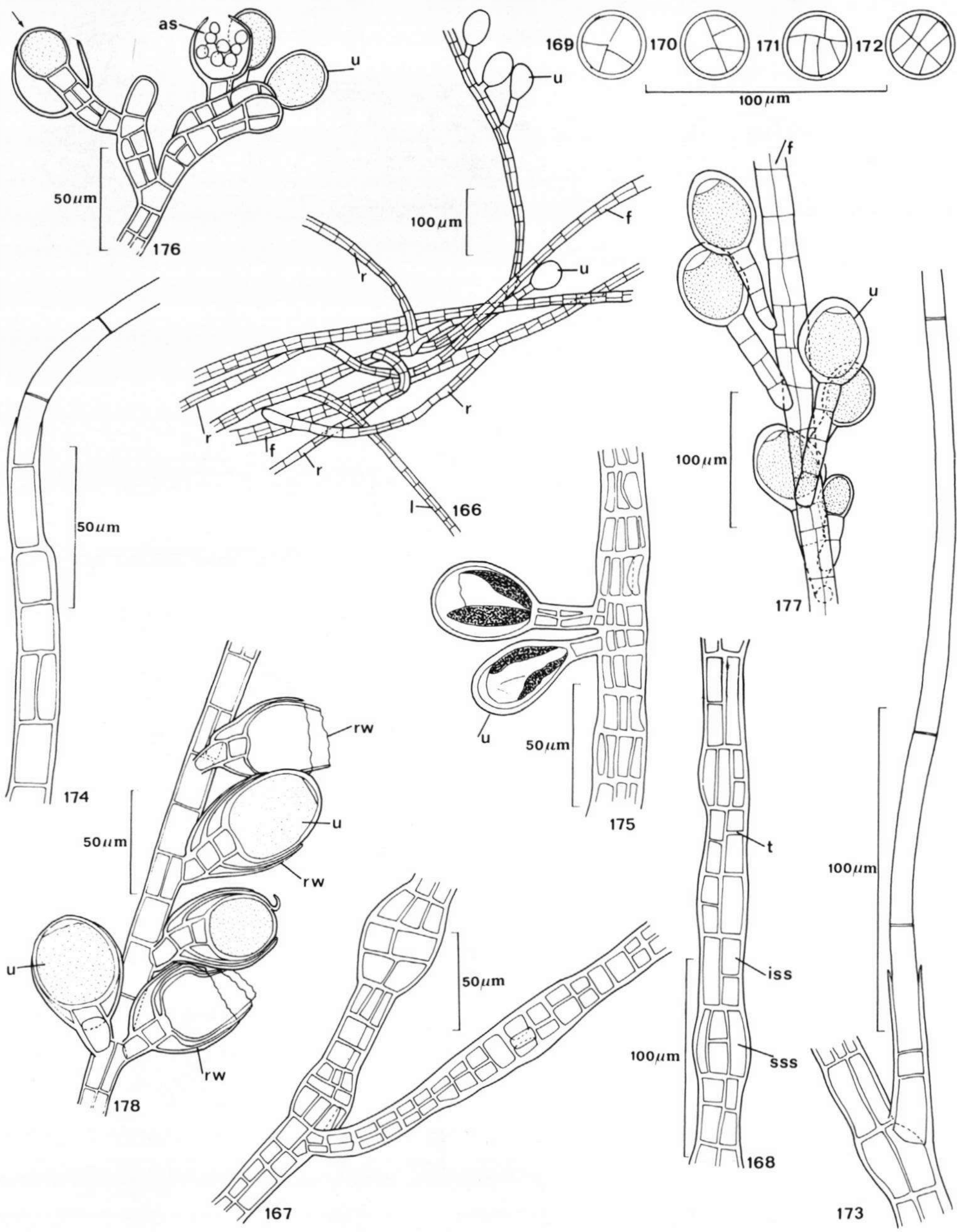


Fig. 166–178. Sphacelaria nana. 166. Erect filaments and intricate rhizoids; 167, 168. Parts of erect filaments with swellings; 169–172. Cross-sections of erect filaments with swellings; 173, 174. Hairs; 175–178. Unilocular zoidangia. as. aplanospore; f. erect filaments; iss. Inferior secondary segment. r. rhizoid; rw. remnants of the wall of a zoidangium; sss. superior secondary segment; t. secondary transverse cell-wall; u. unilocular zoidangium. 166. Culture 67-34-3; 167. Culture 67-77-1; 168. Culture 66-3-4; 169–172. St. Andrews, *Prud'homme van Reine 71-17* (permanent microslides); 173, 174. Culture 67-31-1; 175. Heligoland, *Kuckuck* (C, microslide); 176. Culture 67-64-4; 177. Saltholm, *Lund* (C, microslide); 178. Culture 66-3-5.

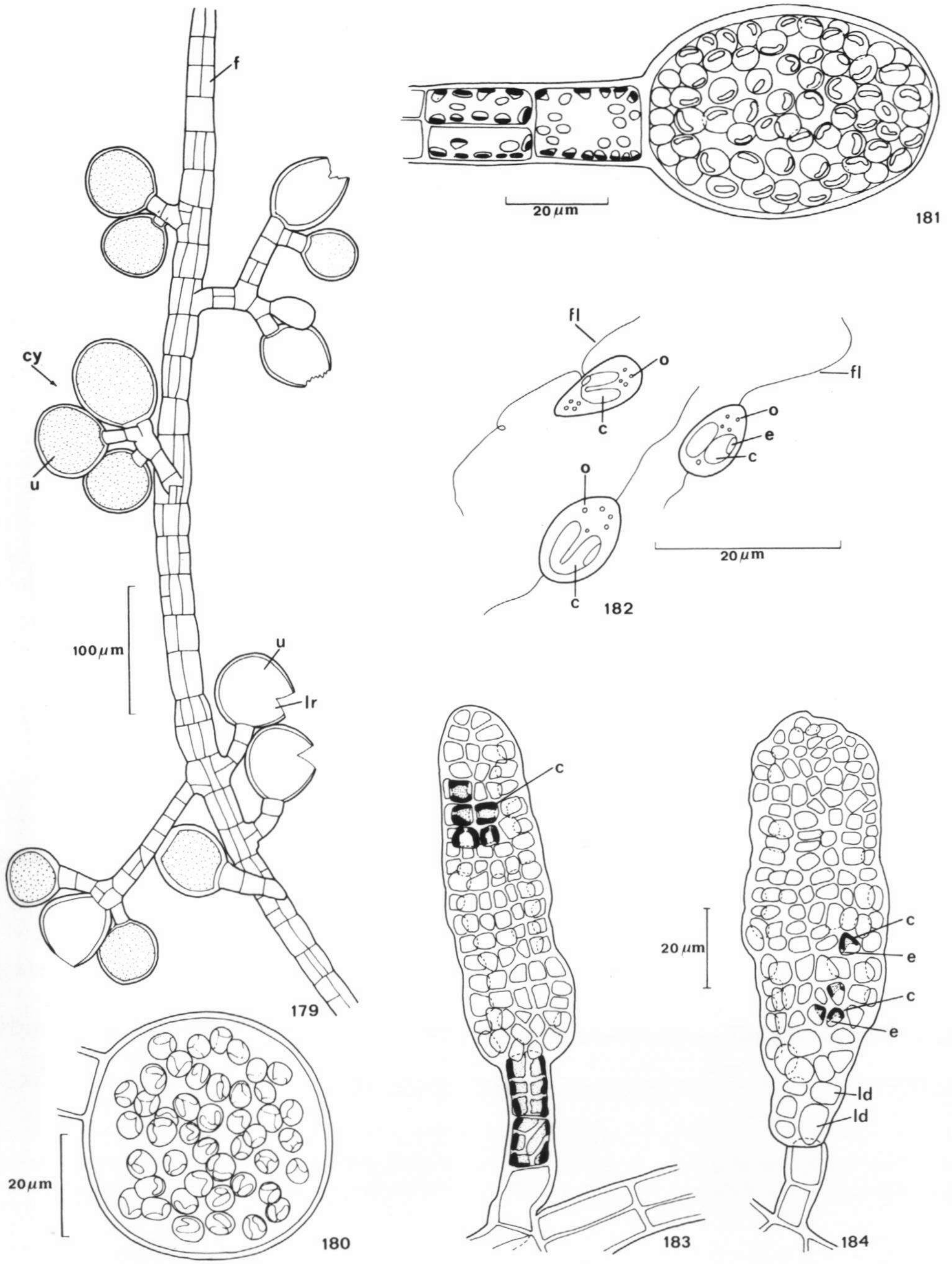


Fig. 179–184. Sphacelaria nana. 179–181. Unilocular zoidangia; 182. Unizoids; 183, 184. Plurilocular zoidangia (183. Dark-coloured; 184. Light-coloured). c. chloroplast; cy. cyme; e. eye-spot; f. erect filament; fl. flagella; ld. less-divided cells; lr. lateral rupture; o. oil-like drop; u. unilocular zoidangium. 179. Culture 67-71-1; 180. Culture 72-13; 181. St. Andrews, *Prud'homme van Reine 71-17* (fresh); 182. Culture 67-64-4; 183, 184. Culture 66-3-6.

locular zoidangia has been observed (fig. 179). Unilocular zoidangia are (sub)spherical (fig. 164; 179; 180), ellipsoid (fig. 181), or (ob)ovoid (fig. 175; 177) when mature, ovoid or ellipsoid when young. Unizoids are pear-shaped, or somewhat rounded. They have a chloroplast which is folded in two and on which an eye-spot is located (fig. 182).

Unilocular and plurilocular zoidangia are located on separate plants. The plurilocular zoidangia have a uniseriate (fig. 183–186; 189; 190) or a polysiphonous stalk (fig. 187) with 2–4 (to many) segments. Occasionally young lateral plurilocular zoidangia develop from the stalk of an older one (fig. 188). Plurilocular zoidangia are solitary or arranged in small groups (fig. 189; 190), usually on the proximal parts of erect filaments, on creeping filaments, or on basal discs (fig. 191). Occasionally small plants are almost fully covered by plurilocular zoidangia (plate 4). Mature plurilocular zoidangia are usually elongate and irregularly cylindrical (fig. 183–187; 189; 190; 192), and often somewhat curved (fig. 189; 190). The 3–6 segments of a plurilocular zoidangium (fig. 192) each form many loculi and usually a central schizogenous cavity can be observed in one or several of these segments (fig. 187;194). Plurizoids have not been observed, but individual pores in loculi of discharged plurilocular zoidangia have often been found (fig. 194; 195). In loculi of (almost) mature plurilocular zoidangia a chloroplast and an eye-spot can be observed (fig. 183–186; 192).

Dimensions: Plants up to 1 cm high (usually less) and mats sometimes covering an area of several m². Diam. basal discs (100–) 320–480 μm., of rhizoids 12–15 (–20) μm. Angle of ramification in erect filaments 0–50°, in stolons 80–90° (erect filaments), or 20–50° (lateral stolons). Diam. of stolons 21–35 μm, in local swellings 37–45 μm, diam. of erect filaments (12–) 16–23 (–30) μm, in local swellings 30–38 μm. Height of secondary segments of erect filaments 8–40 (–50) μm. Hairs 10–12 μm in diam. (with sheath), or 5–9 μm (without sheath). Chloroplasts 2–5 X 3–7 (–9) μm (see fig. 196). Unilocular zoidangia (21–31) –33–58 (–70) μm in diam., stalks (9–) 12–17.5 μm in diam. Unizoids 6–11 X 4.5–7 μm. Plurilocular zoidangia (33–) 50–130 (–180) X 16–33 (–41) μm, loculi (3–) 4–6 (–8) X (2–) 3–4 (–5) μm, stalks 10–15 μm in diam.

Distribution. Greenland. Europe: Iceland, Faeroes, Norway, Sweden, Denmark, Heligoland, The Netherlands, United Kingdom, Eire, French Atlantic coasts.

The species is also known to exist on the northern American coasts of the Atlantic Ocean. It has also been noted in localities in Spain, Italy (Adriatic Sea), U.S.S.R. (Black Sea), and on Madeira.

European localities have been listed and are given in fig. 193. In most herbaria specimens of *S. nana* have been named *S. britannica*. It is almost impossible to distinguish sterile *S. nana* from sterile filaments of the haploid generation of *S. rigidula* when growing in small patches.

For an extract of the list of collections and references see below.

GREENLAND. West coast. Three collections/references.—East coast. Kap Dalton (Jónsson, 1904, p. 41).—Without exact locality. 'e Groenlandia', (as *S. simpliciuscula*), *Gieseke*, 14/3/1818 (C, LD, PC).

ICELAND. (I have not seen any sample of *S. nana* from Iceland, and specimens in C named *S. nana* by Jónsson are *S. radicans*. According to literature on Iceland *S. nana* grows always together with *S. radicans*. The figure by Jónsson (1903, p. 159, f. 16) is quite characteristic).—Northwest coast. Dyrafjördur (Munda, 1972b, p. 13).—Southwest coast. Borgarfjördur (Munda, 1978b, p. 459).—North coast. Three references.—South coast. Vestmanneyjar (Jónsson, 1903, p. 159).

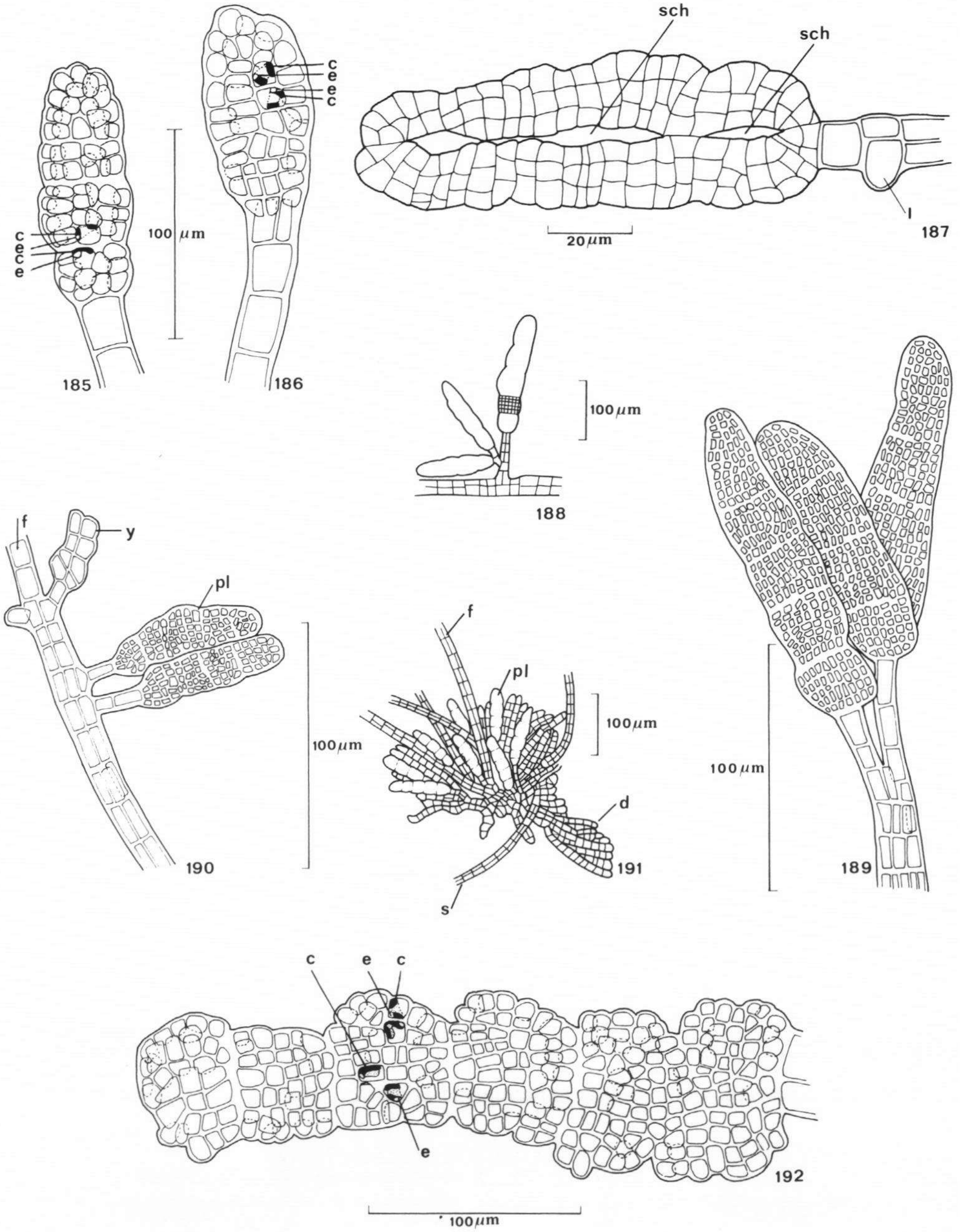


Fig. 185–192. Sphacelaria nana. Plurilocular zoidangia. 185. Light-coloured; 186. Dark-coloured; 187. Optical section. c. chloroplast; d. basal disc; e. eye-spot; f. erect filament; l. lateral initial; pl. plurilocular zoidangium; sch. schizogenous cavity; y. young plurilocular zoidangium. 185, 186. Culture 68-53-1; 187. Culture 66-3-6; 188, 191. Culture 67-31-1; 189. Heligoland, *Kuckuck* (C, microslide); 190. Hirsholmene, *Lund* (C, microslide); 192. Culture 67-64.

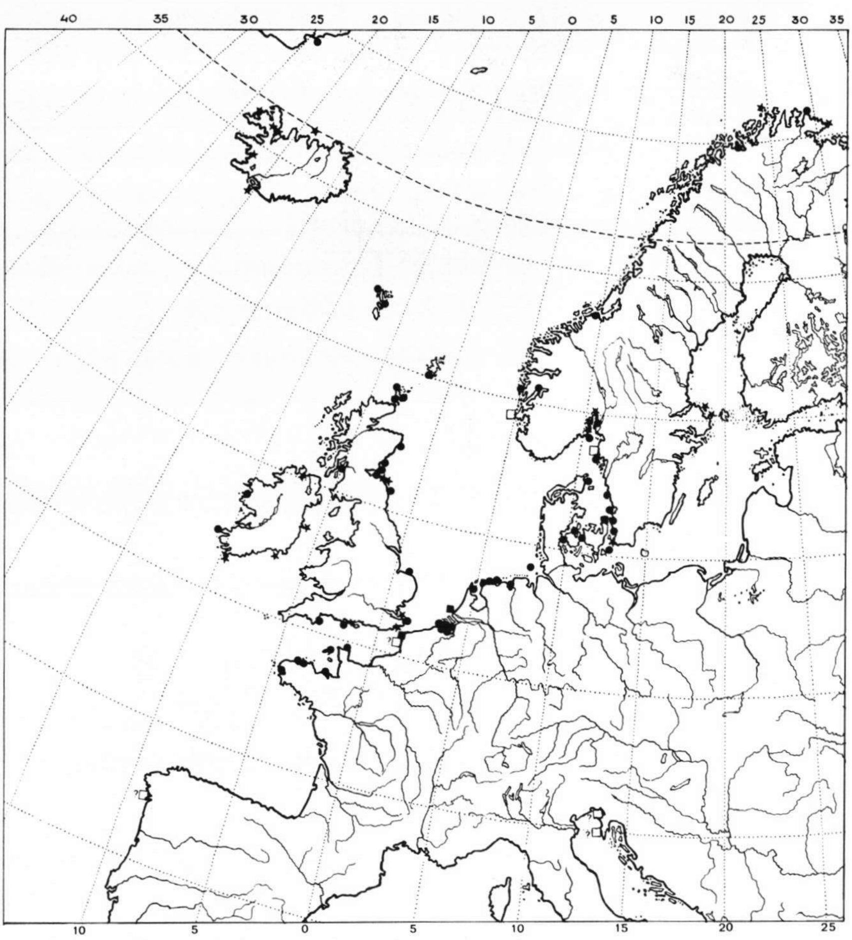


Fig. 193. Distribution of *S. nana* in Europe.

● = Material seen by the author; *S. nana.*
■ = Material seen by the author; *S. nana* or *S. rigidula* ?
★ = According to literature, most probably *S. nana.*
□ = Uncertain material or locality.
? □ = According to literature, but probably *S. rigidula.*

FAEROES. Two collections.

NORWAY. Finmarken. Four collections/references, amongst which Altenfjord: Talvik, *Kjellman*, 7/9/1876, in Areschoug: Algae Scand. exs. ser. nov. n. 410 (BG, GB, HBG, L, PC, W).—Nordland. Without exact locality: (as *S. arctica*), *Kleen* (UPS, mixed with *S. radicans*).—Sör Tröndelag. Trondheimsfjord: Selva, on wood, *Polderman*, 14/8/1973 (L).—Hordaland. More than three collections.—Rogaland. Haugesund: Kvalin, (as *S. olivacea*), *Norum* (?, BG).—Vestfold. Three collections/references.—Buskerud. Oslofjord: Tofteholmen (Sundene, 1953, p. 157).—Akershus. More than six collections/references.

SWEDEN. Bohuslän. Two collections/references.—Halland. Varberg. Subbe: (as *S. olivacea*), *Hylmö*, 12/1920 (LD, mixed with *S. radicans*).—Skåne (Kristianstads Län). Hallands Väderö: Lilla Orskär, (as *S. radicans*), *Suneson*, 5/7/1939 (LD).—Skåne (Malmohus Län). Three collections/references.—Stockholms Län. Two references.

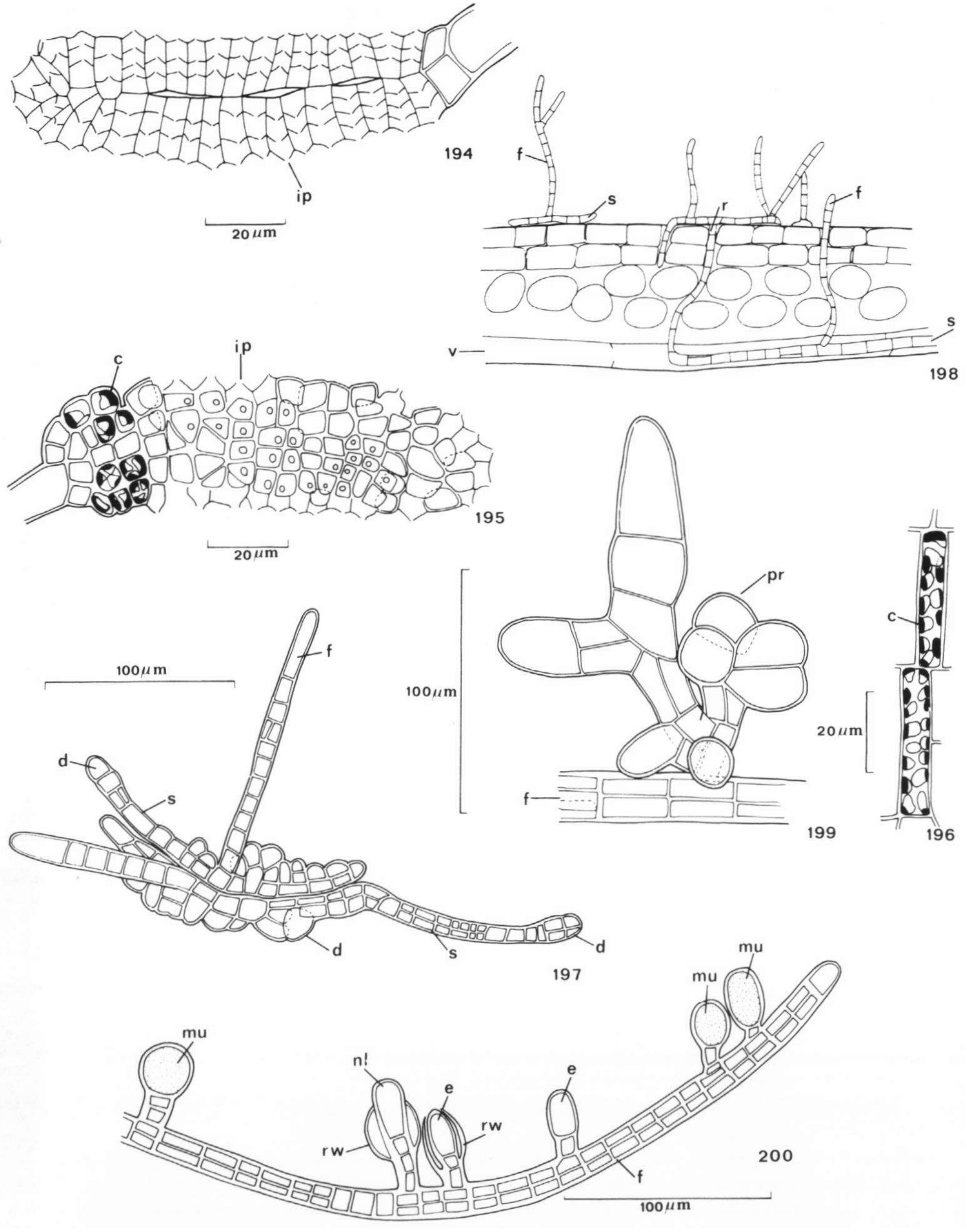


Fig. 194–200. Sphacelaria nana. 194, 195. Old plurilocular zoidangia (194. Optical section); 196. Vegetative cells; 197. Two filamentous germlings forming a basal disc together; 198. Growth of *S. nana* on a dead rhizome of a salt-marsh phanerogram (semi-diagrammatic); 199. Proliferation; 200. Mini-zoidangia. c. chloroplast; d. basal disc; e. empty; f. erect filament; ip. pores of individual loculi; mu. mini-zoidangium; nl. new lateral; pr. proliferation; r. rhizoid; rw. remnants of the wall of a mini-zoidangium; s. stolon; v. vessel. 194, 195. Culture 66-3-8; 196, 197. Culture 67-31-1; 199. Culture 72-13; 200. Culture 67-64-5.

DENMARK. Kattegat. Two collections.—Samsø area. Two collections.—Lille Baelt. Aarösund: Mole, (as *S. olivacea*), *Rosenvinge 9371*, 16/6/1922 (C).—Store Baelt. Kerteminde: Havnemole, Yders, *Rosenvinge 9176*, 9/6/1922 (C).—Öresund. Saltholm: on stones, 1 m deep, *Lund*, 17/4/1947 & 24/1/1948 (C, mixed with *S. radicans*).

GERMANY. Heligoland. Two collections.

THE NETHERLANDS Wadden Islands. Texel: Mokbaai, salt-marsh, *Huwae*, 28/4/1977 (L). Terschelling: six collections. Ameland: Ballumerbocht, Stroomleidam, on limestone, *Huwae*, 15/2/1977 (L). Schiermonnikoog: Westerkwelder, salt-marsh with *Puccinellia*, *Huwae*, 14/2/1977 (L).—Dollard. Punt van Reide: on wood, *Huwae*, 28/12/1976 (L).—Zuid-Holland. Hoek van Holland: Northern mole, on wood, *Van den Hoek 1151*, 23/1/1954 (?L, mixed with *S. rigidula*).—Zeeland. Tholen: three collections. Walcheren: two collections. Zuid Beveland: more than thirteen collections. Zeeuws Vlaanderen: more than four collections.

UNITED KINGDOM. Shetland. Mainland: Spiggie, Peerie Geo, cave wall, *Irvine*, 24/4/1963 (D. Irvine, pers. coll.).—Orkneys. Four collections.—Scotland. Bute: Cumbrae, Clash Farland Point, (as *S. fusca*), *Fucus serratus* belt, *Van den Hoek 2140*, 4/9/1954 (L, mixed with *S. radicans* and *Cladostephus spongiosus*). Aberdeen: (as *S. olivacea*) *Dickie*, (BR, L, both mixed with *S. radicans*). Angus: Arbroath, Mason's Cave, *Jack*, 5/5/1893 (STA). Fife: more than three collections/references. Midlothian: Edinburgh, Leith, Black Rocks, (as *Conferva olivacea*), *Berkeley*, 3-1821 (BM; CONC and PC mixed with *S. radicans* and *Cladostephus spongiosus*). East Lothian: Dunbar (Traill, 1890, p. 282). Berwickshire: Cove Harbour (Norton, 1976, p. 23).—England. Northumberland: more than three collections, amongst which Berwick-upon-Tweed, *Batters* in Hauck & Richter, Phycoth. Univ. n. 320 (BM and many other herbaria; in L and ZA mixed with *S. radicans*); and in Holmes, Algae Brit. rar. exs. n. 96 A (BM, BR, KIEL, OXF). Norfolk: Holkham, *Polderman NF24*, 30/4/1973 (L). Kent: two collections/references. Devon: Torquay, (as *S. nana* and *S. radicans*), *Nägeli K. 214*, 1845 (CN, CO, FI; in HBG, L, M, and W mixed with a few filaments of *S. radicans*). Dorset: two collections. Hampshire: Keyhaven (Polderman, 1978, p. 237). Sussex: Hastings (Tittley & Price, 1978, p. 505).—Channel Islands. Guernsey: two collections.—Northern Ireland. Lough Foyle (Blackler, 1951, p. 126).

EIRE. Mayo: Roonah, cave, on boulders, (as *S. radicans* var. *olivacea*), *Cotton 198*, 15/2/1911 (BM). Kerry: three collections. Dublin: Lambay (Batters, 1907, p. 109). Cork: Loch Ine (Cullinane, 1973, p. 40). Waterford: Dunmore (Cullinane, 1973, p. 80).

FRANCE. Atlantic coasts. Pas-de-Calais: two doubtful references. Manche: Le Béquet, walls of the harbour, together with *Cladostephus spongiosus* and *S. radicans*, *Prud'homme van Reine 467*, 29/3/1968 (L). Ille-et-Vilaine: St. Lunaire, St. Enogat, cave, *Prud'homme van Reine 297*, 17/3/1968 (? L). Finistère: more than three references.

Doubtful references:

SPAIN. Ria de Arosa (Donze, 1968, p. 187).
MADEIRA. Madeira and Porto Santo (Levring, 1974, p. 28).
ITALY. Trieste (Giaccone, 1969, p. 499).
YUGOSLAVIA. Istria (Giaccone, *l.c.*).
U.S.S.R. Black Sea. Crimea (A. Zinova, 1967, p. 150, as *S. saxatilis*).

Notes on nomenclature. (1) Not all material marked 'Torquay, *K.214*, 1845, *S. radicans*' is type-material of *S. nana*. In CN, CONC, and FI I found only *S. radicans* in this material, and in HBG, L, M, and W always some filaments of *S. radicans* were found amongst the many filaments of *S. nana*.

(2) The descriptions and synonymy of *S. olivacea* by Greville, J. Agardh, and De Toni were partly based on *Conferva olivacea* Dillwyn (= *S. radicans*), partly on *S. caespitula* and *S. nana*. Sauvageau based his concept of *S. britannica* on Hauck & Richter 320.

(3) Kuckuck based his description of *S. furcigera* var. *saxatilis* on two different entities: small bushes with filaments with hairs and propagules (= *S. furcigera* → *S. rigidula*), and velvety mats with unilocular and plurilocular zoidangia on separate but entangled filaments (= *S. saxatilis* → *S. nana*).

Notes on morphology. In the secondary segments of *S. nana* only few longitudinal walls are formed. All walls are more or less radial, never periclinal. All mature cells are peripheral and can function as branch-initials, except cells in which secondary transverse walls have been formed. Large pericyst-like cells have never been observed. Usually the diameter of erect filaments varies considerably within short distances. The outline of the filaments is often undulate (fig. 164; 167; 179) and occasionally the diameter may become twice its normal dimension in local swellings (fig. 167). Laterals are not formed from immature secondary segments as is normal in most other *Sphacelaria* species. Erect filaments are often devoid of laterals, or few laterals are formed at a considerable distance from the apical cell. These laterals are not comparable with normal hemiblastic laterals, but they are adventitious or secondary laterals, as described by Sauvageau (1903, p. 334, = R. 268) for *S. radicans*. Laterals do not always sprout from superior secondary segments. They may also arise from two successive secondary segments, or laterals may be separated by two (or another even number) of secondary segments.

In specimens with a conspicuous basal part the monostromatic or polystromatic discs are often covered by intricate growth of stolons and rhizoids. In genuine polystromatic basal discs distinct vertical files of cells can be observed. In *S. nana* often no genuine discs are formed, but irregular clumps of cells which can grow in all directions. These nodules do not attach to the substrate, but are embedded between grains of sand, other algae, and rhizoids and stolons of the *S. nana* mats. There is no strict difference between basal discs and irregular nodules. The basal part of the specimen in fig. 156 is intermediate. Usually basal discs of neighbouring germlings do not grow over each other, but they form together a new disc (fig. 197).

Notes on ecology. The dense carpets of *S. nana* can be found on sheltered, humid, and shaded localities in the upper part of the littoral zone in northern Norway, on Heligoland, in the northern part of The Netherlands, on the coasts of the North Sea of Scotland and England, and in some localities along the southern coast of England (Torquay, Swanage). These dense carpets can be found on rocks in Norway, Heligoland, Scotland, and England, but also in salt-marshes, as observed in The Netherlands and in Great Britain. In St. Andrews, Scotland, I observed on the rocks a continuous band of *S. nana* mats which was about 30 cm broad. It was situated just above a similar band which consisted mainly of *S. radicans*. Both bands were found on steep (almost vertical) north-facing cliffs and above the zone where *Fucus spiralis* grew. Often *Blidingia minima* could also be found growing between the filaments of both species of *Sphacelaria*. These two species grew together in a very narrow transitional zone, but in the distinct bands they formed almost pure growths. In large caves *S. nana* formed a much broader band (up to 1 m broad) just below a zone of *Waerniella lucifuga*. In these caves the ceiling and the darkest walls were covered with *Rhodochorton purpureum*. The latter species also formed a felty layer in a band below the broad band of *S. nana*. In February 1971 *S. nana* formed many unilocular zoidangia when growing on the north-facing cliffs, but the specimens in the caves were always sterile. When growing in those distinct bands the felty mats of *S. nana* were lighter brown and less thick than those of *S. radicans*, but always darker brown and thicker than the mats of *Waerniella lucifuga*.

In the dense carpets from Berwick-upon-Tweed and Torquay usually some filaments of

S. radicans can be found. In places where no distinct felty mats of *S. nana* occur, small patches of *S. nana* can often be found together with *S. radicans* and/or *Rhodochorton purpureum*. It is sometimes difficult to separate the prostrate narrow filaments of *S. nana* form those of *S. radicans* (see also section 'Notes on morphology' of *S. radicans*, p. 73). Van den Hoek (1958b, p. 188–193) described the algal vegetation of caves and shaded habitats near Roscoff and from the Boulonnais (northern France). He named this vegetation the association of *Gelidium pusillum* and *Callithamnion polyspermum*. Around Roscoff he almost always found *S. nana* in this vegetation, and often also *S. radicans*. *Cladostephus spongiosus* forma *spongiosus* has also quite often been found together with *S. nana* and *S. radicans* in shaded localities (see also Van den Hoek, *l.c.*) or in the undergrowth of vegetations dominated by *Fucus vesiculosus* or *Ascophyllum nodosum*.

Jónsson (1912, p. 119 & 123) described the Sphacelarietum britannici which forms part of the *Rhodochorton*-association. On Iceland this community can be found in shady places in the *Fucaceae* belt and also higher up in the littoral zone. *Sphacelaria nana* has been found in the *Fucaceae* belt in Norway, The Netherlands, Great Britain, and France. It occurred in the lower part of the belt of *Pelvetia canaliculata* (Norway, Espegrend), in the *Fucus spiralis*, *Fucus vesiculosus*, and *Ascophyllum nodosum* belts at many localities and occasionally in the *Fucus serratus* belt (Kattendijke, The Netherlands). In some cases in The Netherlands *S. nana* has been found together with *S. rigidula*. It is, however, impossible to separate sterile filaments of *S. nana* from narrow sterile filaments of *S. rigidula* (see also section on 'Taxonomic position', p. 113). It is quite possible that both species occur more often together, but that in those cases the filaments of *S. nana* have not been recognized so far.

In brackish waters with a salinity that does not vary much (i.e.: the Baltic) *S. nana* has been found permanently submerged. Lund (1950, p. 22 as '*S. britannica*' and p. 27 as '*S. saxatilis*') found it at depths of 1 and 4–10 m, respectively, in Dènmark. Hylmö found it at a depth of 5 m near Vikhög, Skåne, Sweden (acc. to specimen in LD), and Waern (1945, p. 403 and 1952, p. 96) found it at depths from 3.5–11.5 m in the Swedish Öregrund Archipelago. In the last-mentioned locality it still grew together with *Rhodochorton purpureum* and *S. radicans* in the undergrowth of the *Fucus vesiculosus* belt which is also sublittoral there. In the narrow middle part of the Oslofjord, where salinity may vary slightly during the year *S. nana* has been found just above the low-water line. It has, however, also been found at depths of 1–5 m, often together with *Fucus vesiculosus*. In brackish waters where salinity varies more during the year or even during the day (like the Hardangerfjord in Norway and the Westerschelde in The Netherlands) *S. nana* has only been found high up in the littoral, however. Von Wachenfeldt (1975, p. 216) classified it as a polyhalobe, pleioeuryhaline species.

A curious mode of growth is shown by *S. nana* when growing on wood. Sauvageau (1901, p. 61 = R. 76) discussed specimens collected by Kjellman at Talvig, Norway, found growing on wood of a Conifer and named by Kjellman *S. olivacea*. The sterile specimens formed stolons which grew through the tracheids of the wood and flexuous erect filaments which grew out of the wood through the pits of these vessels. Sauvageau compared this mode of growth with that of saprophytic fungi. I observed this peculiar habit also in dead stems and rhizomes of salt-marsh plants (fig. 198). Young plants formed stolons and erect filaments inside the dead salt-marsh plants. Rhizoids may find a possibility (an aperture or a weak spot between two epidermal cells) to grow in between the cells and into the dead tissue of the salt-marsh plant. When such a rhizoid entered a vessel it changed into a stolon which may form erect filaments. These erect filaments grew more or less perpendicularly to the stolons and grew out of the tissue again. I observed this particular habit in specimens from Talvik, Norway (Areschoug: Algae Scand. exs. 410, in coniferous wood); Selva, Norway (*Polderman*, in coniferous wood); Terschelling, The Netherlands (several collections, in salt-marsh plants); and several other localities in The Netherlands: Punt van Reide, Vlissingen, Sas van Goes, Yerseke, Wemeldinge, Strijenham, Nummer Een, Hoofdplaat, Walsoorden and Baalhoek (all in wood) and from St. Andrews, Scotland (r. Eden, in salt-marsh plants). If growing on wood in which the vessels or tracheids were perpendicular to the surface, the rhizoids grew deep in the wood but the prostrate stolons could only be found creeping over the surface.

Sphacelaria rigidula has also been found growing on wooden poles. In some cases it could be found on the same pole as *S. nana*, but usually most plants of *S. rigidula* grew on a lower part of the pole than most plants of *S. nana*. In Vlissingen (The Netherlands) Huwae found both species growing together in a small transitional zone. Later he also found both species together on poles in The Netherlands at the Punt van Reide and at Hoofdplaat (Huwae pers. comm.). In Hoek van Holland Van den Hoek probably found this mixture as well (see section 'Systematic position', p. 113).

As described above, *S. nana* can grow in dead salt-marsh plants. On most salt-marshes, however, it grows directly on the soil, usually on places where not much silt will be deposited. On steep sandy or clayey walls on the terminal part of small creeks, it may form its velvety patches or it may grow in more flaccid mats in which the prostrate filaments dominate over the erect ones. I found the velvety patches on the Orkney Islands, near St. Andrews, near Hasmark on Fünen, Denmark, and on the salt-marsh of De Kom on the island of Terschelling. Vegetations on salt-marshes in Dorset and Hampshire (Polderman, 1978, p. 237) were probably also of this type. The flaccid mats were found by Huwae on the salt-marshes of the Dutch Wadden Islands Texel and Schiermonnikoog. Occasionally *S. nana* has been found as intricate prostrate filaments growing in between other algae, especially between *Catenella caespitosa*. This type of growth has been found on a clayey dike in Norfolk (Polderman, 1974a, p. 19); on the Dutch salt-marshes 'De Dellewal' (Terschelling) and 'De Slurf' (near Sas van Goes, Zuid-Beveland) and on a clayey dike near Nummer Een, Zeeuws-Vlaanderen (Polderman, 1974b, p. 93).

Form range and cultures. Morphological variation in the erect filaments of *S. nana* is insignificant. Variation occurs mainly in the number of secondary transverse walls in the secondary segments. Variation in the prostrate part of the plant is much larger. In Scandinavia (Iceland, Norway, Denmark) and in Heligoland often distinct polystromatic basal crusts can be found, but specimens in the United Kingdom, The Netherlands, and in France are usually devoid of distinct basal discs and form small occasional monostromatic discs by proliferating stolons. Stolons of specimens from the latter area (but also in specimens growing on and in wood from Norway) may be long (several mm or even several cm). Usually specimens with polystromatic basal crusts form many short thick stolons and intricate rhizoids, which cover the crusts. In specimens from the southwestern part of the area usually the many long stolons grow radially from the central part of the plant. The diameter of these stolons is only a little larger than that of the erect filaments. In the central parts of the plants stolons, intricate rhizoids and small discs concentrate, and form many erect filaments. Usually many plants grow together to form velvety mats. The erect filaments are usually perpendicular laterals of the first order of the prostrate stolons, only occasionally erect filaments grow directly from basal discs. In many specimens the erect filaments are devoid of laterals of the second order, especially when growing in wood. In the velvety mats cells in the proximal part of erect filaments usually form scattered secondary laterals. The angle of branching in the erect filamentous parts of *S. nana* is usually narrow and often the laterals bend directly to grow parallel to the filament from which they sprouted.

Cultures have been isolated from material collected from the coasts of Norway (Espegrend, Øystese, Tjøme, Drøbak), The Netherlands (Terschelling, Sas van Goes, Kattendijke, Walsoorden, Baalhoek), England (Norfolk), and France (Le Béquet, St. Enogat, Térénez and Roscoff). Some of these cultures and their subcultures have been maintained during more than ten years. *S. nana* grew well in culture at 4°C, 12°C, and 20°C, but at higher light-intensities (2500–5500 Lx) often many apical cells died off and later many other cells too. At 20°C few straight erect filaments could be found, most erect filaments and their laterals bent downwards and grew into rhizoids. At 12°C at light-intensities of 700–1400 Lx rhizoidal growth was still conspicuous, but at light-intensities of 400–700 Lx the straight or slightly curved erect filaments were in a majority.

Usually in cultures started from isolated fragments of sterile erect filaments the algae did not grow attached to the substrate. When larger fragments of plants, provided with stolons and/or rhizoids were transferred into new culture-tubes or in petri-dishes they often attached quite easily. In unattached specimens the erect filaments grew radially in all directions and rhizoids and irregular clumps of cells often formed a solid centre of the growing algal balls. In attached specimens the number of stolons, their mode of growth, and the extent of proliferation to form basal discs varied considerably within each isolate, but usually in cultures of Norwegian material the basal discs were more prominent than in Dutch material. When *S. nana* in cultures sporulated the germlings attached well to the walls of culture-tubes and petri-dishes and usually the number of discs increased. The morphology of erect filaments was similar in all cultures. Some specimens formed peculiar proliferations in culture (fig. 199).

Reproduction and life-history. Unilocular zoidangia are well known, but plurilocular zoidangia have only been observed by Kuckuck (1897, p. 373, as *S. furcigera* var. *saxatilis*), Lund (1950, p. 27, as *S. saxatilis*), Sundene (1953, p. 158, as *S. saxatilis*), Jaasund (1965, p. 70, as *S. saxatilis*), and Blackler & Jackson (1966, p. 85, as *S. britannica*). In March 1968 I found many specimens of *S. nana* with long plurilocular zoidangia among filaments of *S. nana* with unilocular zoidangia. These filaments grew together with filaments of *S. radicans*, also with unilocular zoidangia. The specimens had been collected from the northern wall of the old mole of the harbour of Roscoff, a well-known locality for both species.

In culture specimens originating from Norway (Espegrend, Øystese, Drøbak), The Netherlands (Kattendijke), and France (Roscoff, Le Béquet) formed plurilocular zoidangia after having been kept for several years. Usually these plurilocular zoidangia were found at 4°C on germlings from unizoids, only occasionally on larger plants grown from fragments from plants collected from nature (Øystese, Roscoff).

Unilocular zoidangia are common in specimens collected in winter and early spring. I obtained them also in culture in specimens originating from Norway (Espegrend, Øystese, Drøbak), The Netherlands (Kattendijke), and France (Roscoff, Le Béquet). In most cultures these unilocular zoidangia were found on normal plants (or even on unattached plants) grown at 4°C from fragments of sterile specimens found in nature. Usually they have short uniseriate or somewhat polysiphonous stalks. In some cultures, however, many apical cells of erect filaments were transformed into unilocular zoidangia. The diameter of the often almost spherical normal mature unilocular zoidangia is 40–60 (–70) µm, but in some cultures also very small unilocular zoidangia have been observed (fig. 200). These mini-zoidangia have a diameter of 22–31 µm. I have not seen any mature zoids in the mini-zoidangia, but often they seem to be empty. Waern (1952, p. 96) found no normal unilocular zoidangia in the Baltic, but he observed some of these mini-zoidangia. De Haas-Niekerk (1965, p. 152) found these mini-zoidangia too, according to the variations in diameter of unilocular zoidangia she published.

In most cultures with normal unilocular zoidangia the unizoids were released through a narrow apical pore in the wall of the zoidangium (fig. 176).

Occasionally the walls of unilocular zoidangia were ruptured apically (fig. 178) or laterally (fig. 179). As described for *S. radicans* (see p. 79), the unizoids were usually enclosed in a common mucilage-envelope. When the elastic membrane of this envelope bursts the unizoids separate from each other. The zoids with their sharply curved chloroplast (fig. 182) on which the eye-spot is not always distinct did not move very fast and usually they attached within 20 minutes after release.

Often not all unizoids were released, and the remaining spores (fig. 176) did not form flagella (or if they did, they shed them very soon). These aplanospores germinated in situ into filamentous germlings. Occasionally all or almost all spores in a unilocular zoidangium formed filaments and the basal parts of these filaments formed irregular clumps of cells ('nodules') which later were often covered by rhizoids. The newly formed filaments grew among the filaments of the old plant and together they formed in culture velvety patches or algal balls again. Occasionally a distal cell of the stalk grew into the empty unilocular zoidangium and formed a new zoidangium (fig. 176; 178) or a vegetative filament. In some cases this process may be repeated several times, resulting in small unilocular zoidangia with a collar made of the remnants of the walls of several older ones (fig. 178). Stalks of unilocular zoidangia are usually not branched, but occasionally they sprout laterally and form lateral unilocular zoidangia (fig. 179).

The attached unizoids are globose and they grow into germlings without embryospore formation (fig. 201). Occasionally the wall of the original unizoid is more prominent than that of the other cells of the germlings (fig. 202; arrows). In cultures originating from material from Kattendijke, The Netherlands, most germlings were filamentous (fig. 202) or only a small disc was formed (fig. 203). Most filaments of these germlings were prostrate and functioned as stolons, but erect filaments also occurred (fig. 204). Germlings with a well-developed basal disc are of less frequent occurrence in these cultures (fig. 158; 159). In cultures originating from material from Espegrend, Norway, germlings from unizoids usually started to form monostromatic discs (fig. 205) and later also stolons (fig. 206). In cultures originating from material from Drøbak, Norway, the discs of the germlings are usually conspicuous (fig. 157). On these germlings plurilocular zoidangia were formed from unizoids in all cultures. The plurilocular zoidangia started to grow from the basal discs (fig. 191) or stolons, but later they could also be found on erect filaments (fig. 190; plate 4). I have not

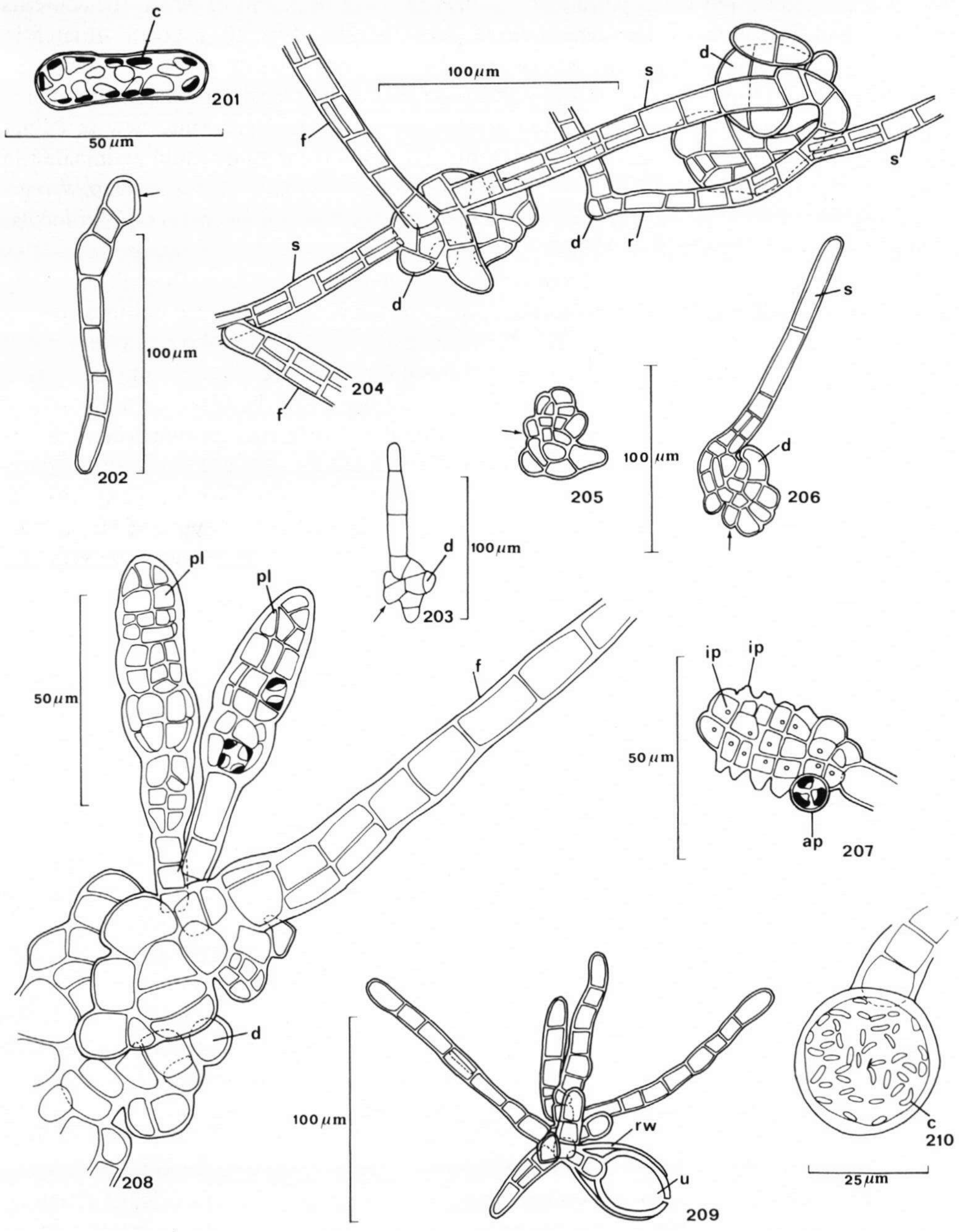


Fig. 201–210. ***Sphacelaria nana.*** 201–206. Germlings; 207, 208. Plurilocular zoidangia; 209. Fertile germling; 210. Mini-zoidangium. ap. aplanospore; c. chloroplast; d. basal disc; f. erect filament; ip. pores of individual loculi; pl. plurilocular zoidangium; r. rhizoid; rw. remnants of the wall of a unilocular zoidangium; s. stolon; u. unilocular zoidangium. 201, 205, 206. Culture 67-31-1; 202–204. Culture 72-13; 207. Culture 68-53-1; 208. Culture 67-64; 209. Culture 66-3-8; 210. Culture 67-64-5.

seen any plurizoids, but often plurilocular zoidangia could be found of which the contents of loculi had been released through a narrow pore (fig. 194; 195; 207). Loculi situated in deeper layers of the plurilocular zoidangia released their contents into the superposed loculi (fig. 194). Often some loculi did not release their contents which remained immobile (aplanospores). These aplanospores often germinated in situ and grew into new germlings (fig. 207). Occasionally all loculi of a segment of a plurilocular zoidangium germinated in this way or entire plurilocular zoidangia transformed into vegetative tissue. This new vegetative tissue may grow into a nodule or into a basal disc and erect filaments; new plurilocular zoidangia may arise from it (fig. 208).

In some cultures two different types of plurilocular zoidangia occur. They differ mainly in colour, one being dark brown, the other type being very light. In some cultures (66-3-5 & 66-3-6, both from Kattendijke, The Netherlands) I thought to observe a very slight difference in the dimensions of the loculi of those different types, but drawings made from this material did not endorse this (compare fig. 183 and 184). In other cultures (67-64, from Øystese and 68-53-1 from Le Béquet) I found no difference in dimensions of the loculi, only in the dimensions of the chloroplasts (compare fig. 185 and 186). In the dark-brown zoidangia it is often impossible to locate the eyespots (they have not been drawn in fig. 183). It is tempting to think about the possibility that these two types of plurilocular zoidangia may contain ♂ and ♀ gametes, but since no gametes have been observed, this assumption cannot be affirmed. Perhaps those different types represent different stages of growth, maturation, or vitality of the plurilocular zoidangia.

In most culture-tubes, containing specimens with plurilocular zoidangia, after a few months germlings occurred. These germlings did not differ from germlings of unizoids. In some cultures these germlings, presumptive of plurizoids, formed zoidangia again. The majority of the fertile new germlings formed unilocular zoidangia, occasionally on very small plants (fig. 209). In some cultures, however, germlings with plurilocular zoidangia have been found as well. In my cultures of material originating from Roscoff all germlings of plurizoids formed new plurizoids.

Apart from germlings with normal unilocular zoidangia in culture 67-64 also germlings have been found which formed many unilocular zoidangia of much smaller dimensions and a 1–2-celled stalk. These mini-zoidangia have often been found on germlings which grew among germlings with plurilocular zoidangia (fig. 200; 210). I never observed mature unizoids in these mini-zoidangia. Occasionally the chloroplasts were arranged in a similar way as in almost mature normal unizoidangia (fig. 210). Often the contents of many mini-zoidangia seemed to have been released (fig. 200). In many of these empty mini-zoidangia I observed no pore, however. Occasionally mini-zoidangia had a collar of remnants of the walls of older ones (fig. 200). More frequently filaments have been formed from the cells of the stalks of mini-zoidangia (fig. 200), in several germlings all laterals had such a collar. Germlings with mini-zoidangia have been isolated and cultured in separate culture-tubes. In some of these tubes after 2–3 months new germlings could be found, while the original germlings had grown into mature plants, still covered with mini-zoidangia. On some erect filaments of these mature plants, apart from mini-zoidangia, also few subspherical structures could be detected growing on multicellular stalks. These subspherical structures resembled unilocular zoidangia but did not manifest any sign of formation of zoids. The newly formed germlings bore once more either plurilocular zoidangia or mini-zoidangia. The diameter of the laterals of mature plants with mini-zoidangia was similar to that of the narrow filaments bearing plurilocular zoidangia (see table VIII). These plants with mini-zoidangia are probably comparable to the haploid unilocular zoidangia-bearing phase described for *S. rigidula* (see Van den Hoek & Flinterman, 1968, p. 207–208, as *S. furcigera*).

Owing to the lack of caryological investigations in *S. nana* the life-history of this species cannot be described in full. In accordance with the observations of Van den Hoek & Flinterman (*l.c.*) a hypothetical life-history of *S. nana* may be drafted. The data are compatible with the image of a slightly heteromorphic diplo-haplontic life-history with plurilocular gametangia and unilocular asexual zoidangia (fig. 211).

Systematic position. Two well-known entities, *S. britannica* and *S. saxatilis*, merge into the circumscription of *S. nana*. Several authors, viz. Sauvageau (1901, p. 53 = R. 69), Waern (1945, p. 402), Kylin (1947, p. 29), Lund (1950, p. 29), Irvine (1956, p. 26), and Jaasund (1965, p. 69) discussed the characters of these two entities. Often they decided that there was not much difference. Jaasund (*l.c.*) suggested that the two taxa might be united into one species, but he did not make a formal decision. It had been assumed that the two entities differ in prostrate parts and in propagation. The plurilocular zoidangia of *S. saxatilis* had been described as elongate (see also table IX), but similar organs in *S. britannica* were unknown until Blackler & Jackson (1966, p. 85) described them. It was stated that the difference in diameter between prostrate filaments and erect filaments was more prominent in *S. saxatilis* than in *S. britannica*. *S. saxatilis* had mainly been described from localities in Norway, southwestern Sweden, Denmark, and Heligoland. *Sphacelaria britannica* was reported from a much wider area, including the coastal regions where *S. saxatilis* had been found (except Heligoland) but also the coasts of Greenland, Iceland, the Faeroes, the

TABLE VIII. Diameter of mature erect filaments (in µm) in S. nana

culture	reproductive structure on filaments		
	unilocular zoidangia	plurilocular zoidangia	mini-zoidangia
66–3–5	(15–) 20–25		
66–3–6	20–23	15–17.5	
66–3–7	18–22.5		
66–3–8	16–22.5		
66–6–1	20–22.5		
67–31–1	16–22.5	13.5–18	
67–34–3	20–22.5	11–16 (–18)	
67–57		16–18	
67–64–1	(15–) 20–23	(9–) 11–16 (–18)	16–18
67–64–4		12–16 (–22.5)	(7–) 16–18 (–22)
67–77–1	(16–) 20.5–23 (–31)		
68–49–3		14–17	
68–53–1	22.5–27	9–16 (–18)	
variation in diameter	(15–) 18–25 (–31)	(9–) 11–18 (–22.5)	(7–) 16–18 (–22)

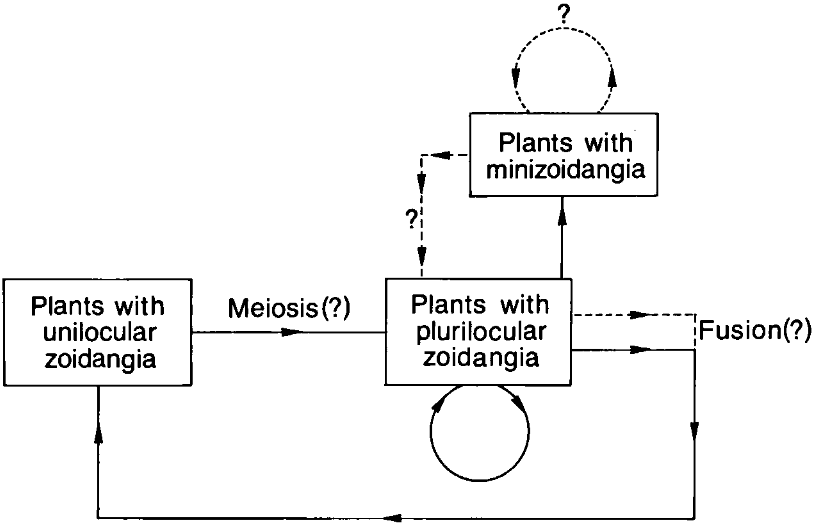


Fig. 211. Diagram of the hypothetic life-history of *S. nana.*

United Kingdom, Eire, and France. Sundene (1953, p. 157) found both species occurring together in Oslofjord. Recently Kornmann & Sahling (1977, f. 83 B) published a photograph of a typical specimen of *S. britannica* (as *S. radicans* with stalked unilocular zoidangia on its rhizoids).

In my cultures of material from Norwegian origin the basal parts were usually much better developed than the basal parts of material originating from localities in The Netherlands or in France. In some of my isolates from Kattendijke (The Netherlands), however, the development of the basal parts was similar to the Norwegian ones. When comparing old isolates of different origin, not having been transferred into new culture tubes for several months, the differences in development of basal discs had disappeared. When plurilocular zoidangia had been formed in culture, isolates of Norwegian origin usually possessed mainly distinctly elongated plurilocular zoidangia, while isolates originating from Dutch or French localities often formed less elongated plurilocular zoidangia (compare fig. 188; 191; 192 of Scandinavian isolates with fig. 183; 184; 187; 194, and 195 of Dutch isolates, and fig. 185; 186, and 207 of isolates of French origin). When measuring the dimensions of the plurilocular zoidangia, however, differences in proportions or length/width ratio of these plurilocular zoidangia were not established (see table IX). The dimensions given for the width of plurilocular zoidangia by Blackler & Jackson (1966, p. 85) are larger than all others. They found only a small number of plurilocular zoidangia and they did not succeed in isolating plurizoids or germlings (Jackson, 1966). It is possible that the plurilocular zoidangia found by Blackler & Jackson were old ones similar to somewhat aberrant ones that occasionally have been found in cultures (fig. 192).

I consider both entities to belong to the species *S. nana.* The differences between the populations are small and gradual, and there are no boundaries between the entities. It is even impossible, therefore, to circumscribe the assumed entities *S. saxatilis* and *S. britannica* as infraspecific taxa within *S. nana.* De Haas-Niekerk (1965, p. 152) synonymized *S. saxatilis*

TABLE IX. Dimensions of plurilocular zoidangia in S. nana

origin	culture or reference	zoidangia dimensions in µm	length/width ratio
Heligoland	Kuckuck (1897)	70–120 x 22–28	2.5–5.5
Denmark	Lund (1950)	33–150 x 16–25	1.3–7.8
Norway (Oslofjord)	Sundene (1953)	60–120 x 30–35	1.7–4.0
N. Norway	Jaasund (1965)	70–130 x 20–27	2.5–6.5
Scandinavia	var. in S. saxatilis (litt.)	33–125 x 16–35	1.3–7.8 (av. 2.0–6.5)
Norway, Espegrend	67–31–1	117–160 x 25–33	3.5–6.5
Norway, Espegrend	67–34–3	45–90 x 22.5–29	1.5–4.0
Hardangerfjord	67–57	68–110 x 25–30	2.3–3.7
Oslofjord	67–64	95–130 x 35–40	2.4–3.7
Oslofjord	67–64–1	60–90 x 16–23	2.6–5.6
Oslofjord	67–64–3	70–85 x 21–23	3.0–4.0
Oslofjord	67–64–4	60–95 x 25–30	2.0–3.8
Oslofjord	67–64–5	85–135 x 20–30	2.8–6.4
Isolates from Norway	var. cultures	45–160 x 16–40	1.5–6.4 (av. 2.5–4.7)
Scandinavia	var. cultures + litt.	33–160 x 16–40	1.3–7.8) (av. 2.3–5.3)
Scotland	Blackler & Jackson (1966)	88–125 x 33–41	2.0–3.8
The Netherlands	66–3–5	43–120 x 22–28	2.0–6.0
The Netherlands	66–3–6	50–60 x 25	2.0–2.4
The Netherlands	66–6–1	56–150 x 21–25	2.2–7.1
France, Roscoff	68–49	68–180 x 18–33	2.0–10.0
France, Le Béquet	68–53–1	45–55 x 22–25	1.7–2.5
Isolates from Scotland, The Netherlands, France	var. cultures	43–180 x 18–33	1.7–10.0 (av. 2.0–5.6)
	var. cultures + litt.	43–180 x 18–41	1.7–10.0 (av. 2.0–5.3)

with her *S. fusca* (= *S. rigidula*) and considered *S. britannica* to be a separate species. Van den Hoek & Flinterman (1968, p. 213), however, declared it to be reasonably certain that *S. furcigera* (= *S. rigidula*), *S. saxatilis*, and *S. britannica* are synonymous. De Haas-Niekerk and Van den Hoek & Flinterman based their conclusions on the description by Kuckuck (1897, p. 373) of *S. furcigera* var. *saxatilis*. This description, however, was an amalgamation of descriptions of two different entities, *i.e.* *S. rigidula* and *S. nana* (see also notes on nomenclature 3, p. 104).

Vegetative filaments of *S. nana* cannot be separated from vegetative filaments of the haploid phase of *S. rigidula* and from the narrow filaments occasionally formed by *S. radicans*. To name such filaments they have to be cultured. An extra difficulty is that *S. nana* can often be found together with these narrow filaments of *S. rigidula* or of *S. radicans*. For comparison between the *Sphacelaria* species with narrow filaments see tables X and XI.

Van den Hoek & Flinterman (1968) isolated their cultures for their investigations on the life-history of *S. rigidula* from narrow sterile filaments collected at Hoek van Holland. In an earlier publication Van den Hoek (1958a, p. 204) supposed similar filaments belong to *S. britannica*. In one collection at the Leiden herbarium (*Van den Hoek 1151*) I found

TABLE X. Comparison of some Sphacelaria-species which may have narrow filaments

	S. nana	S. rigidula	S. radicans	S. arctica	S. caespitula
diameter of narrow filaments	(12–)16–23(–30)	13,5–32(–37)	20–24	20–30	(13–)18–30(–35)
secondary transverse cell walls	few	occasional	few	few	many
propagation organs on narrow filaments	uni- and plurilocular zoidangia	small unilocular zoidangia, plurilocular gametangia propagules	none	unilocular zoidangia	uni- or plurilocular zoidangia
In plants with normal mature erect filaments					
diameter of filaments	(12–)16–23(–30)	13,5–32(–37) (haploid phase)	(19–)25–60	25–45(–49)	(13–)18–30(–35)
secondary transverse cell walls	few	occasional	many	many	many
marked pericysts	absent	absent	present	absent	of irregular occurrence
polystromatic basal disc	occasional	absent	occasional	usually present	present
pluriloc. zoidangia:					
dominant form	long cylindrical	stout cylindrical	stout cylindrical	long cylindrical	stout cylindrical
dimensions: l	(33–)50–130(–180)	60–130(–200)	65–115(–170)	65–200	75–125(–160)
b	16–33(–41)	(25–)50–60	37–60(–63)	25–50(–55)	(40–)60–95(–130)
uniloc. zoidangia:					
arrangement	solitary, stalked	solitary, stalked	geminate, sessile	solitary or in racemes, stalked	solitary, stalked
dimension: l	(21–)33–58(–70)	45–85	(40–)42–65	(40–)45–60(–75)	80–110
b	(21–)29–57(70)	45–85	(30–)40–60	(37–)40–55(–62)	60–100
mini-zoidangia:					
diameter:	21–31	20–25	-	-	-

dimensions in µm

TABLE XI. Comparison of sterile filaments of S. tribuloides, S. rigidula, and S. nana

	S. tribuloides	S. rigidula	S. nana
tufts	usually dense	usually dense	quite open
basal discs	small, monostromatic	small, monostromatic or polystromatic	small or extensive, monostromatic or polystromatic
diameter erect filaments (in µm)	(20–)23–50(–70)	(10.5–)16–45(–52)	(12–)16–23(––30)
branching	absent or scattered	scarce or frequent	absent or scarce
rhizoids	usually absent	often formed from laterals	often formed from laterals
secondary transverse cell-walls	rare	occasional	occasional
solitary hairs	usually frequent	absent, scarce or frequent	usually absent

narrow *S. nana*-like sterile filaments together with broader filaments of *S. rigidula*. The cultures of Van den Hoek & Flinterman formed propagules at 12°C and at 20°C, a phenomenon never observed in cultures of *S. nana*. Germlings of unizoids of Van den Hoek & Flinterman's isolates formed plurilocular gametangia which were mainly of a stout cylindrical type. Only occasionally plurilocular zoidangia of a slender cylindrical type occurred. In *S. nana* most plurilocular zoidangia are of a slender cylindrical type (see also table X).

Sphacelaria nana is not to be synonymized with *S. rigidula*. These species are not even closely related: *S. rigidula* with its many propagules is doubtless a member of the section *Furcigerae* of the subgenus *Propagulifera*, while *S. nana*, which is always devoid of propagules, evidently does not belong to that subgenus. Another main differentiating character can be found in the formation of the laterals. In *S. rigidula* laterals are usually formed by normal hemiblastic branching, so from young secondary segments. Laterals of *S. nana*, however, sprout from cells of mature segments, which are usually located at the proximal part of the erect filaments. These laterals of *S. nana* can be considered to be secondary laterals. In *S. radicans* and *S. caespitula* laterals are usually also secondary in origin. For that reason it is reasonable to relate *S. nana* to these two species, which can be grouped together in the subgenus *Sphacelaria*. When using numerical taxonomic methods to classify the European *Sphacelariales* (Prud'homme van Reine, 1978) I usually found *S. radicans*, *S. caespitula*, and two entities of *S. nana* (*S. saxatilis* and *S. britannica*) in one cluster. In dendograms, clustered by single linkage, the two entities of *S. nana* were always found together in a cluster of two, within the nearest cluster *S. radicans* and *S. caespitula*. Because I found no arguments to the contrary I decided to incorporate *S. nana* into the subgenus *Sphacelaria*.

Figures of *S. nana* (as *S. britannica*) published by Lund (1950, especially f. 3E and 3F) are very similar to the figures published by Reinke (1892, t. 46) as *S. olivacea*. Specimens collected by Reinke and named *S. olivacea* will be discussed in the section 'Notes on nomenclature' of *S. arctica* (p. 153). There I consider it plausible that Reinke's specimens belong to *S. arctica*. The specimens collected and discussed as '*S. britannica*' by Lund (*l.c.*), however, were correctly assigned to that entity. My figures 156 and 177 have been made from the same slides Lund used to make his drawings.

II. Subgenus Pseudochaetopteris Batters

Sphacelaria subgenus *Pseudochaetopteris* Batters (1889) 63.—Type species: *S. plumigera* Holmes.
Chaetopteris Kützing (1843) 293 (as genus).—Type species: *Chaetopteris plumosa* Lyngbye.
Sphacelaria subgenus *Sphacelaria*, Prud'homme van Reine (1978) 309 & 312 (*nom. inval.*).

Plants are small (less than 2 cm high) or large (up to 11 cm high), attached by a polystromatic basal crust. Determinate hemiblastic laterals, which vary in number between few and many, arise from the erect filaments. The secondary segments of the main filaments contain many secondary transverse walls and generally a large number of longitudinal walls, which arise in a periclinal pattern. Hairs are absent or occur in fours or in pairs, occasionally solitary. Propagules are absent.

IIa. Section Pseudochaetopteris Prud'homme van Reine *nov. sect.*

Sphacelaria sect. *Pseudochaetopteris* Prud'homme van Reine (1978) 312 (*nom. inval.*).—Type species: *S. plumigera* Holmes.
Sphacelaria sect. *Sphacelaria*, Prud'homme van Reine (1978) 312 (*nom. inval.*).
Chaetopteris Kützing (1843) 293 (as genus).—Type species: *Chaetopteris plumosa* Lyngbye.

For discussion see p. 130.

Thalli compositi e crusta basali crassa, dura et filamentis pinnatis erectis. Filamenta principalia erecta corticata, vagina densis, e rhizoideis crescentibus inferne e cellulis parvis peripheralibus filamentorum principalum. Zoidangia in filamentis distinctis parvis fertilibus.

Thalli consist of a thick, hard, basal crust and pinnate erect filaments. Main erect filaments are corticated by a compact sheath of downward growing rhizoids arising from small peripheral cells of these filaments. Zoidangia occur on specialized, small, fertile filaments.

5. Sphacelaria plumosa Lyngbye—Fig. 212–263

Sphacelaria plumosa Lyngbye (1819) 103, t. 30C f. 1 & 2; C. Agardh (1824) 166, (1828) 24; Harvey (1833) 324 (*p.p.*); Postels & Ruprecht (1840) II; Fries (1846) 128; Harvey (1847) t. 87 (*p.p.*); Waern (1945) 404; Irvine (1956) 40; Jorde & Klavestad (1960) 97; Prud'homme van Reine (1974) 174; Russell & Fletcher (1975) 766; Kornmann & Sahling (1977) 156, f. 85; Rueness (1977) 185, f. 109, t. 24, 5; Prud'homme van Reine (1978) 303.—*Cladostephus plumosus* Sprengel (1827) 346; Fries (1835) 313; Holmes (1883) 142; Traill (1888) 161.—*Chaetopteris plumosa* Kützing (1843) 293, (1845) 241; J. Agardh (1848) 41; Kützing (1849) 468, (1856) 3, t. 6 f. 1; Geyler (1866) 511, t. 36 f. 1–5 (*p.p.*); Magnus (1872a) 74, (1873b) 133, t. 1 f. 15–20, t. 2 f. 33–37; Kleen (1874) 35; Areschoug (1875) 20, t. 2 f. 4; Kjellman (1877a) 32, t. 2 f. 2 & 3, (1877b) 42, (1877c) 28; Gobi (1878) 63; Wollny (1880) 65 (*p.p.*), (1881) 42 (*p.p.*); Kjellman (1883) 273; Hauck (1885) 348, f. 146; Strömfelt (1886) 52; Batters (1889) 64, t. 10 f. 4–6; Reinke (1890a) 209, (1891) 17, (1892) 69, t. 49 & 50; De Toni (1895) 511; Rosenvinge (1898) 99; Sauvageau (1901) 144 (= R. 106); Jónsson (1903) 161, (1904) 40; Børgesen (1905) 775; Kylin (1907) 66; Kuckuck (1912) 180, t. 8 f. 5; Printz (1926) 165; E. Zinova (1929) 77; Newton (1931) 193, f. 121 (*p.p.*); Kylin (1947) 31, t. 2 f. 7; Lund (1950) 55, (1951) 13; Sundene (1953) 159; A. Zinova (1953) 115; Lund (1959) 98; Jaasund (1965) 72; Pankow (1971) 165.—*Cladostephus distichus* Holmes in Traill (1882) 188, *nom. illegit.*; superfluous *nom. nov. pro Chaetopteris plumosa.*—*Ceramium pennatum auct. non* Roth: Hornemann (1813) t. 1481, *excl. descr. et syn.*; C. Agardh (1817) 68; Wahlenberg (1826) 905 (*p.p.*).—Lectotype: *Lyngbye s.n.* Hofmansgave, Island of Fyn, Denmark, January 1816 (C).—See notes on nomenclature 1.

Sphacelaria plumosa var. *β divaricata* Lyngbye (1819) 103, t. 30C f. 3 & 4.—Type: *Lyngbye s.n.* Oxefjord (= Oksöyfjorden) near Kristiansand, Vest-Agder, Norway, detached specimens (C, lecto; BR, KIEL, LD).—See notes on nomenclature 2.

Conferva pennata auct. non Hudson: Wahlenberg (1812) 512 (*p.p.*); *Wahlenberg s.n.* Finmarken, 26 April 1802, *sub nomine 'Conferva pectinata* in Diar' (UPS).

Sphacelaria heteronema Postels & Ruprecht (1840) II, *nom. nud.*—Type: *Baer s.n.* Nova Zembla, 1837 (LE).

Plants are shrubby, erect and sometimes complanate, when all axes and main branches are arranged in one plane; light to dark brown or olivaceous; solitary, but sometimes gregarious; epilithic or epiphytic. One to many branched main axes arise from a thick, polystromatic, hard, dark brown or black, perennial basal crust (fig. 212; 213), but young crusts may also give rise to many narrow determinate filaments.

In early stages the basal part is a circular basal disc with marginal growth. The young disc is monostromatic and consists of a number of radiating, branched, coalescent, creeping filaments with apical growth (fig. 214–216). Upward growth and subsequent division of the intercalary cells of the coalescent creeping filaments results in the formation of a polystromatic disc (fig. 217; 218). Gradually the crust is thickened and enlarged by downward growing rhizoids from the axes spreading over the disc (fig. 218). Often several discs grow over one another. Occasionally creeping filaments function as stolons (fig. 219).

The erect parts of the plants are composed of one or more main axes and indeterminate hemiblastic laterals of up to the third or fourth order. The distal parts of the main filaments are pinnate and clothed with opposite determinate hemiblastic laterals (fig. 212; 220; 221; 228). These ultimate pinnate parts have an ovate or lanceolate outline and are light brown or olivaceous. In winter they are dilapidated because determinate laterals break off (fig. 213). In spring one or more main axes of the second generation may arise from the apical parts of the remaining main filaments. These new axes will be lined with determinate and indeterminate laterals of the second generation. There are no anatomic differences between comparable parts of different generations.

Many downward growing closely appressed rhizoids arise from the main erect filaments at a variable distance from the apex, forming a compact cortication (fig. 223–226). Especially the proximal corticated parts are often very dark; they are bare by having shed the determinate laterals and more or less wiry (fig. 212; 213).

The dimensions of the inferior and superior secondary segments of the main filaments are usually equal to each other (fig. 221; 222), but in some specimens the inferior secondary segments are slightly longer than the superior ones (fig. 220). In narrow proximal parts and in ultimate and penultimate laterals secondary segments are often longer than they are wide (fig. 227), but in the thick distal parts most secondary segments are somewhat wider than they are long (fig. 221; 222).

The secondary segments are subdivided by radial, periclinal, and transverse walls into a few-celled medulla and many peripheral cells. In the medulla almost no transverse walls are formed and the long cells are quadrangular in cross-section. In the main erect indeterminate filaments this medulla is well developed (fig. 225; 226; 235–245), but in the other indeterminate laterals the medulla consists of only a few cells (fig. 246–249). The many peripheral cells are separated by walls which are more or less radial. In lateral view often 10–14 longitudinal walls can be observed in large secondary segments (fig. 220; 221). The

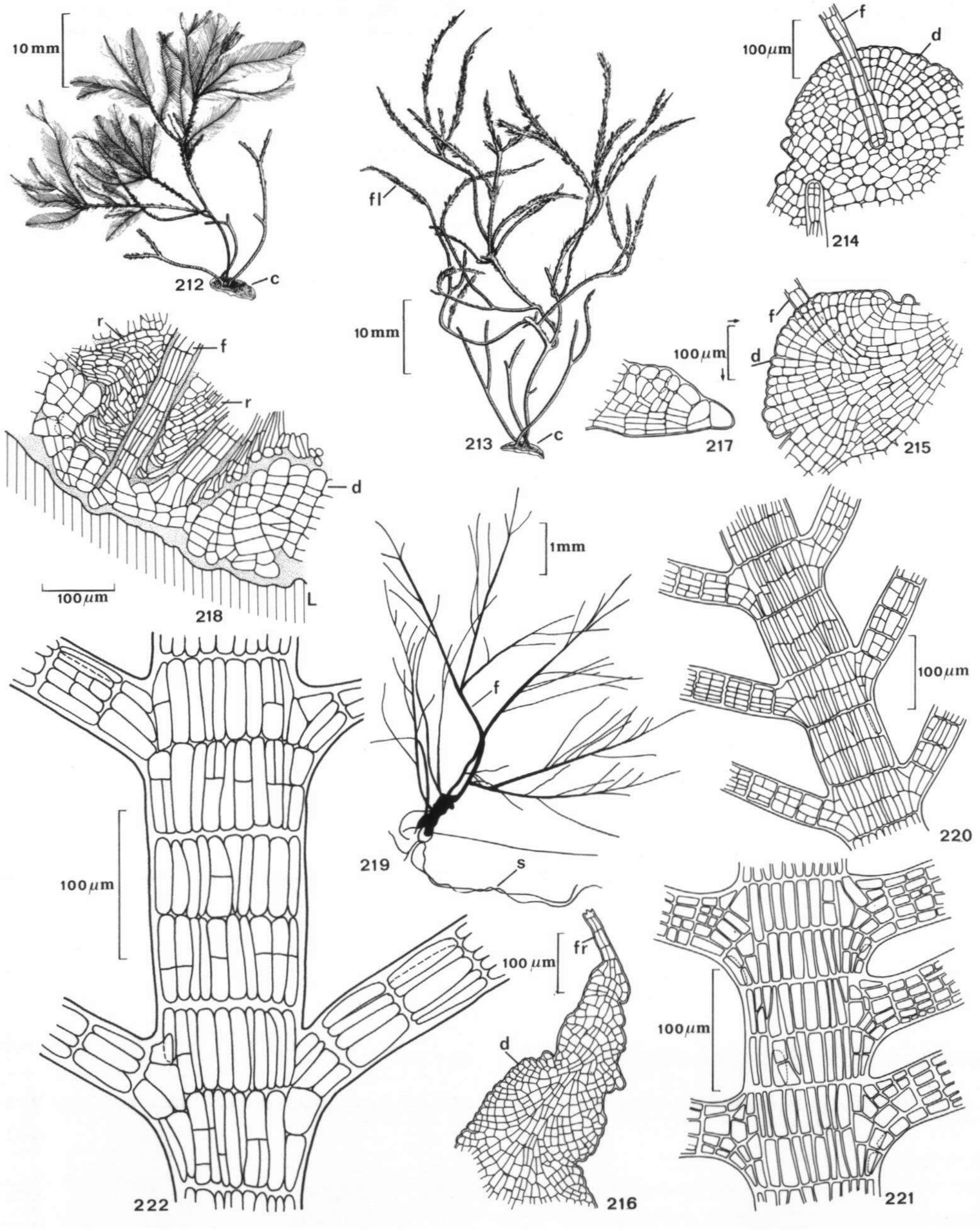


Fig. 212–222. Sphacelaria plumosa. 212. Summer habit; 213. Winter habit; 214–217. Basal disc (214. From above; 215, 216. From below; 217. Section); 218. Basal crust, section; 220–222. Branching of erect filaments. c. basal crust; d. basal disc; f. erect filament; fl. fertile laterals; fr. loose fragments of a filament, proliferating into a basal disc; L. *Laminaria hyperborea*; r. rhizoids; s. stolon. 212. Heligoland, *Sonder* (L, sheet 936.24-15); 214, 215, 217. Culture 67-24-2; 216. Culture 67-49-2; 218. Skjerholmen, Espegrend, *Prud'homme van Reine 67-24* (formalin); 219. Culture 67-53-1; 220. Lysekil, *M.G.R.* (S, soaked); 221. Kirkegrund, *Rosenvinge 4043* (C, soaked); 222. Jørgen Brønlundfjord, *Holmen* (S, soaked).

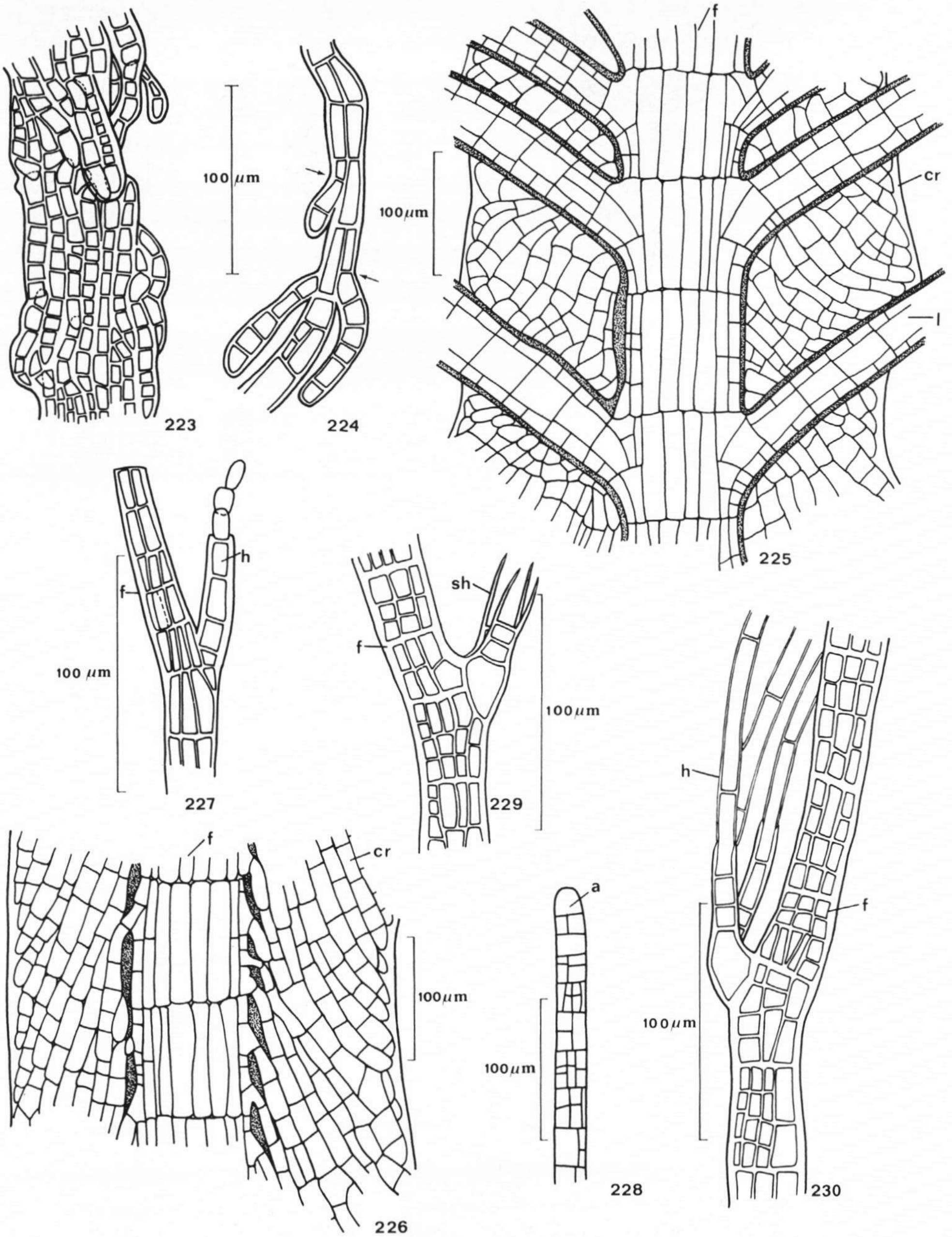


Fig. 223–230. Sphacelaria plumosa. 223, 224. Corticating rhizoids. 225, 226. Longitudinal section of corticated main filament (225. In the plane of branching; 226. Perpendicular to that plane); 227–230. Hairs; 231. Apex of a determinate lateral. a. apical cell; cr. corticating rhizoids; f. erect filament; h. hair; l. lateral; sh. sheath of a hair. 223, 224. Culture 67-49-1; 225, 226. Aarhus, *Mathiesen 1–3* (L, microslides); 227. Lysekil, *M.G.R.* (S, soaked); 228. Svartholm, Espegrend, *Prud'homme van Reine 67-49* (formalin); 229, 230. Kristineberg, *Prud'homme van Reine 67-12* (formalin).

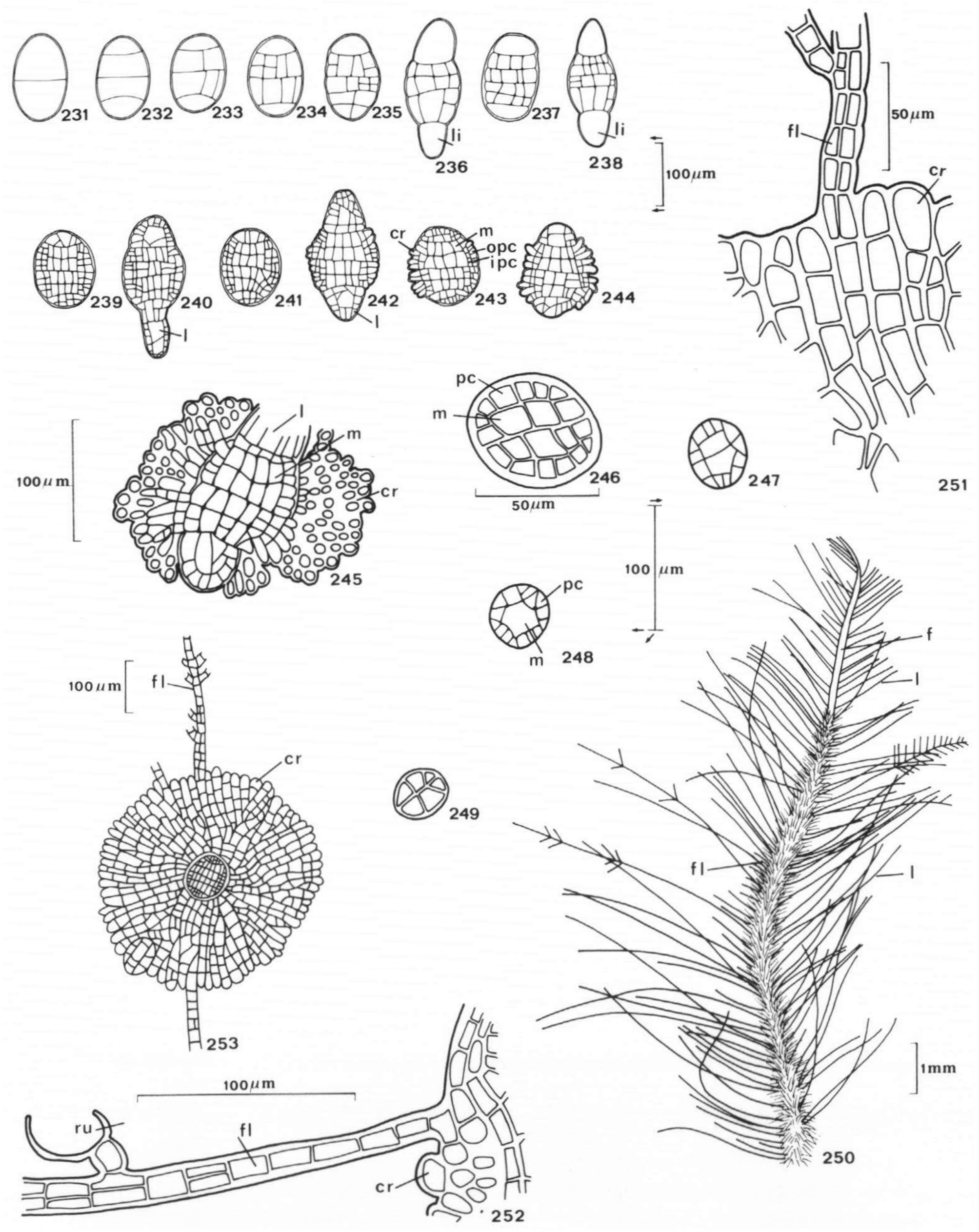


Fig. 231–253. Sphacelaria plumosa. 231–249, 253. Cross-sections of erect filaments (231–244. Subsequent secondary segments of a main filament; 245, 253. Main corticated filaments; 246. Indeterminate lateral; 247–249. Determinate laterals); 250. Part of an erect filament; 251, 252. Fertile laterals. cr. corticating rhizoids; f. (main) erect filaments; fl. fertile laterals; ipc. inner peripheral cells; l. lateral; li. lateral initial; m. medulla; opc. outer peripheral cells; pc. peripheral cells; ru. remnants of unilocular zoidangium. 231–244, 247, 248, 250–253. Kristineberg, *Prud'homme van Reine 67-12* (formalin); 245. Aarhus, *Mathiesen 1–3* (L, microslide); 246. Culture 67-24-2; 249. Culture 67-21-1.

layer of peripheral cells is often divided into an inner and an outer layer by periclinal walls (fig. 225; 226; 235–244), and the long peripheral cells are often divided into several shorter ones by 1–5 transverse walls (fig. 220–222; 225; 226).

Nearly every outer peripheral cell in the corticated parts forms a branched or unbranched rhizoidal outgrowth and the thick rhizoidal cortex obscures the septation of the main filaments (fig. 223–226; 245).

The opposite determinate unbranched laterals arise from the superior secondary segments of all axes and indeterminate laterals (fig. 220). Sometimes inferior secondary segments also form these determinate laterals (fig. 221; 225). Secondary segments of determinate laterals are usually longer than wide except near their tips (fig. 228). The medulla is hardly developed in these laterals and the peripheral cells are not divided into an inner and outer whorl of cells (fig. 247; 248). Corticating rhizoids are lacking on these laterals. Some of the determinate laterals, located at irregular distances, may change into indeterminate laterals in a later stage of growth.

Hairs may arise by acrohomoblastic branching on the ultimate and penultimate laterals, but not on the main erect filaments. On the penultimate laterals the hairs only occur on or near the apex, but the ultimate laterals may be clothed by several hairs spreading in many directions. Hairs are solitary or geminate, sometimes occurring in bundles of four or more together (fig. 227; 229; 230). Rarely the base of a hair is multicellular and coloured like a lateral. In these cases other hairs may arise from this coloured base.

There are no propagules, but parts of the plant may occasionally break off and form new plants that secondarily attach to the substrate by newly formed rhizoids or small basal discs (fig. 216; 219).

Zoidangia are usually formed on short and thin specialized laterals arising from the rhizoids without order and very close to each other (fig. 213; 250–254). These laterals are mostly unbranched, rarely branched (fig. 255; 256). They are slightly curved upward and form approximately right angles to the axis. The secondary segments of these laterals are undivided or divided by 1–2 (–3) longitudinal walls and rarely also by a transverse wall. The superior segments of the fertile laterals (sometimes all superior segments in such a lateral, in other cases only one or two of them) bear zoidangia with short hemiblastic 1–2 (–5)-celled stalks (fig. 255–259). Especially on bare parts of the main filaments these closely packed small fertile laterals may cover fairly large areas as a dense felt (fig. 250). The fertile laterals may persist more than one year, when new fertile laterals arise. Occasionally zoidangia arise from the normal pinnate laterals (fig. 260).

Unilocular and plurilocular zoidangia rarely occur on the same plant. Unilocular zoidangia are spherical or somewhat ellipsoid when mature, more or less clavate when young (fig. 255; 256; 259). Plurilocular zoidangia are shortly cylindrical when mature, sometimes, however, ellipsoid or ovoid (fig. 257–259). Zoids have been observed by Kuckuck (1912). According to him zoids from unilocular zoidangia are pear-shaped, the single dark brown chloroplast is sometimes folded to give the suggestion of two chloroplasts. The eyespot, located on the chloroplast, is very clear. Phototactic movements are quite slow. The zoids of the plurilocular zoidangia are very similar, but their dimensions differ.

Dimensions: Plants up to 11 (–14) cm high. Width of distal pinnate parts 4–10 mm. Diam. basal crusts 1–10 mm. Diam of stolons 35–65 μm, of rhizoids 8–20 μm. Angle of ramification (25–) 40–50 (–70°); however, in loose-lying plants 65–80°. Diam. corticated

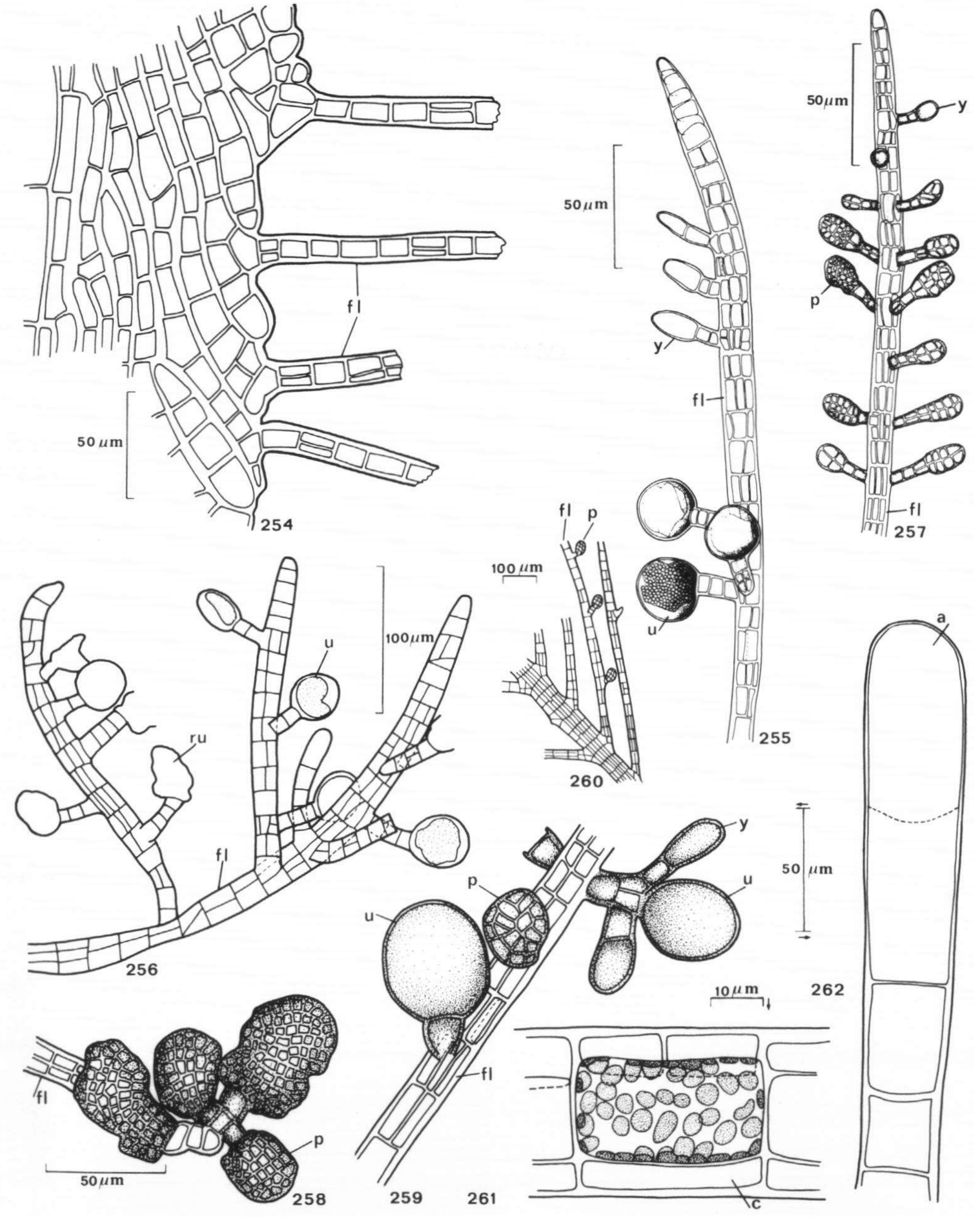


Fig. 254–262. Sphacelaria plumosa. 254. Longitudinal section of a main filament; 255, 256. Unilocular zoidangia; 257, 258, 260. Plurilocular zoidangia; 259. Unilocular and plurilocular zoidangia; 261. Cells of a narrow erect filament; 262. Distal part of main axis of a young plant. a. apical cell; c. chloroplast; fl. fertile lateral; p. plurilocular zoidangium; ru. remnants of unilocular zoidangium; u. unilocular zoidangium; y. young. 254. Kristineberg, *Prud'homme van Reine 67-12* (formalin); 255. Lysekil, *Kjellman* (UPS, soaked); 256. Hofmansgave, *Lyngbye* (C, soaked); 257. Lysekil, *Kjellman* (HBG, soaked); 258. Bülk, Hauck & Richter Phycoth. Univ. n. 318 (ZA, soaked); 259. Mosselbay, *Kjellman* (HBG, soaked); 260. Culture 67-49-2; 261, 262. Culture 67-53-1.

parts up to 700 μm, but without rhizoidal sheath (10–) 75–120 μm. Diam. penultimate laterals 30–50 μm and ultimate determinate laterals 20–32 μm. Height of secondary segments of corticated parts 40–100 μm. Number of cells in the medulla of the main indeterminate filaments 12–16; in other indeterminate laterals 2–4, and in determinate laterals (0–) 1–2. Hairs 7–12 μm in diam. (without sheath). Chloroplasts 2.25–4.5 X 3.5–7 μm in surface view (fig. 261). Fertile laterals 400–1000 μm long; diam. 15–25 (–30) μm. Unilocular zoidangia diam. 32–55 μm. Plurilocular zoidangia 35–60 (–67) X 25–35 (–42) μm, diam. loculi 3–6 μm. Zoids unilocular zoidangia 11–11.3 X 5–7.8 μm; zoids plurilocular zoidangia 7.5–9 X 4.5–5 μm.

Distribution. Greenland. Europe: Iceland, Spitzbergen, Faeroes, Norway, southwest Sweden, U.S.S.R. (Arctic coasts), Germany (B.R.D.: Baltic coasts and Heligoland), Denmark, Shetland and the Orkneys, Scotland, Isle of Man, north Wales, north England, Northern Ireland, Eire.

The species is also known to exist in the Asian and American Arctic Ocean, the Bering Sea, the Okhotsk Sea, and on the eastern coasts of Canada.

European localities have been listed and are given in fig. 263.

For an extract of the list of collections and references see below.

GREENLAND. West coast. 23 collections/references.—East coast. More than 12 localities/references.—Without locality. Three collections.

ICELAND. Northwest coast. Two collections/references.—North coast. Five collections/references.—East coast. Eskifjördur (Strömfelt, 1886, p. 52).—Southwest coast. Three references.

SPITZBERGEN. Many localities/references, amongst which Bellsound, *Kjellman* in Schiffner, Algae mar. exs. n. 1152, 1873, (L, S, W, WU).

FAEROES. Three collections.

NORWAY. Finmarken. Twelve collections/references.—Troms. Two collections.—Nordland. Five collections.—Tröndelag. Three collections/references.—Möre og Romsdal. Three collections.—Sogn & Fjordane. Stensundholmen: *Boye*, 7/4/1894 (GB).—Hordaland. Many localities/references.—Rogaland. Four collections/references.—Vest-Agder. More than six collections/references.—Aust-Agder. Three collections.—Telemark. Jomfruland (O).—Vestfold. Nine collections.—Buskerud. Tofteholmen (Sundene, 1953, p. 159).—Akershus. Nine collections.—Ostfold. Six collections/references.

SWEDEN. Bohuslän. Many collections, amongst which Lysekil: Areschoug, Algae Scand. exs. ser. nov. n. 408 (L, and several other herbaria); *Ibidem*, n. 107 (L, and many other herbaria). 'Bahusia': Rabenhorst, Algen Europ. n. 1459 (L, and many other herbaria). 'I hafvet Bohusl.': Akermark, Typsamling n. 61 (BR, and several other herbaria).—Halland. Many collections, amongst which Varberg: *Hylmö*, in Schiffner, Algae mar. exs. n. 867 (BM, and several other herbaria).—Skåne. (Kristianstad Län). Six collections.—Skåne. (Malmöhus Län). More than seven collections.

U.S.S.R. Western Arctic coasts. Twelve collections/references.—Novaya Zemlya. More than seven localities/references.—Kara Sea. Four collections/references.

GERMANY. Baltic coasts. Many localities/references, amongst which Kieler Förde: Bülk, 5–15 m deep, on shells and stones, *Reinke* in Hauck & Richter, Phycoth. Univ. n. 318, 10/1888 (L, and many other herbaria). Kieler Bucht: Boje C, 8–9 m, Schiffner, Algae mar. exs. n. 1470, 12/9/1924 (BM, S). 'Mer baltique' in: Lenormand Coll. Hydroph. n. 347 (L, MEL).—North Sea coast. Heligoland: Many collections, amongst which Biol. Station, in Schiffner, Algae mar. exs. n. 398, 4/1929 (BM, WU).—Without exact locality: Threde, Die Algen der Nordsee... n. 93 (BM; in HBG partly *S. plumigera*, in many other herbaria all material under this number is *S. plumigera*).

DENMARK. North Sea. Four collections/references.—Skagerrak. Eight collections/references.—Kattegat. More than six collections/references. N.B. Material from Frederikshavn by *Børgesen* is *S. plumigera*.—Samsø area. More than twelve collections/references.—Lillebaelt. More than three collections/references.—Sydfynske Øgaard. See Lund (1950, p. 58).—Storebaelt. More

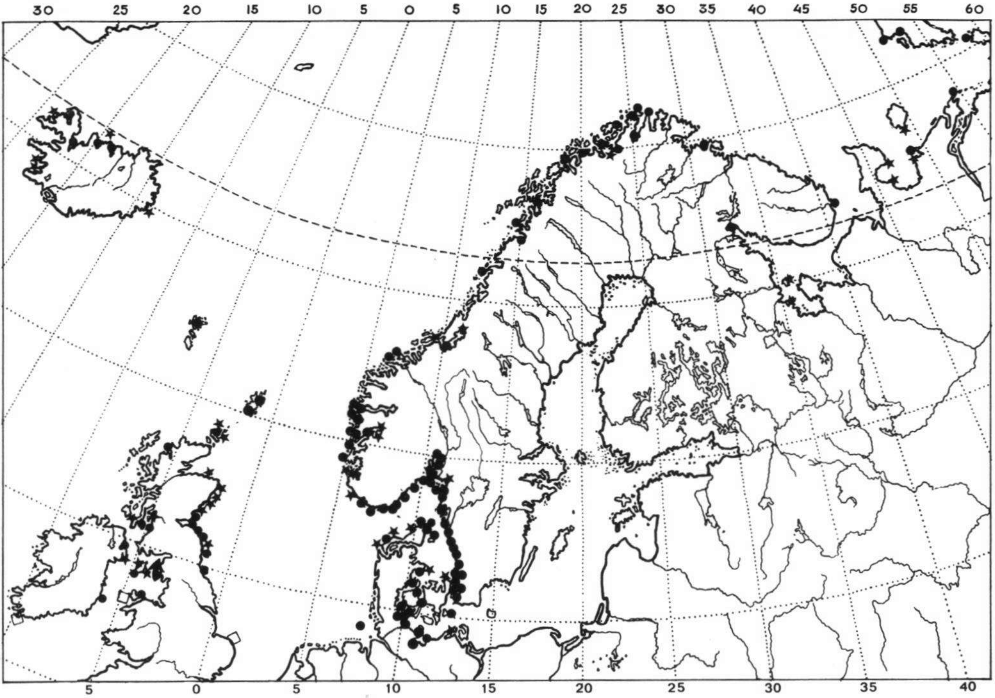


Fig. 263. Distribution of *S. plumosa* Lyngbye in Europe.

● = Material seen by the author. ★ = According to literature. ☐ = Doubtful locality.

than three collections/references.—Øresund. More than four collections/references.—Baltic Sea. Møens Klint, 21 m deep, loose?, *Rosenvinge 4882*, 25/7/1894 (C). See also Lund (*l.c.*).

UNITED KINGDOM. (N.B. in many herbaria most material under this name from the U.K. is *S. plumigera*). —Shetland. Four collections.—Orkneys. Four collections/references.—Scotland. Ross & Cromarty: Taner Mhor, Summer Isles, *Farnham*, 10/6/1971 & 7/9/1972 (PORT). Argyllshire: two references. Colonsay (Norton *et al.*, 1969, p. 130). Buteshire: Great Cumbrae Island (Batters, 1902, p. 39). Arran: two collections. Ayrshire: four collections, amongst which Ardrossan, (as *Cladostephus plumosus*). *Landsborough*, in Holmes, Algae Brit. rar. exs. n.1. (BM, and several other herbaria). Dumfriesshire: Brighthouse Bay, Solway Firth (?) (Burrows, 1960, p. 24). Banffshire: Macduff; Aberdeenshire: Peterhead and Bay of Nigg; and Kincardineshire: Stonehaven (Batters, 1902, p. 39). Fife: four collections. East Lothian: Dunbar, from a shaded pool at about half tide level under shelving rocks, *Traill*, 4/1890 (BM, E).—Isle of Man. Three collections/references.—Wales. Anglesey: Two collections/references. ? Caernarvonshire: Port Dinorwic, *Griffith* (Davey, 1953, p. 285).—England. ? Cheshire: Hilbre Island (Batters, 1902, p. 39). Northumberland: three collections/references. Durham: three collections/references. ? Norfolk, Scolt Head (Chapman 1937, p. 242).—Northern Ireland. Down: two collections/references.

EIRE. Wicklow: (as *Cladostephus distichus*), *Harvey*, 1833 (TCD). ? Cork: Lough Ine near Baltimore (Rees, 1935, p. 128).

Specimens which have been found, according to the labels, in Brazilia (*Hagendorf*, herb. Kützing, L) and Adria or Dalmatia (in L, M, PC) seem to have been mislocated. Specimens distributed under this name for localities in France proved to be misnamed.

Notes on nomenclature. (1) Typification of *S. plumosa.* The specimen figured by Hornemann is not preserved. A specimen in the Lyngbye herbarium marked: '*Sphacelaria plumosa, ad littus Frederitiae Cimbriae. Prof. Hornemann* aestate 1812, *dedit* Hornemann 12/12/1818' is a small *Stypocaulon scoparium* (L.) Kütz. The specimen of *S. plumosa* marked: 'Hofmansgave, 1816, Januari, *cum delineat.* 4 juny 1818' was selected as the lectotype. Its general habit corresponds very well with Lyngbye's drawing and description, from which it differs, however, by having unilocular zoidangia. Lyngbye did not mention fructification at all, but most of the specimens in his herbarium are fertile. So it can be presumed he overlooked the zoidangia.

(2) *Sphacelaria plumosa* var. *β divaricata.* No material marked with this name could be located, but much material bearing the not published name *S. plumosa* var. *intricata* was found in several herbaria. This material is often mixed with *S. plumigera* ecad *pinnata.* The specimen marked '*cum Delineat.* d. 4 Juny 1818, *Sphacelaria plumosa* var. *intricata. Ceramium pennatum* fl. Dan. d. Juny 1816 *in Fucis ad rupes ante ostium sinus Oxefjord Norvegiae*' was selected as the lectotype. The material consists of specimens that have lost their contact with the substrate. From the basal disc new filaments arise in all directions, and the plants get a more or less spherical outline. The morphological characters of the plants do not differ from the specimens still in contact with the substrate. So there is no reason to separate them as a variety. As will be seen further on, some other loose fragments of *S. plumosa* may show particular morphological characters.

Notes on morphology. The prominent elongate apical cells of the indeterminate filaments are often a little wider than the primary segments. The latter normally divide into two secondary segments (fig. 262).

Geyler (1866) observed in his material of '*Chaetopteris plumosa*' the sequence of division within the secondary segments. His material originated from Denmark and Great Britain. The latter material was probably of *S. plumigera* and of the five figures Geyler depicted in his Tafel 36 only fig. 4 & 5 are positively *S. plumosa.* According to Geyler the first longitudinal wall in the secondary segment is in the plane of branching. Every half is divided again by another longitudinal wall, perpendicular to the primary longitudinal wall. After that in every of the four 'quadrants' periclinal walls split off two or three primary peripheral cells. The figures of cross-sections of filaments given by Geyler are all of secondary segments that are already divided by many longitudinal walls. Magnus (1873b) affirmed the observations of Geyler and so did Sauvageau (1901). These observations are, however, not correct.

In young, indeterminate filaments the first longitudinal wall in a secondary segment is always median and perpendicular to the plane of branching, as can be observed in cross-sections (fig. 231). The next walls are not radial and perpendicular to the primary longitudinal wall, but periclinal and parallel (fig. 232). These periclinal walls split off two primary peripheral cells, forming the branch-initials in all superior and some inferior secondary segments. Shortly after the formation of these periclinal walls other periclinal and also radial walls are formed, the early ones perpendicular to the primary longitudinal wall (fig. 233; 234). The central cells divide by crosswise division in 16 (or more) long medullar cells, in which no transverse walls occur. In the peripheral parts rather irregular periclinal and anticlinal walls occur, followed by transverse septation (fig. 225; 226; 235–241). The superior secondary segments nearly always form two opposite laterals and the inferior secondary segments occasionally do the same. But even if the pattern is not disturbed by the formation of laterals, the septation of the peripheral parts in the plane of branching is more irregular than in other peripheral regions (fig. 239; 240; 244).

In the laterals the pattern of septation is less regular. This was already observed by

Magnus (1873b). In many indeterminate laterals only a few medullar cells are formed in the secondary segments (fig. 246). In the penultimate laterals and the terminal parts of the other indeterminate laterals only the primary longitudinal wall is present, and the other walls are mainly periclinal. This results in two fairly large central cells and a whorl of peripheral cells around it (fig. 247). Sometimes even the primary longitudinal wall is not radial but periclinal, resulting in one central cell surrounded by peripheral ones (fig. 248) or even no central cell at all (fig. 249).

Corticating rhizoids arise from nearly all outer peripheral cells of the main erect filaments, but not from those localized in the plane of the pinnate branching (fig. 225; 226; 242–245). The possible gap in the cortex is filled up by rhizoids that are bent towards the plane of branching.

According to Magnus (1873b) branching of the rhizoids is similar to the formation of solitary hairs of *Sphacelaria*, so acrohomoblastic. No figures are given by Magnus, but Reinke (1892) depicts some young branching rhizoids. These figures make clear that the description by Magnus can be correct, but that also hemiblastic branching occurs.

In the present study branching of rhizoids has not been studied in detail. Some of the microslides contain sections that suggest acroblastic branching of rhizoids, but it is possible that this is in part a hemiblastic branching that is deformed by lack of room in the rhizoidal cortex.

Young basal discs are monostromatic. Further development to a polystromatic disc is very similar to the process described for *S. mirabilis* (p. 172 and fig. 388), but the upright filaments are not so much branched (fig. 217; 218 and Sauvageau 1901, fig. 24) and the apical cells of these upright filaments are not as small as in *S. mirabilis.*

The rhizoids of the cortex extend partly to the basal disc and spread over it, sometimes forming a thick layer. The discs may become multi-layered crusts if vigorously growing parts overlap one another. A similar result can be obtained when the old disc is overgrown by discs of other individuals or by germinating spores.

Basal discs can also originate form parts of stolons or from loose fragments of erect filaments (fig. 216). In these cases the cells in contact with the substrate give rise to prostrate coalescent filaments together forming a new basal disc. Stolons can be formed as continuations of radial filaments of basal discs. Sometimes laterals of rhizoids may function as such, while occasionally in cultures filaments that were originally erect later bend downward and get a stolon-like prostrate habit (fig. 219). New basal discs as well as erect filaments can originate from these stolons.

Hairs of *S. plumosa* are mostly geminate (fig. 229), but solitary hairs have also been found (fig. 227), and sometimes small groups of hairs occur (fig. 230). In most cases the acroblastic origin of these hairs is distinct (fig. 227; 229), but sometimes it looks as if they have been formed by hemiblastic branching (fig. 230).

In fertile specimens many small laterals arise radially from the rhizoidal cortex of the thick axes (fig. 213; 250–254). These small filaments are sometimes continuations of the rhizoidal filaments, but more often they arise laterally at the spot where the rhizoids reach the periphery of the cortication (fig. 254).

Notes on ecology. *Sphacelaria plumosa* is a sublittoral, permanently submerged species. In Iceland and on the southwest coast of Sweden it occurs near low-water mark and sometimes in permanent pools in the eulittoral zone; but in most cases it is an inhabitant of deeper water. In Spitzbergen, Iceland, and Heligoland, it is found down to a depth of 15–20 m; in north Norway and arctic U.S.S.R. it descends to 30 m and on the coasts of Greenland and middle Norway it has been found down to a depth of 40 m. *Sphacelaria plumosa* grows on several kinds of substrates like rocks, stones, gravel, shells, and large algae. It is a common inhabitant of the shell-grounds in the Kattegat (Waern, 1958) but it also grows on the hapteres and stems of Laminarias, especially *Laminaria hyperborea.* In the inner parts of Hardangerfjord it is a common constituent of the undergrowth of the *Fucus serratus* zone.

In most cases *S. plumosa* is found scattered, but sometimes it forms dense carpets. Kjellman (1878, p. 19) describes a '*Chaetopteris*-formation', that is almost a monoculture of *S. plumosa* with some *Zostera marina* and *Stictyosiphon tortilis* in between. This formation was growing near Fiskebäckskil on silty grounds at a depth of 2–3 m. But the author mentions *S. plumosa* for six of his other formations.

Plants of *S. plumosa* that do not grow attached to any substrate are rare. These unattached specimens have been found in North Greenland (Jørgen Brønlund Fjord) and in Denmark (Møens Klint and Kirkegrund) (fig. 221; 222). The specimens described by Lyngbye (1819, p. 103) as *S. plumosa* var. *divaricata* were also unattached, but these were probably specimens or fragments of specimens that originally grew attached and became detached by the influence of storms etc.

Sphacelaria plumosa is a marine species which can penetrate into brackish areas. Data from two areas where the species is common are discussed to illustrate this.

In the Baltic *S. plumosa* has been observed in the westernmost parts only. Fertile specimens have been found in the German Belt Sea and in the Øresund where salinity (S) varies between 8 and 15‰. Sterile and sometimes unattached specimens have been found in parts of the Arkona Sea, where salinity varies between 7.5 and 11‰.

In the Hardangerfjord *S. plumosa* is a common inhabitant of the innermost branches (Granvinfjord, Eidfjord, and Sørfjord) where in summer salinity in surface waters decreases to values below 10‰, due to the discharge of water from melting glaciers. In winter salinity in these areas is high (> 30‰). According to Alstadsaeter (1954, p. 113) the inner limit of this species coincides with the inner limit for salinities of 10‰ in June, but her own observations in the Eidfjord do not confirm this.

In other fjords where *S. plumosa* occurs it is mostly scattered in the sublittoral all over the area. In these fjords yearly fluctuations of salinity are mostly not as large as in the innermost branches of Hardangerfjord, nor does salinity decrease to values below 10‰ for any longer period.

Jorde & Klavestad (1960, p. 99) suggest: 'the species needs high salinity at least at one time of the year, either when it is fertile (in winter, when salinity is high in Hardangerfjord), or during the growth period. Its frequency in the inner part of Hardangerfjord indicates that it is indifferent to the variations of salinity occurring there, and perhaps that it needs some shelter'.

The environmental conditions at the moment the zoids or fused gametes have to attach to a substrate are probably the most important. Possibly *S. plumosa* is abundant in the innermost parts of Hardangerfjord because the motile stages attach to the substrate in winter and early spring, when salinities are high.

Form range and cultures. In *S. plumosa* the morphological variation seems to have no taxonomical implications. The dimensions of tufts and basal discs, the number of axes and laterals and the diameter of these filaments show sometimes rather large variations from one plant to another. Laterals grow out from the superior secondary segments only or from some or from all inferior secondary segments (fig. 220–222; 225). The amount of hairs and rhizoids is also variable and so is the colour of herbarium specimens. But in many cases all or nearly all these variations can be found in one area and perhaps even in one population. In arctic regions large specimens exist (a specimen from Spitzbergen was 14 cm high) and in the northern Atlantic Ocean and in the North Sea the dimensions of the tufts are smaller, viz. 1–4 (–5) cm high. Along the Swedish west coast an increase in height of plants is observable from the north towards the south, so in the direction of the Baltic. In Halland specimens of 10 cm have been found and in the Danish archipelago even specimens of 12.5 cm. But more to the south the size of the plants diminishes again.

The habit of the plants varies with the season (fig. 212; 213). In early spring new pinnate sprouts arise from the old axes. The determinate laterals of parts formed during the next months are longer than the ones formed in the first period of the growth season. In autumn the length of the determinate laterals diminishes and growth by the apical cells ceases altogether. In early winter most determinate laterals detach and on the bare corticated axes felted areas of short fertile laterals are formed. In early spring the young sprouts arise again and the whole sequence is repeated.

Cultures have been isolated from material collected on the coasts of southwest Sweden (Kristineberg), southwest Norway (Bergen-Espegrend and Hardangerfjord-Øystese), and southeast Norway (Oslofjord-Drøbak and Tjøme). Most cultures have been maintained during six years but during that time many subcultures had to be made because of the often occurring infections by rapidly growing green and bluegreen algae. Subcultures originating from one specimen and cultured in separate tubes filled with culture medium from one bottle may vary considerably, even when cultured under identical conditions. So it is possible that one subculture shows small dark and hard basal clumps of cells and radial growth of short unbranched filaments while another subculture shows well-grown pinnate plants with stolons or basal discs.

Sphacelaria plumosa grew very slowly in culture. Under the daylight conditions in culture (1400–2800 Lx) the apical cells died off very often and growth of specimens in culture-rooms with a temperature of 4°C (short day) or 12°C (long day) was often very stunted. In most cases these specimens died within three years. Specimens transferred from low light intensities to higher ones showed a quick increase of corticating rhizoids.

At 20°C most specimens died within a few months. At 4°C and 12°C and under lower light intensities (100–700 Lx) the specimens seemed to grow better. In general the plants had a healthy and normal appearance. The plants became 15–20 mm high and the diameter of the main axes varied between 50 and 92 μm (in corticated parts: 150–210 μm). In some cases a small basal disc was formed and by means of this disc, the plant grew attached to the wall of the culture tube. In most cases, however, the disc lost contact with the wall of the tube and then it formed a dark-coloured irregular cell-mass with a firm structure. Form this cell-mass determinate and indeterminate filaments grew in all directions forming a soft more or less spherical plant with a radial construction and a hard and dark central part. In some other cases the pinnate fragments used to start cultures functioned as stolons and these fragments adhered as creeping filaments to the wall of the culture tubes. From these fragments erect branched and unbranched filaments arose together with creeping filaments. The latter had the habit of stolons and rhizoids and sometimes formed small discs. Stolon-like growth also occurred occasionally in cultures where pinnate erect plants adhered to the wall of the tube with their rhizoids but without forming a basal disc (fig. 219). In those cases sometimes thicker creeping filaments are formed in between the rhizoidal mass and from these creeping filaments new pinnate parts arose. In culture media composed with artificial sea-water more rhizoids and especially more stolons occurred than in other media. I never observed any stolons in nature.

In culture in the pinnate parts the laterals were in many cases not arranged in one plane, but they often formed spirals around the main axis. In some specimens the angle between the planes of branching of two successive segments was 90°. This phenomenon was probably due to differences in the angle of incidence of the light in the culture tube. Very occasionally four laterals arose from one secondary segment. In these cases the laterals were arranged in two planes at angles of 90°.

In many cases small fragments of specimens in culture spontaneously broke off and formed new plantlets adhering to the wall of the tube by rhizoids, stolons, or small discs (fig. 216). Sometimes these fragments remained loose in the tube and then they either formed balls of radially growing filaments or irregularly branched loosely interwoven systems of filaments. After some months from these balls or from the irregular filaments, pinnate parts arose, even if the plantlets were not attached. In these cases the angle between the axis and the laterals varied between 40 and 60 degrees, and this is also the variation found in specimens in culture that were attached. So the large ramification-angles found in loose-lying material (fig. 221; 222) from nature have not been found in culture.

Hairs were rarely found in culture. In one culture, growing under low light intensities at 12°C (long day) many hairs occurred on one occasion (fig. 229; 230), but not at other times. In another culture hairs were found on two occasions, and this material grew under normal light intensities at 4°C (short day).

Reproduction and life-history. Unilocular and plurilocular zoidangia are known to exist, but no specialized propagules. Vegetative reproduction can take place by means of detached fragments which easily attach to the substrate and form new plants (fig. 216).

In culture plurilocular zoidangia (fig. 260) were observed but no unilocular ones. In fertile material with plurilocular zoidangia collected in St. Andrews in February 1971 and similar material collected in January 1974 in Frederikshavn by *Mrs. R. Nielsen* the zoids did not swarm during a three-day period of observation. I observed no swarming of plurizoids in culture either. Kuckuck (1912, p. 180) who observed the release of zoids by both unilocular and plurilocular zoidangia also made remarks about a period of one to several days before release of plurizoids took place.

Unilocular and plurilocular zoidangia mostly occur on separate plants. On specimens collected by *Kjellman* during the winter of 1872–1873 in Mosselbay, Spitzbergen, both unilocular and plurilocular zoidangia have been found mixed on the thallus (fig. 259). The small stalks of the plurilocular zoidangia consist mostly of 1–3 cells (fig. 257) but in material from Kiel (Phycotheca universalis 318) in the herbarium in Zagreb branched stalks have been observed (fig. 258) and the number of cells in the stalks was much higher. The observations made by Kuckuck about the zoids are already mentioned in the description (p. 220).

Areschoug (1875) was the first to describe and depict plurilocular zoidangia. He also described presumptive unilocular zoidangia, but these are probably deformations due to the activities of a marine fungus growing in the apical cells of the small laterals. The genuine unilocular zoidangia have been observed by Kjellman (1875; 1877a) who also supplied a characteristic drawing. The unilocular zoidangia described by Wollny (1880, 1881) are the fructifications of *S. plumigera* and not of *S. plumosa.* Fructification occurs always in late autumn and in winter. Young special fertile laterals appear in July or August, but the zoidangia are rarely met before November. Fructification ceases in March, but occasional zoidangia have been found in other months. According to Kjellman (1875) plurilocular zoidangia occur less often than unilocular ones, but in the material collected in winter, specimens with plurilocular zoidangia form more than 50% of the total number of fertile specimens. All fertile specimens from Heligoland had plurilocular zoidangia only.

In my cultures I only very occasionally observed plurilocular zoidangia, which were, however, always growing on normal pinnate laterals and not on specialized narrow filaments (fig. 260).

Schreiber (1931, p. 236) carried out copulation experiments with zoids from plurilocular zoidangia of separate plants, but without observing any copulations.

From the incomplete observations cited above it is clear that no reasonably complete picture of the life-history of *S. plumosa* can be obtained, in particular because there have been no caryological investigations whatever, and the development of the zoids has not been studied. In accordance with the observations of Van den Hoek & Flinterman (1968) on *S. rigidula* (as *S. furcigera*) a hypothetical life-history may be drafted. The data are not incompatible with the image of an isomorphic diplo-haplontic life-history with plurilocular isogametangia, unilocular zoidangia, and perhaps also plurilocular asexual zoidangia. Perhaps the supposed gametes may also function as asexual zoids if copulation fails to occur. There are no indications for the existence of male microgametangia, so the occurrence of isogamy is probable. The material in Schreiber's experiments may have consisted of asexual plurilocular zoidangia or of plurilocular gametangia that were all male or all female.

Systematic position. Kützing (1843, p. 293) separated the genus *Chaetopteris* from *Sphacelaria* because of the thick cortex of the former. The only species in his new genus was *Chaetopteris plumosa* (Lyngbye) Kützing. During a long period most authors followed Kützing by keeping *Chaetopteris plumosa* separate from the genus *Sphacelaria.* Even the discovery of a cortex in *S. plumigera*, *S. arctica*, and other species did not change this practice. Holmes (in Traill, 1882) discovered the cortical origin of the fertile laterals, and Hauck (1885, p. 348) and Batters (1889, p. 64) used this datum as the main character to separate *Chaetopteris* from *Sphacelaria.* Waern (1945, p. 404) points out that there is no distinct generic delimination between the two genera, since in some other species of *Sphacelaria* zoidangia may also be attached to cortical filaments or rhizoids. If the zoidangia would exclusively be formed on specialized fertile filaments, it would probably be opportune to place *S. plumosa* in a separate section. My observations of plurilocular zoidangia on normal pinnate laterals of specimens in culture, however, demonstrate that the differences between *S. plumosa* and the related *S. plumigera* are not as large as thought before by most authors. For that reason I bring both species together in the section *Pseudochaetopteris*.

In *S. plumosa* nearly all peripheral cells of the main axes form rhizoidal outgrowths, whereas in *S. plumigera* only the peripheral cells in the plane of branching form rhizoids. The species of the section *Pseudochaetopteris* are always distinctly corticated. In the related section *Racemosae* in *S. arctica* the rhizoids arise very irregularly and *S. racemosa* is usually devoid of rhizoids.

6. Sphacelaria plumigera Holmes—Fig. 264–317

Sphacelaria plumigera Holmes (1883) 141; Hauck (1885) 348; Traill (1885) 16; Holmes (1885) 61; Batters (1889) 63, t. X, f. 1–3; Reinke (1890a) 209, (1891) 12, (1892) 66, t. 47, f. 1–5; De Toni (1895) 506; Sauvageau (1901) 115 (= R. 98), f. 22; Newton (1931) 191; Waern (1945) 405, f. 6 (*p.p.*), (1952) 99 (*p.p.*); Irvine (1956) 40; Den Hartog (1962) 81; De Haas-Niekerk (1965) 159, f. 64, 66, 67–72; Prud'homme van Reine (1968) 116, f. 1, (1974) 174; Russell & Fletcher (1975) 766; Prud'homme van Reine (1978) 303.—*Sphacelaria plumigera* forma *typica* Lund (1950) 50, f. 11.—*Sphacelaria arctica* Harvey forma *plumigera* Pankow (1971) 164 (*p.p.*); (1975) 803 (*p.p.*).—Type: *W. Borrer s.n.* Eastbourne, Beachy Head, in pools left by the tide, 2/10/1808, *sub nomine Conferva pennata* Huds. (BM, lecto; LD, TCD).

Sphacelaria recemosa var. *arctica* forma *pinnata* Reinke (1892) 66, t. 45, f. 11, 12; Levring (1940) 44 (as *Sphacelaria racemosa* forma *pinnata*).—*Sphacelaria plumigera* forma *pinnata* Lund (1950) 50; Prud'homme van Reine (1978) 303.—Type: *Brandt*, Hoburg Bank, South of Gotland, Sept. 1887 (KIEL, lecto; S).—See notes on nomenclature 1.

Sphacelaria plumigera var. *patentissima* Sauvageau (1903) 50 (= R. 233).—*Sphacelaria plumigera* forma *patentissima* Lund (1950) 54.—Holotype: *Rosenvinge 4455* Denmark, Sundet, North of Lous' Flak, (C).—See notes on nomenclature 2.

Sphacelaria plumigera Holmes 'dwarf form' Waern (1945) 404, f. 5.

Sphacelaria plumigera Holmes 'loose-and-entangled status' Waern (1952) 99, f. 40 & 47a.

Conferva pennata auct. non Hudson: Dillwyn (1806) t. 86, f. B, (1809) 87; Smith & Sowerby (1812) T. 2330, middle f.

Sphacelaria plumosa auct. non Lyngbye: Greville (1824b) 313 (*excl. syn.*); Harvey (1833) 324 (*p.p.*), (1841) 38 (*p.p.*), (1847) t. 87 (*p.p.*).—*Chaetopteris plumosa auct. non* Kützing: Geyler (1866) 511 (*p.p.*); Wollny (1880) 65 (*p.p.*), (1881) 42 (*p.p.*); Newton (1931) f. 121 C, D.

Plants are shrubby, erect, and sometimes complanate when all main erect filaments are arranged in one plane, light brown to olivaceous; solitary, but sometimes gregarious; epilithic, occasionally epiphytic or unattached. Several branched main axes arise from a thick, polystromatic, coriaceous, dark brown, perennial basal crust (fig. 264–267) which is, however, lacking in the unattached plants (fig. 268; 269). Often also many determinate filaments arise from these crusts. The pinnate parts of the plants have a linear outline and are light brown or olivaceous.

In early stages the basal part is a circular basal disc with marginal growth. The young disc is monostromatic and consists of a number of radiating, branched, coalescent, creeping filaments with apical growth (fig. 270; 271). Upward growth and subsequent divisions of the intercalary cells of the coalescent creeping filaments results in the formation of a polystromatic disc (fig. 272; 274). Gradually the crust thickens and enlarges by rhizoids growing downward from the axes and spreading over the disc. Only rarely discs grow over one another (fig. 274). Often filaments function as stolons, giving rise to new axes and discs (fig.. 266; 267).

The erect parts of the plants are composed of several main axes and indeterminate hemi-

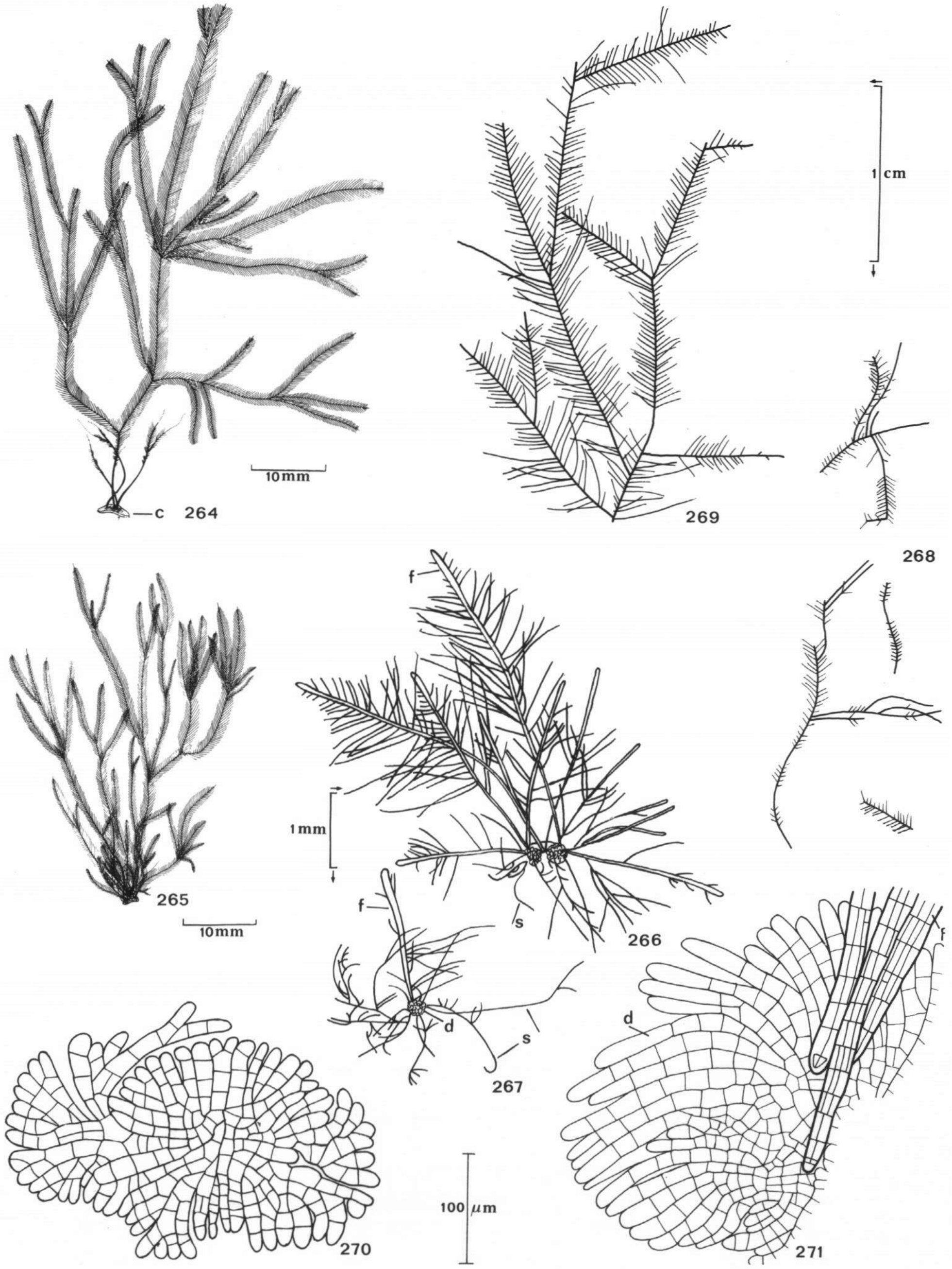


Fig. 264–271. Sphacelaria plumigera. 264–269. Habit (268 & 269. Ecad *pinnata*); 270, 271. Basal disc (270. From below; 271. From above). c. basal crust; d. basal disc; f. erect filament; s. stolon. 264. Joppa, *Traill* (L, sheet 937.71-751); 265. Vlissingen, *Prud'homme van Reine 557* (L, sheet 972.088-198); 266. Culture 71-22-2; 267. Culture 71-22-1; 268. Ekerö, *Häyrén* (H, soaked); 269. Kirkegrund, *Rosenvinge 4043* (C, soaked); 270, 271. Culture 68-3-1 (formalin).

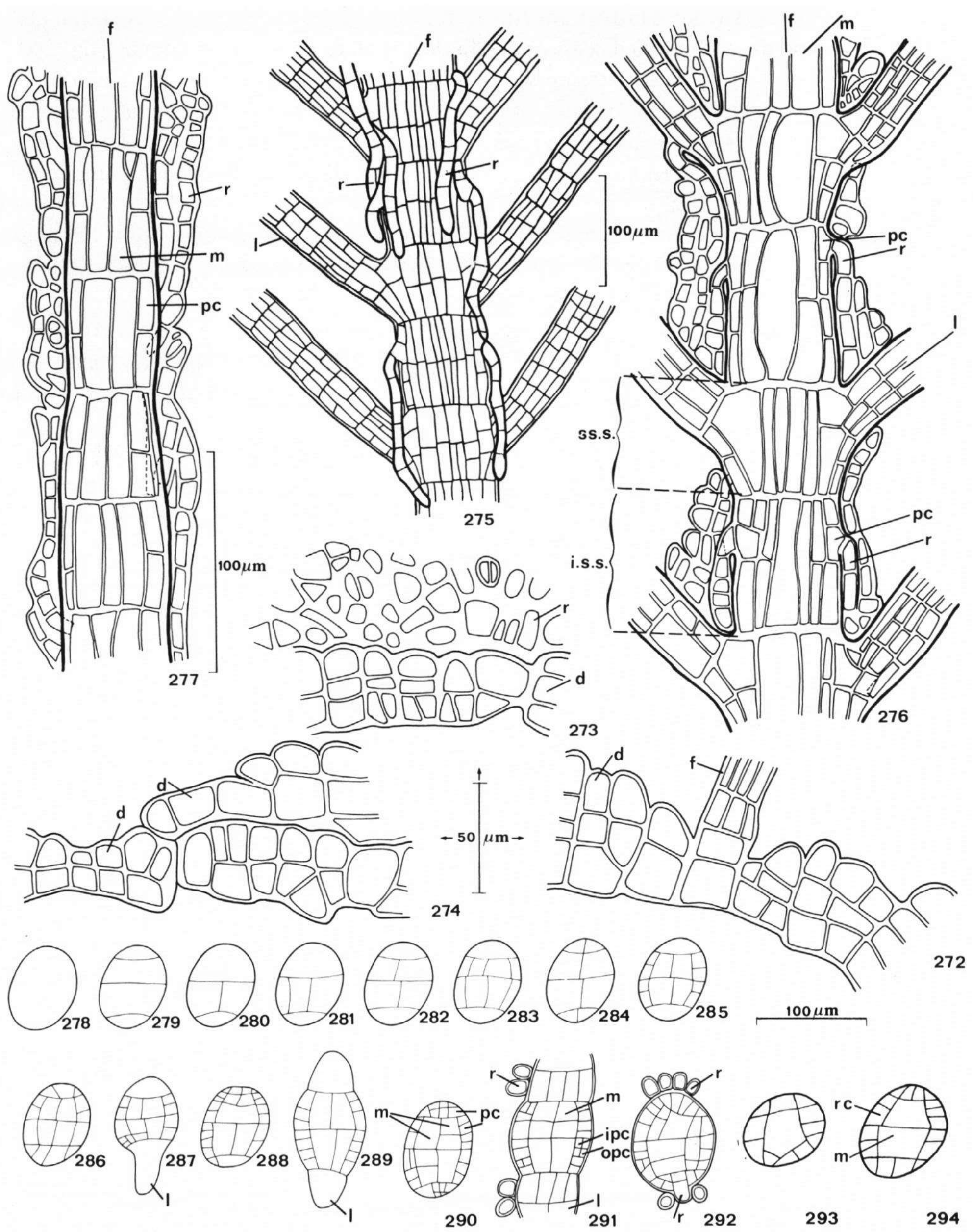


Fig. 272–294. Sphacelaria plumigera. 272–274. Sections of basal parts; 275. Part of a branched erect filament; 276, 277. Longitudinal sections of erect filaments (276. In the plane of branching; 277. In a perpendicular plane); 278–293. Cross-sections of filaments (278–291. Of subsequent secondary segments of a main filament; 292, 293. Of determinate laterals). d. basal disc; f. erect filament; ipc. inner peripheral cell; iss. inferior secondary segment; l. lateral; m. medulla; opc. outer peripheral cell; pc. peripheral cell; r. rhizoid; sss. superior secondary segment. 272–274, 276, 277. Vlissingen, *Prud'homme van Reine 68-3* (formalin); 275. St. Andrews, *Prud'homme van Reine 71-17* (microslide); 278–294. Vlissingen, *Prud'homme van Reine 68-9* (microslides).

blastic laterals of up to the third or fourth order. Most parts of the main indeterminate filaments are pinnate and clothed with opposite determinate hemiblastic laterals (fig. 264; 265; 268; 269). In winter most determinate laterals do not break off. In spring one or more main axes of the second generation may arise from the apical parts of the remaining main indeterminate filaments of the first generation. Such new axes will be lined with determinate laterals of the second generation. There are no anatomic differences between comparable parts of different generations.

Rhizoids, if present, arise from the main filaments at a variable distance from the apex and in the plane of branching (fig. 275; 276; 292; 295). They are loosely appressed and form a more or less complete cortication.

The inferior and superior secondary segments of the filaments are usually of equal dimensions and often wider than they are long (fig. 275; 295–297). In fast growing narrow filaments the secondary segments may become somewhat longer than they are wide (fig. 276; 277).

The secondary segments are subdivided by radial, periclinal, and transverse walls into a few-celled medulla and many peripheral cells (fig. 276–294). In the medulla almost no transverse walls are formed, and the long cells are quadrangular in cross-section. The medulla is best developed in the main indeterminate filaments (fig. 283–292) and consists of only one or two cells in each secondary segment of the smaller indeterminate laterals (fig. 293; 294). Walls between the peripheral cells are more or less radial.

In large secondary segments of the main filaments often 6–10 longitudinal walls can be observed in lateral view (fig. 275; 295–298). Some peripheral cells in the main filaments may be divided into an inner and an outer peripheral cell by a periclinal wall (fig. 276; 290; 291), and the long peripheral cells are often divided into 2–4 shorter ones by transverse walls (fig. 275–277; 296).

The peripheral cells in the inferior secondary segments of the main filaments may form branched (hemiblastic) or unbranched rhizoidal outgrowths but only in the plane of branching of the filaments. These corticating rhizoids grow downward and may encircle the filaments (fig. 275; 276; 292; 295). In the proximal parts of the thallus the cortication is compact and closed, but in the distal parts often gaps in the cortication occur through which the peripheral cells of the filaments can be observed.

The opposite determinate unbranched laterals arise from the superior secondary segments of all indeterminate axes and laterals (fig. 275; 295; 296; 298). Occasionally inferior secondary segments also form these determinate laterals. Secondary segments of determinate laterals are usually as long as they are wide; but near the apex of the determinate laterals they are often wider than they are long (fig. 299). Some of the determinate laterals, especially when located directly below damaged parts of the main filaments, may change into indeterminate laterals in a later stage of growth.

Hairs may arise by acrohomoblastic branching (fig. 297; 300) or occasionally by hemiblastic or meriblastic branching (fig. 297; 310). They usually occur on ultimate and penultimate laterals, spreading in many directions. Occasionally they can also be found on the main filaments (fig. 297). Hairs may be solitary (fig. 297; 300; 310) or geminate (fig. 297; 300) and occasionally a few of their basal cells may contain chloroplasts.

There are no propagules, but parts of the plants may occasionally break off and form new plants that secondarily attach to the substrate by newly formed rhizoids or small basal discs (fig. 301).

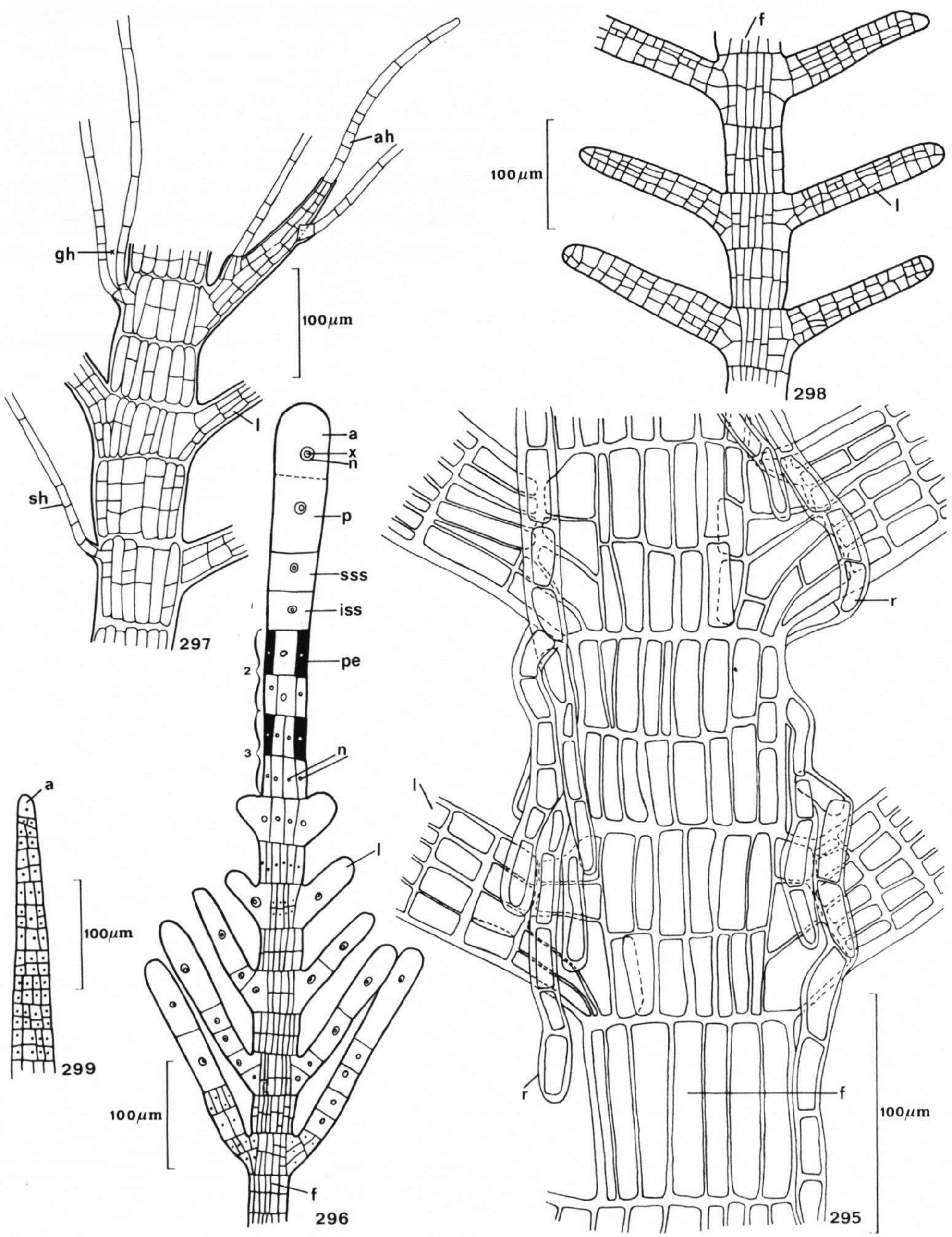


Fig. 295–299. Sphacelaria plumigera. 295–298. Parts of erect filaments (295, 298. Ecad *pinnata*); 299. Determinate lateral. a. apical cell; ah. apical hair; f. erect filament; gh. geminate hairs; iss. inferior secondary segment; l. lateral; n. nucleus; p. primary segment; pe. peripheral dark cell; r. rhizoid; sh. solitary hair; sss. superior secondary segment; x. nucleolus. 295. Kirkegrund, *Rosenvinge 4043* (C, soaked); 296, 299. St. Andrews, *Prud'homme van Reine 71-17* (microslides, coloured with acetocarmine); 297. Culture 66-1-1; 298. Ekerö, *Häyrén* (H, soaked).

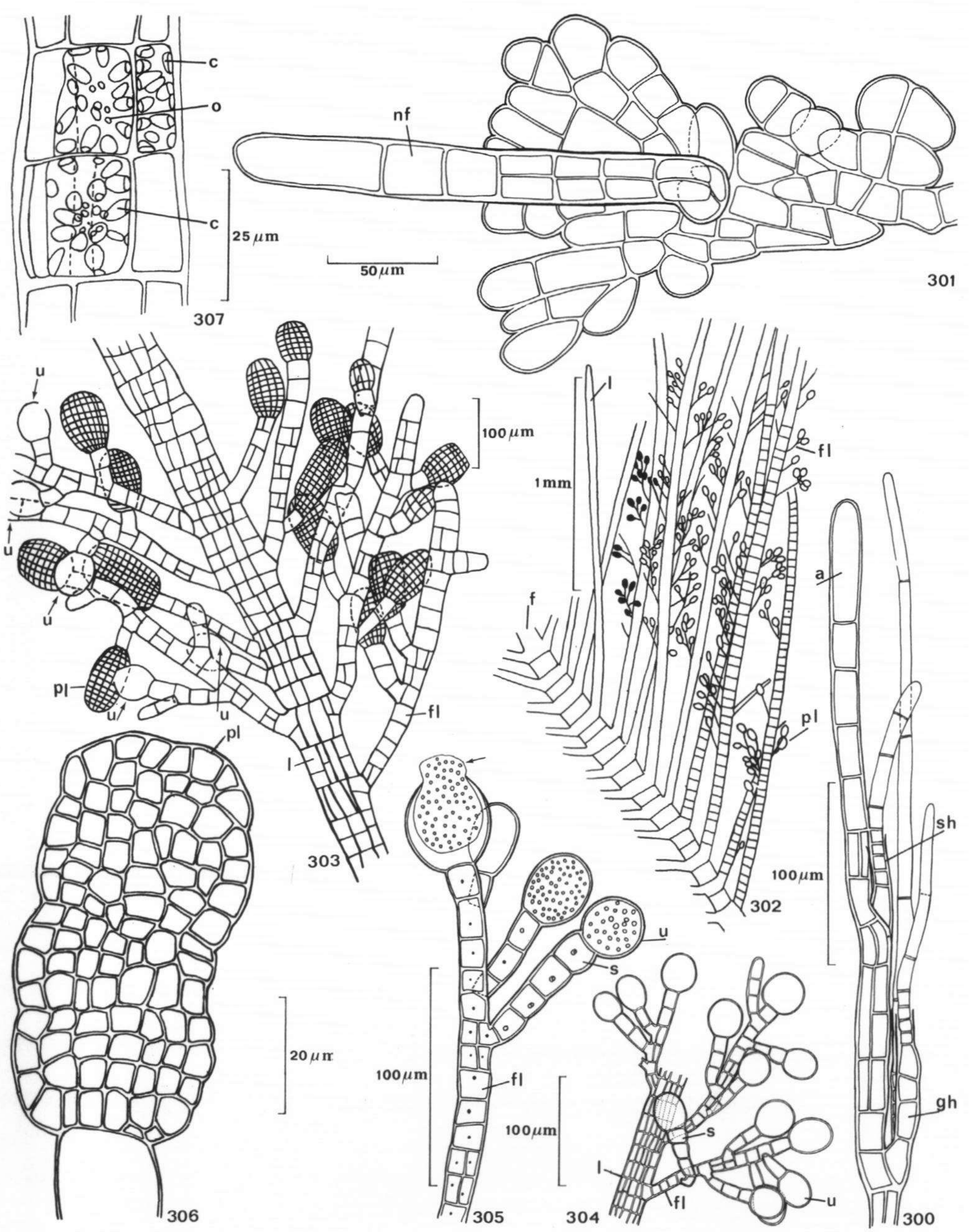


Fig. 300–307. Sphacelaria plumigera. 300, 307. Parts of laterals; 301. Fragment of an erect filament, forming a secondary basal disc; 302–306. Zoidangia. a. apical cell; c. chloroplast; f. erect filament; fl. fertile lateral; fr. fragment of an erect filament; l. lateral; nf. new filament; o. oil-like drop; pl. plurilocular zoidangium; s. swollen cell; sh. solitary hair; u. unilocular zoidangium. 300. Culture 68-5-1; 301. Culture 67-1-3; 302, 303, 306. Vlissingen, *Prud'homme van Reine 68-5* (fresh); 304. Vlissingen, *Prud'homme van Reine 71-25* (alcohol); 305. Vlissingen, *Prud'homme van Reine 71-22* (fresh); 307. Culture 66-1-1.

Zoidangia are formed on small, short, thin, specialized laterals, arising in irregular rows and with 1–3 together from superior and inferior secondary segments of the ultimate and penultimate determinate laterals (fig. 302–305). These specialized laterals are unbranched and slightly curved upward. The secondary segments of these special laterals are undivided or divided by 1–2 longitudinal walls and have no transverse walls. From these segments the short, hemiblastic, uniseriate, 1–4 celled stalks arise (fig. 303–305). The fertile laterals are shed soon after the fruiting season.

Unilocular and plurilocular zoidangia occasionally occur on the same plant (fig. 303). Unilocular zoidangia are spherical or somewhat ovoid when mature, more or less clavate, obovoid or ellipsoid when young (fig. 304; 305). Plurilocular zoidangia are cylindrical when mature, sometimes, however, ellipsoid or obovoid (fig. 303; 306). Zoids were not studied in detail.

Dimensions: Plants up to 11 cm high. Width of distal pinnate parts 0.5–5 (–8) mm. Diam. basal crusts 1–5 mm. Diam. of stolons 30–60 (–75) µm, of rhizoids (8–) 10–20 µm. Angle of ramification (25–) 40–50 (–70)°. Diam. corticated parts up to 450 µm, but without rhizoidal sheath (10–) 53–100 µm. Diam. penultimate laterals 40–60 µm and ultimate determinate laterals 20–60 µm. Height of secondary segments of corticated parts 20–60 µm. Number of cells in the medulla of main indeterminate filaments 4–6 (–8); in other indeterminate laterals 2–4 and in determinate laterals 1 (–2). Hairs 7–12 µm in diam. (without sheath). Chloroplasts in surface-view 2–3 µm (fig. 307; 309). Fertile laterals 100–200 (–300) µm long, diam. 10–15 (–20) µm. Unilocular zoidangia (30–) 45–70 (–85) X (25–) 40–60 (–65) µm. Plurilocular zoidangia 45–80 X 30–40 µm; loculi 5–7 X 3–4 (–5) µm.

Ecads. Ecad *pinnata* (fig. 268; 269; 295; 298). Small, light brown, pinnate, sterile, unattached plants which are usually entangled with other algae. A plant is composed of one or more branched main filaments, which are arranged in one plane. Rhizoids are only occasionally formed.

Distribution. Europe: southwest Sweden, Finland, Germany (Baltic coasts of B.R.D. and Heligoland), Denmark, The Netherlands, Scotland, Isle of Man, Wales, England, Jersey, Eire. Doubtful references from: Greenland, southwest Norway (Oslofjord), and the Orkneys. The species is also reported from the southeastern coasts of Canada, the northeastern coasts of the U.S.A., and on the coasts of Sakhalin (northeast Asia).

European localities have been listed and are given in fig. 308.

For an extract of the list of collections and references see below.

GREENLAND. Without exact locality. (as *S. plumosa*), (MEL, doubtful, locality correct ?).

NORWAY. Oslofjord. Two doubtful references.

SWEDEN. Bohuslän. Three collections/references.—Halland. Laholmsbukten, on shells, 16 m deep (Waern, 1964, p. 313).—Skåne (Kristianstads Län). All specimens are of ecad *pinnata*. Two collections.—Skåne (Malmohus Län). Three collections/references.—Blekinge. All ecad *pinnata*. More than five collections.—Småland (Kalmars Län). All ecad *pinnata*. Two collections. —Gotland. All ecad *pinnata*. Two collections.—Södermanlands Län. Ecad *pinnata*. Trosa Archipelago: between Persö and Gråskär, 11–13 m deep, with *S. arctica*, *Prud'homme van Reine 67-86*, 20/6/1967 (L).—Stockholm Län. Ecad *pinnata*. Stockholm Archipelago: Huvudskär (Waern 1952, p. 99).—Uppsala Län (Uppland). All ecad. *pinnata*. Six references.—Västernorrlands Län (Ångermanland). Ecad *pinnata*. Närke: (as *S. cirrosa*), *Krok*, 6/1868 (S).

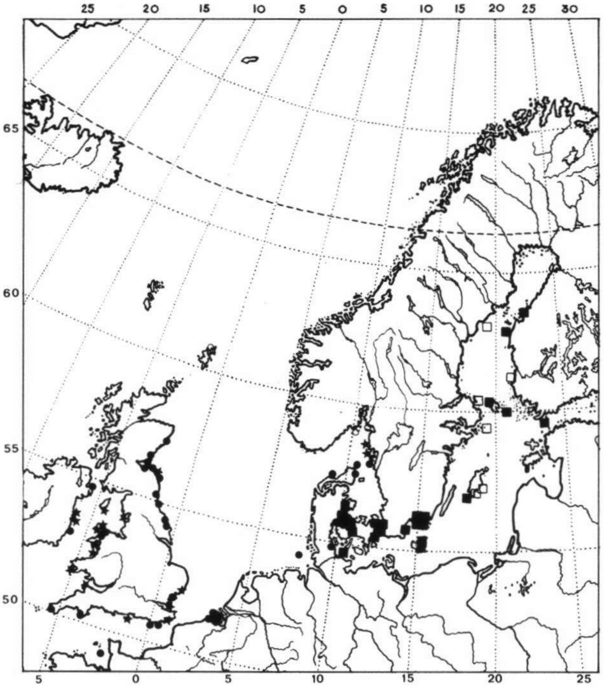


Fig. 308. Distribution of *S. plumigera* in Europe.

● = Material seen by the author.
★ = According to literature.
□ = Ecad *pinnata*; according to literature.
■ = Ecad *pinnata*; material seen by the author.
○ = Doubtful locality.

FINLAND. All ecad *pinnata.*—Ostrobottnia media. Nykarleby (= Uusikaarlepyy) Archipelago: Tonskär, *Storå*, 24/9/1953 (H, in mixture together with *S. arctica* and *Stypocaulon scoparium* forma *scoparioides*).—Ostrobottnia australis. Bergö: Rönnskärs Lotsplatz, Fälliskär, harbour bay, 4 m deep, *Häyrén*, 5/7/1952 (H, in mixture together with *S. arctica*, *S. radicans*, and *Stypocaulon scoparium* forma *scoparioides*).—Satakunta. Luvia (South of Björneborg = Pori): Säbbskär, *Häyrén* (Waern 1952, p. 99).—Alandia. Two collections.—Nylandia. Ekenäs rural: near Tvärminne Zoölogical station, Tvärminne Långskär, (as *S. racemosa*), *Nordman*, 22/6/1922 (H, mixed with *S. arctica*).

GERMANY. Baltic coasts. Bülk bei Kiel: (as *S. arctica*), *Reinbold*, 3/1890 (PC, ecad *pinnata*, mixed with *S. arctica*). Flensburg (as *S. plumosa β divaricata*), *Frölich* (herb. Binder in HBG).—Heligoland. More than ten collections, amongst which Threde, Die Algen der Nordsee.... n. 93 (HBG, together with *S. plumosa* with identical label; L, M, MEL, O. Without exact locality but 'Helgoland' is given on the label in O. In BM all material of this number is *S. plumosa*).

DENMARK. Skagerrak. Three collections.—Kattegat. More than seven collections.—Samsø area. Six collections, five of which are ecad *pinnata.*—Lillebaelt. Lyngsodde near Frederica: *Rosenvinge 8515*, 11/8/1915 (C).—Storebaelt. Ecad *pinnata*. Bovense: off Strandskoven, 11 m deep, loose, *Rosenvinge 4243* (C, mixed with *S. cirrosa* ecad *patentissima*).—Øresund. Three collections, all ecad *pinnata.*—Western Baltic (between Sjaelland and Bornholm). Stevns Lighthouse: N. to W¼W, hardly 13 miles, 24 m deep, loose, *Rosenvinge 5048*, 2/8/1894 (C, ecad *pinnata*).—Bornholm area. Four collections, all ecad *pinnata*.

THE NETHERLANDS. Schouwen-Duiveland. Eight collections/references.—Tholen. Oosterschelde. Gorishoek: sublittoral, on stones, *Nienhuis*, 11/1/1966 (L).—Noord-Beveland.

Five collections/references.—Zuid-Beveland. Two collections.—Walcheren. More than five collections.

UNITED KINGDOM. Shetland. Sullom Voe (Tittley *et al.*, 1976, p. 408, doubtful).—Orkneys. Doubtful, (Traill, 1891, p. 313).—Scotland. Buteshire: five references. Kircudbrightshire: two collections. Dumfries: (as *S. plumosa*), Richardson (E). Aberdeen: (as *S. plumosa*), *Dickie* (LISU). Fife: eight collections. Midlothian: more than four collections, amongst which Joppa, *Traill*, in Holmes, Algae Brit. rar. exs. n. 23, 12/1881 (BM, KIEL, LD). Eastlothian: Longniddry (Traill, 1885, p. 16). Without other data: (as *S. plumosa*), in Greville, Algae Brit. n. 25 (BM). Berwickshire: two references.—Isle of Man. (Holmes & Batters, 1891, p. 81).—Wales. Anglesey: three references. Caernarvonshire: three collections, amongst which Caernarvon, (as *S. plumosa*), in Wyatt, Algae Danm. n. 209 (BM, E, KIEL, L). Merionethshire: Barmouth, and Cardiganshire: Aberystwyth (Rees, 1929, p. 252). Southwest Pembrokeshire: McLean (Thomas, 1953, p. 571).—England. Lancashire: two references. Devonshire: two collections/references. Northumberland: more than four collections. Durham: four collections/references. Yorkshire: two collections. Essex: Harwich, Holmes & Traill, 7/1889 (BM, E, NMW). Kent: three references. Cornwall: two collections, amongst which Penzance, (as *S. plumosa*), in Hohenacker, Algae mar. sicc. n. 266 (L, M, MEL, PC, W). Isle of Wight: Steephill (Foslie, 1892, p. 14). Sussex: five collections.—Channel Islands. Jersey: pools between tides, *Meinertzhagen*, 5/1930 (BM).—Northern Ireland. Co Down: Bangor, (as *Chaet. plumosa*), without other data (E).

EIRE. Co Dublin: two references. Co Wicklow: (as *Chaet. plumosa*), *Suringar* (L, MEL). Without locality: (as *Conferva pennata*), *Dillwyn* (C, LD).

Notes on nomenclature. (1) Reinke (1892) did not give a description of forma *pinnata*. He only remarked: 'Die forma *pinnata* ward bisher nur im losgerissenen Zustande beobachtet', but his figures 11 and 12 of plate 45 are sufficiently distinctive to enable separation of this taxon from the rest of his var. *arctica*. Especially when *Sphacelaria* is supposed to be a microscopic plant Reinke's figures are adequate and the name of the forma can be considered as validly published (Stafleu *et al.* 1978, art. 25, 32 & 44).

Levring (1940, p. 44) rejected Reinke's var. *arctica*, but accepted three forms of *S. racemosa*: forma *typica*, forma *arctica*, and forma *pinnata*.

(2) Sauvageau (1901, p. 140 = R. 102) was well aware of the forma *pinnata* described by Reinke, but he was uncertain about the question whether or not this infraspecific taxon belonged to *S. plumigera*. His name *S. plumigera* var. *patentissima* (Sauvageau 1903, p. 50 = R. 233) is based on a separate type.

Notes on morphology. The prominent elongate apical cell of the indeterminate filament (fig. 296; 309) functions like the one in *S. plumosa*, but the sequence of the divisions within the secondary segments is different. In most cases the first longitudinal walls in the secondary segments are two periclinal and parallel walls that are always perpendicular to the plane of branching. These periclinal walls split off two primary peripheral cells, forming the branch-initials in almost all superior and some inferior secondary segments. The formation of the two periclinal walls is followed by the formation of a median longitudinal wall, parallel to the periclinal walls (fig. 279). In some cases, however, the formation of one of the periclinal walls is delayed (fig. 280; 281). The absence of a radial longitudinal wall at the time of the formation of the primary peripheral cells can also be observed in fig. 296 (compare ss 2 and is 2 with ss 3 and is 3) and in fig. 1 of plate 36 in Geyler (1866).

In the central part (the medulla) of the main indeterminate filaments four cells are formed, in which no transverse walls occur. They may be divided by perpendicular walls and this results into a maximum of eight medullar cells. In the peripheral layer several radial, periclinal, and anticlinal walls are formed, followed by transverse septation (fig. 283–292; 296). The septation of the peripheral layers in the plane of branching is more intense than

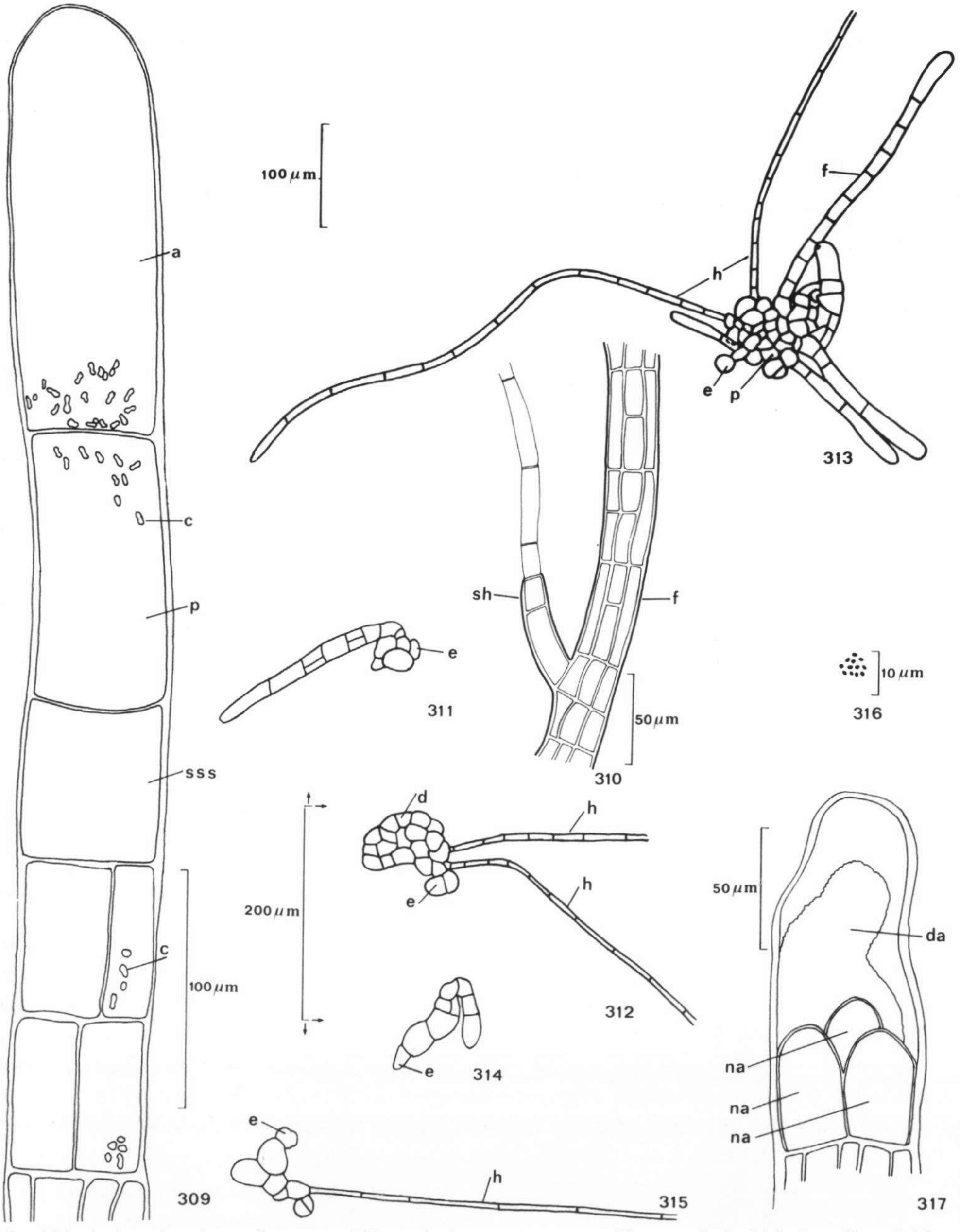


Fig. 309–317. Sphacelaria plumigera. 309. Apical part of an erect filament; 310–315. Germlings (311–315. One month old; 310, 314, 316. From plurizoids, in 310 a part of an erect filament; 311–313. From unizoids); 316. Mitosis-metaphase or early anaphase of a haploid nucleus in a young unilocular zoidangium; 317. Dead apical cell replaced by three new apical cells. a. apical cell; c. chloroplast; d. basal disc; da. dead apical cell; e. empty cell; f. erect filament; h. hair; na. new apical cell; p. primary segment; sh. solitary hair; sss. superior secondary segment. 309. Culture 68-5-1; 310, 314, 315. Culture 71-22-1; 311–313. Culture 71-22-2; 316. Vlissingen, *Prud'homme van Reine 71-25* (coloured with acetocarmine); 317. Culture 66-1-1.

in other peripheral regions (fig. 290; 292). In the laterals the pattern of septation is not as regular as in the main filaments and very similar to that of S. plumosa (compare fig. 293 & 294 with fig. 246–248). Normally the dimensions of the inferior and superior segments are equal to each other, but in one year old plants grown from plurizoids a succession of short superior segments (53–63 μm) and longer inferior segments (63–70 μm) has been observed in the main indeterminate filaments.

In the filaments of the ecad *pinnata* the medulla of the secondary segments always consists of only one or two large cells, the same number as can be found in the secondary segments of the laterals of attached *S. plumigera*. The main filaments of ecad *pinnata* are always laterals of old decayed thalli and so the structure of the medulla is not aberrant. Most filaments in this ecad are branched in the same plane, but sometimes the pinnate laterals of the second order arising from an indeterminate lateral of the first order are in a plane perpendicular to the original plane of branching. In this case the indeterminate lateral often curves in such a way that the pinnate parts are spread in a plane parallel to the original plane of pinnate branching.

Young basal discs are monostromatic. Further development is very similar to the process described for *S. mirabilis* (p. 172 and fig. 388), but the upright filaments are rarely branched and they are few-celled (fig. 272–274 and Sauvageau, 1901, f. 22B). The crusts become multi-layered when the rhizoids of the cortex extend to the basal disc and spread over it (fig. 273). In culture the basal holdfast is sometimes more developed than in nature. Basal discs can also originate from parts of stolons or from loose fragments of erect filaments (fig. 301).

Hemiblastic hairs often occur on the erect filaments of germlings (fig. 300; 310). Solitary hairs may also arise from cells of the basal discs of germlings (fig. 312; 313; 315). Some acrohomoblastic hairs have also been found on the erect filaments of germlings (fig. 300).

Notes on ecology. Sphacelaria plumigera is a sublittoral species that also can grow in permanent and shaded pools in the lower parts of the eulittoral. At LWS, and especially at ELWS, the plants may emerge for a short time. In Denmark and Sweden it has been found down to a depth of 15–28 m; near Heligoland between 2–10 m, and in The Netherlands down to a depth of 2–3 m. On the British Isles it has almost exclusively been found in pools. *S. plumigera* grows on rocks, stones, gravel, shells and peat-banks and it occurs often on mud- or sand-covered substrates. It has been found on the shell-grounds in the Kattegat (Waern, 1958) where it sometimes grows in equal quantities as *S. plumosa*. In Denmark and Heligoland it has sometimes also been found mixed with *S. plumosa* but the latter species is more common there. On the British Isles *S. plumigera* is apparently far more common than *S. plumosa*. This may be the consequence of the occurrence of *S. plumigera* in parts of the shore that can be more easily explored.

Sphacelaria plumigera has more often been collected in winter than in summer because this perennial species can be more easily detected when the many epiphytic and epilithic *Rhodophyceae* and *Chlorophyceae* are not too numerous.

In St. Andrews (Scotland) the species grows in shallow sandy pools in the shade of the cliffs about H.W.N.; so quite high on the shore. In February these pools are inhabited by three *Sphacelaria* species: *S. mirabilis, S. plumigera*, and *S. radicans*. The latter two species often grow on the crusts of *S. mirabilis* (fig. 401; 402).

Sphacelaria plumigera ecad *pinnata* has always been found in the sublittoral between depths of 5 and 38 m, as unattached plants. It is often found entangled in the epilitic algae, in most cases in tufts of *S. arctica.* In other cases the filaments are part of algal balls (aegagropilae), often together with other *Sphacelariales.*

In material from Malmö (Limhamn, *Hylmö*, as *S. radicans* forma *aegagropila* in LD) *S. plumigera* ecad *pinnata* is mixed with *S. cirrosa*, *S. radicans* ecad *libera*, and *S. arctica.* In material from Finland (Åland, Ekerö, *E. Häyrén*, 13/6/1949; in H), *S. plumigera* ecad *pinnata* is mixed with *S. radicans* ecad *libera, S. arctica*, and *Stypocaulon scoparium* forma *scoparioides*, and a similar mixture has been found near Karlshamn in Sweden (*Levring*, 13/6/1936, in GB). In Odensefjord (*Lyngbye*, 13/1/1816, in C) it is mixed with *S. cirrosa* ecad *patentissima*, *S. reticulata*, and *Stypocaulon spinulosum*, and at the Kirkegrund in the Samsö-area in Denmark (*Rosenvinge 4043*, 18/9/1893, in C) it occurs together with *S. cirrosa* ecad *patentissima*, a loose-lying *S. plumosa*, and *Stypocaulon spinulosum.*

Apart from its ecad *pinnata S. plumigera* does not penetrate very far into brackish waters. The normal form has been found in the Lillebaelt where salinity (S) varies between 20 and 25°/oo.

Sphacelaria plumigera ecad *pinnata* in the Baltic is always sterile and rarely forms a few rhizoids. Thus it is incapable of attaching to the substrate. Many other algae in this brackish area present this loose-and-entangled growth habit.

In the Bothnian Gulf *S. plumigera* ecad *pinnata* has been found as far to the north as to Nykarleby, where salinity (S) varies between 3 and 4°/oo. In Kalø Vig (where the ecad also had been found) the salinity may rise as high as 20°/oo.

The area where *S. plumigera* has been found can be described as circum-boreal and non arctic. Fossil remains of this alga have been found in some British pleistocene deposits and have been checked by me. At Renfrew airport near Glasgow the alga has been sieved out of late glacial, grey, silty, fine sands also containing *Desmarestia aculeata* and *Laminaria* species (Brett & Norton, 1969). Small pieces of an alga that is probably *S. plumigera* have been found in the Cromer Forest Bed Series at Mundesley, Norfolk. Fragments of other plants (especially pollen) suggest that these are from a cold near-glacial stage in the lower Pleistocene and laid down in an estuarine habitat (Wilson, 1973). From these observations it looks as if *S. plumigera* did grow in colder waters in the Pleistocene than it does in recent times.

Form range and cultures. In *S. plumigera* the morphological variation seems to have little taxonomic implications. The dimensions of tufts, the number of axes and laterals, and the diameter of these filaments show sometimes rather large variations from one plant to another. The amount of hairs and rhizoids is also variable and so is the colour of herbarium specimens. In some specimens the laterals grow out very rapidly, resulting in a truncate or cuspidate outline of the apex of the feathers (fig. 264), in others these laterals grow more slowly, resulting in a more or less acute or blunt outline of the apex (fig. 265). These variations can be observed in one population. In deeper permanent pools and in the lower sublittoral large specimens exist, but in shallow pools and in the upper sublittoral the specimens are often much smaller.

The habit of the plants does not vary much with the seasons. Except in winter the tufts of *S. plumigera* are usually covered with epiphytes and they are often almost completely hidden by tufts of green and red algae (especially *Ceramium, Polysiphonia*, and *Cladophora* spp.).

In areas where salinity is relatively high (in Denmark) there is not much difference between the attached *S. plumigera* and the loose ecad *pinnata*. The angle of ramification is on an average larger in the ecad *pinnata* and the number of rhizoids is much smaller. In localities with a lower salinity the attached plants disappear and the unattached plants become much smaller and are often lighter in colour. The laterals are shorter and more uniform. They give the impression as to whether the laterals are almost perpendicular to the axes, but actually the angle of ramification is on an average only 5–10° larger than in specimens from localities with higher salinities. The specimens from the Bothnian Gulf are in most cases small and very narrow (pinnate parts ±0.5 mm broad), but the Danish specimens are much more robust and the pinnate parts are up to 1.5 mm broad (fig. 268; 269).

Cultures have been isolated from material collected on several occasions on the coasts of The Netherlands (province of Zeeland). Some cultures and their subcultures have been maintained during seven years. These subcultures showed a similar variation as subcultures of *S. plumosa*.

Only one fragment of *S. plumigera* ecad *pinnata* (from Askö, Trosa Archipelago) has been studied in culture. In some subcultures originating from this fragment rhizoids were formed and the specimens attached themselves with those rhizoids to the wall of the culture-tubes. In an early stage the cultures got lost.

Sphacelaria plumigera grew very slowly in culture. Under the normal day-light conditions in culture at 4°C (1400–2800 Lx) the apical cells died off very often (fig. 317) and the nearby determinate laterals started indeterminate growth. At 4°C and low light intensities (88–500 Lx) the apical cells functioned better and the small plants maintained their characteristic *S. plumigera* habit. Young plants grew best at 12°C (low light intensities) but their growth was only c. 2 mm a month, and in old plants even slower. When more light was given maximum growth was sometimes faster, but plants grown from fragments of c. 1 mm of mature plants had a height of only 15 mm after 3½years in culture and the apical cells died often. At 20°C growth was much faster, but the laterals became determinate after the formation of 10–15 primary segments or less. In many cases no new indeterminate laterals were formed after the death of the apical cell of the main indeterminate filaments at this high temperature.

In many cultures the forming of rhizoids and stolon-like filaments was more extensive than in nature. Often thick basal parts were formed without a definite structure and mainly consisting of creeping rhizoids. When cultured as unattached plants in artificial marine wave conditions (shaken culture) thick, hard, irregular balls, consisting mainly of rhizoids, were formed, without any sign of pinnate branching. In normal non-shaken cultures these hard balls may form normal pinnate filaments again.

Hairs were quite often found in culture, as well at 4°C as at 12°C and 20°C. Especially at 20°C they occurred in an early stage of growth of determinate laterals and this resulted in very short laterals.

Reproduction and life-history. Unilocular and plurilocular zoidangia have been found, but no specialized propagules. Vegetative reproduction can take place by means of detached fragments which easily attach to the substrate and form new plants (fig. 301).

Many fertile plants from nature have been taken into culture, but none of the new plants in culture formed any zoidangia. In fertile material with plurilocular zoidangia swarming of the zoids was not observed. Swarming of unizoids was observed on several occasions within a few hours in freshly collected material. The discharge of these unizoids seemed to take place in exactly the same way as described for *S. radicans* (p. 78). See also my fig. 305 (arrow). The discharge of the zoids, still enclosed in a common mucilage-envelope, took less than one minute at 15°C and within 10–30 seconds the zoids separated from one another. The zoids moved quite quickly and no sign of clumping or copulation was observed.

Fragments of fertile plants with unilocular or plurilocular zoidangia were separately cultured in culture-tubes or hanging drops. After 5½ weeks, young germlings were found at 4° and 12°C (fig. 311–313). The germlings that probably originated from unizoids were disciform or filamentous. In some cases long solitary hairs grew from the basal parts (fig. 312; 313). The filaments often showed apical growth and in some cases the secondary segments were divided by longitudinal walls. In some germlings small round seemingly empty cells could be observed (fig. 313). These empty cells were probably the remnants of the walls of the settled unizoids. The diameter of the discs was 60–100 μm. The filaments were till 275 μm long and 10–18 μm in diameter, while the secondary segments were 10–25 μm long. The germlings that probably originated from plurizoids had the same form as described above (fig. 314; 315), but in most cases they were smaller and the empty cells were less rounded. Solitary hairs were also found (fig. 315). The diameter of the discs was 40–100 μm, and the filaments were not longer than 150 μm. Their diameter was 12–20 μm, while the length of the secondary segments was 20–30 μm.

The germlings grown from unizoids held the lead in growth. When five months old, these germlings were still larger and more robust than the germlings of plurizoids (fig. 266; 267). The dimensions of the segments and laterals, however, were not significantly different.

Unilocular zoidangia have been found on specimens from different parts of Europe. They have already been described by Dillwyn (1809, as *Conferva pennata*) with the remark '... an unusually large variety of this species, with oblong pedicellated capsules.' Wollny (1880) figured the unilocular zoidangia of *S. plumigera*, supposing these were sporangia of *Chaetopteris plumosa*. Later Batters (1889) and Reinke (1892) correctly pictured these unilocular zoidangia of *S. plumigera*.

Plurilocular zoidangia have only been found on specimens collected near Vlissingen in The Netherlands (Prud'homme van Reine, 1968). Some specimens collected by *Traill* in Scotland were annotated 'pluriloc. fruit' by the collector, but in spite of detailed studies of the material no plurilocular zoidangia could be detected. In hundreds of plants I studied at St. Andrews, Scotland, I never saw any plurilocs, nor on plants from other localities in The Netherlands. In most cases plants from Vlissingen with plurilocular zoidangia also bore unilocular zoidangia. These unilocular and plurilocular zoidangia were found on the determinate laterals of different main indeterminate filaments, but sometimes the plurilocular zoidangia occurred on the proximal determinate laterals and the unilocular zoidangia on the distal ones. Rarely unilocular and plurilocular zoidangia occurred on the same determinate lateral and still more rarely on the same fertile lateral (fig. 303, and Prud'homme van Reine, 1968, f. 1d). The number of plants with plurilocular zoidangia was always small (table XII).

Fructification occurs in winter and early spring (March and April) but some fertile plants

TABLE XII. Unilocular and plurilocular zoidangia on S. plumigera from Vlissingen

date of collecting		number of specimens				
		with plurilocs (also unilocs)		with unilocs only	sterile	total
30/1/1967		1	(1)	19	-	20
17/2/1968		2	(2)	28	-	30
1/3/1971	pool 1	1	(1)	90	9	100
	pool 2	5	(3)	43	2	50
	upper sublittoral	-	-	8	17	25

have been collected in other months of the year. From incidental chromosome counts in young unilocular zoidangia I estimated 12 presumably haploid chromosomes (fig. 316).

The available data on the reproductive structures of *S. plumigera* are too scarce to construct a life-history model.

Systematic position. *Sphacelaria plumigera* has often been confused with the very similar *S. plumosa*, especially on the British Isles and on Heligoland. It differs from *S. plumosa* by its elongated and uninterrupted pinnae with their linear outline (compare fig. 264 & 265 with fig. 212). The zoidangia of *S. plumigera* arise from the ultimate and penultimate determinate laterals (fig. 302) and not from the rhizoidal cortex of the main filaments as is usual in *S. plumosa* (fig. 250). The appressed rhizoids, forming a compact cortex, arise in *S. plumigera* exclusively in the plane of branching of the filaments (fig. 275–277; 292), but in *S. plumosa* in all planes except the plane of branching of the filaments (fig. 225; 226; 244; 245).

The material collected by *Brandt* at the Hoburg Bank (containing the type of *S. plumigera* f. *pinnata*), puzzled Reinke much. He at first used the name *S. pseudoplumosa* Crouan for it, but when Kjellman had suggested that it might be a state of *S. cirrosa* or *S. arctica*, he considered it as part of *S. racemosa* (Reinke 1891, p. 12, footnote). Svedelius (1901, p. 99) did not accept the pinnate specimens as a separate taxon within *S. racemosa* forma *notata* C. Ag. (= *S. arctica*), but merely as loose fragments showing the characteristic branching of young specimens. Sauvageau (1901, p. 140 = R. 102), when (wrongly) citing *S. racemosa* var. *pinnata* Reinke, did not give a definite status to this infraspecific taxon, but he only suggested that it might belong to *S. plumigera*. But in a later paper Sauvageau (1903, p. 50 = R. 233) based a new variety on specimens from Denmark he had on hand. Waern (1945, p. 408) stated: 'In my opinion f. *pinnata* (Reinke) is nothing but *Sphacelaria plumigera* Holmes in a specific form so far known only from the Baltic'. He did not make a new combination for these 'loose, sterile dwarf forms of *Sph. plumigera*' and in a later paper (Waern 1952, p. 99) he used the indication'Loose-and-entangled status (f. *pinnata*)'.

Lund (1950, p. 50) distinguished two forms of loose lying *S. plumigera*. According to

TABLE XIII. Comparison between attached S. plumigera, S. plumigera ecad pinnata, and S. arctica

	S. plumigera		S. arctica
	attached plants	ecad pinnata	
rhizoids	from inferior secondary segment and in the plane of branching	almost lacking	from both inferior and superior secondary segments and in all planes
pattern of branching	regularly pinnate	regularly pinnate	regularly or irregularly pinnate
angle of branching	(25–)40–50(–60)°	(40–)50–60(–70)°	0–15–30° (regular) 25–45(–60)° (irregular)
zoidangia	arise from laterals only	absent (plants always sterile)	arise from all parts of the plants
secondary transverse cell walls in secondary segments	in all peripheral cells	in all peripheral cells	in most peripheral cells

him forma *patentissima* has divaricate, often rather long determinate laterals, which issue almost rectangularly, whereas the determinate laterals of forma *pinnata* are shorter, rising at an acute angle. But he also remarks: ‘However, the characters are not distinct’.

There are no distinct differences between the two loose-lying forms of *S. plumigera*, and so it seems better to consider these loose specimens in which rhizoids are lacking or very scarce as one single ecad: ecad *pinnata*.

Plants of ecad *pinnata* can often be found entangled in the tufts of *S. arctica*. It differs from the latter species in its regular pinnate branching, the larger angle between axis and laterals, the permanent occurrence of median transverse walls in the cells of the secondary segments and the (rare) rhizoids always issuing in the plane of branching. These characters (except the angle between axis and laterals, which is larger in ecad *pinnata*) are also those of the attached *S. plumigera*.

Pankow (1971, p. 164) in uniting *S. arctica* and *S. plumigera* as forms of *S. arctica* apparently only studied the loose sterile specimens and not the attached ones. In another paper (1975, p. 803) he tried to elucidate his action and added some arguments based on literature and on personal information from a letter I wrote to him. In my opinion, however, there is no reason to justify the combination of the two species.

The loose sterile specimens are found in a particular area and are quite easily recognisable in the field. For these reasons I prefer to retain a special name for this growth form.

Batters (1889) separated *S. plumigera* from the other species of the genus *Sphacelaria* and placed it in his new subgenus *Pseudochaetopteris*, accentuating its similarity to *S.* (*Chaetopteris*) *plumosa*. After having observed plurilocular zoidangia arising from normal pinnate laterals of *S. plumosa*, I consider *S. plumigera* and *S. plumosa* both as belonging to the section *Pseudochaetopteris* of the subgenus *Pseudochaetopteris*.

In the other section of the subgenus *Pseudochaetopteris*, the section *Racemosae*, both distribution of the cells from which rhizoids arise and branching of the filaments is much less regular than in *S. plumigera*. For comparison between *S. arctica* and *S. plumigera* and its ecad *pinnata* see table XIII, and for comparison between *S. plumigera*, *S. caespitula*, *S. radicans*, and *S. mirabilis* see table VII.

IIb. Section Racemosae Prud'homme van Reine *nov. sect.*

Sphacelaria sect. *Racemosa* Prud'homme van Reine (1978) 312 (*nom. inval.*)—Type species: *S. racemosa* Greville.

Thalli e disco basali tenui et filamentis pinnatis vel irregulariter ramosis erectis compositi. Filamentum erectum principale et disci basales ecorticati vel corticati, rhizoideis laxe appressis crescentibus deorsum, irregulariter emersis ex cellulis filamentorum peripheralibus. Zoidangia racemosa vel solitaria.

Thalli consisting of a thin basal disc and pinnate or irregularly branched erect filaments. Main erect filaments and the basal discs are ecorticate or corticated by loosely appressed downward growing rhizoids, arising irregularly from peripheral cells of these filaments. Zoidangia occur in racemes or solitary.

7. Sphacelaria arctica Harvey—Fig. 318--352

Sphacelaria arctica Harvey (1858) 124; J. Agardh (1871) 1080; Kleen (1874) 36; Kjellman (1875) 96, (1877a) 34, t. 2 f. 4–6, (1877b) 43; Gobi (1878) 62; Kjellman (1883) 275; Waern (1945) 409, t. 1 & f. 2, (1952) 100, f. 41, 43, 44, 47b; A. Zinova (1953) 112, f. 91; Lund (1959) 95; Jorde & Klavestad (1960) 91 (excl. 'large form'); Ravanko (1968) 24; Prud'homme van Reine (1974) 174; Mathiesen (1974) div. pp. + t. II, c; Pankow (1975) 803; Rueness (1977) 181 + f. 106; Prud'homme van Reine (1978) 303.—*Sphacelaria arctica* forma *arctica* Pankow (1971) 164, f. 190, (1975) 804.—*Sphacelaria racemosa* var. *arctica* Reinke (1889) 40, (1892) 66, t. 44 (excl. f. 2) & t. 45 (excl. f. 11 & 12); Rosenvinge (1893) 904, (1898) 100; Jónsson (1904) 40; Lakowitz (1907) 28, f. 17; Skuja (1924) 349, f. p. 352; Lakowitz (1929) 233, f. 328.—*Sphacelaria racemosa* forma *arctica* Sauvageau (1903) 76 (= R. 247); Levring (1940) 44; Lund (1950) 46, (1951) 13; Sundene (1953) 158.—*Sphacelaria racemosa* Greville *emend.* Reinke (1890a) 207 (*p.p.*), (1891) 11 (*p.p.*); De Toni (1895) 505 (*p.p.*); Sauvageau (1901) 137 (= R. 99) (*p.p.*), f. 23.—Type: *Lyall s.n.*, Isle of Disko, E. Greenland, in tide pools, 6/1852 (BM; TCD, holo).

Conferva pennata auct. non Hudson: Wahlenberg (1812) 512 (*p.p.*).—*Ceramium pennatum auct. non* Roth var. β: Wahlenberg (1826) p. 905 (*p.p.*).—Type: *Wahlenberg s.n.* Kjerringöy (as Kierringö), N. Norway, 27/5/1809, as *Conferva scoparia* (UPS).

Sphacelaria cirrhosa ε *notata* C. Agardh (1828) 29.—*Sphacelaria cirrhosa* forma *notata* Hornemann (1837) 694.—*Sphacelaria notata* Kjellman (1890) 67, E. Zinova (1929) 77.—*Sphacelaria racemosa* forma *notata* Svedelius (1901) 98; Skottsberg (1911) 14, Sjöstedt (1920) 24.—Lectotype: Salgö, *n. 84*, probably collected by *C. Aspegren* (LD, Ag. no. 45421).—See notes on nomenclature 1.

Sphacelaria clevei Grunow (1874a) 37, (1874b) 71, (1874c) 174 (all identic).—Type: *Cleve s.n.*, Gotland, 1864 (TCD; UPS; W, coll. Grunow no. 19629).

Sphacelaria radicans auct. non (Dillw.) C. Ag.: Gobi (1874) 8.—*Sphacelaria cirrhosa* forma *corticata et radicans* Areschoug (1876) 33.—*Sphacelaria intermedia* Gobi (1877) 528, *nom. nov. pro Sphacelaria radicans sensu* Gobi.—Type: Coast of Estland (not located).—See notes on nomenclature 2.

Sphacelaria olivacea auct. non (Dillw.) Grev.: Reinke (1890a) 206, f. 1, (1891) 6 (*p.p.*: Ostseeform), (1892) 66, t. 46: *Reinke s.n.* Kieler Föhrde, 12/1887 (HBG, KIEL, MEL, PC).—See notes on nomenclature 3.

Plants are quite stiff; shrubby or tufted (fig. 318; 319); yellowish-brown, reddish-brown, olivaceous, or dark-brown; solitary, gregarious, or caespitose; epilithic or epiphytic. The tufts are often broom-like with narrow base and asymetrical broadened distal ends, or broad-fusiform with an irregular tip.

Several to many branched main axes arise from one to several basal holdfasts, which are very variable in form, structure, and dimensions.

In early stages the basal part is a circular basal disc with marginal growth. The young disc is monostromatic and consists of a number of radiating, branched, coalescent, creeping filaments with apical growth (fig. 320). In later stages the basal disc may become polystromatic by upward growth and subsequent division of the intercalary cells of the coalescent creeping

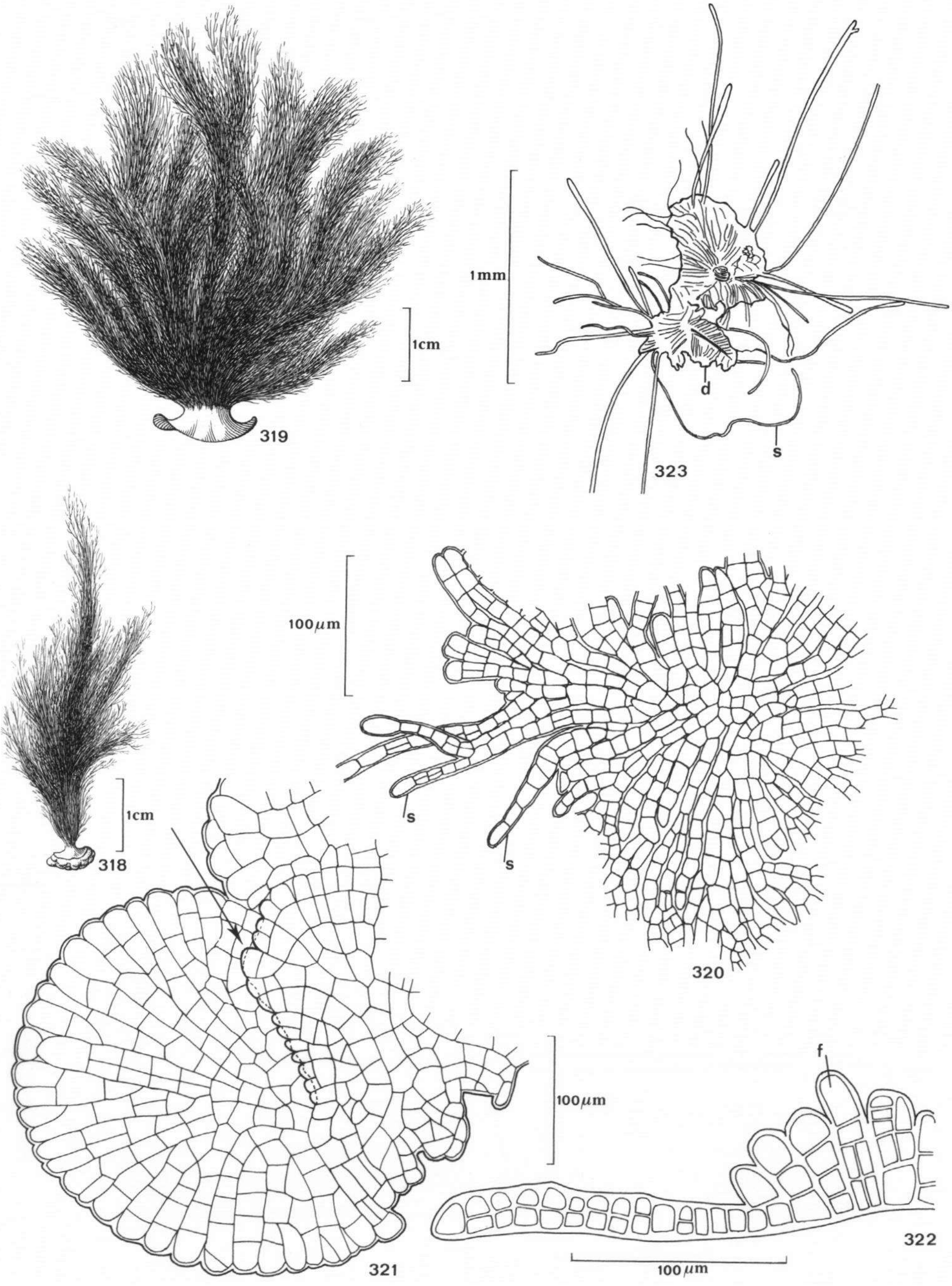


Fig. 318–323. Sphacelaria arctica. 318, 319. Habit; 320–322. Basal disc (320. From below; 321. From above; 322. Section); 323. Young plant. d. basal disc; f. erect filament; s. stolon. 318. Askön, *Prud'homme van Reine 751* (L, sheet 972.046-74); 319. Actinia bay, *Kjellman* (O, soaked); 320–323. Culture 67–89.

filaments (fig. 322). The crust may be gradually thickened and enlarged by downward growing rhizoids from the axes spreading over the disc. Sometimes discs grow over one another, forming thick crusts (fig. 321, arrow). Often rhizoids or creeping filaments function as stolons (fig. 320; 323).

The erect parts of the plants are composed of several main axes and indeterminate hemiblastic laterals of up to the third or fourth order. The pattern of branching is pinnate or irregularly pinnate (fig. 324–326) and even the ultimate laterals often show indeterminate growth. The bases of the laterals are often narrower than their apical parts.

Few to several narrow downward growing, loosely appressed rhizoids arise irregularly from the main erect filaments and descend along these filaments (fig. 326), forming an irregular spiral but sometimes forming a complete cortication.

The dimensions of the inferior and superior secondary segments of the main filaments are mostly equal to each other (fig. 332). In some specimens, however, the inferior secondary segments are longer than the superior ones (fig. 324; 333). Secondary segments are usually slightly longer than they are wide and only occasionally somewhat wider than they are long.

The secondary segments are subdivided by radial, periclinal, and transverse walls into a few-celled medulla and many peripheral cells. In the medulla almost no transverse walls are formed and the cells are quadrangular in cross-section (fig. 327–331; 350). In dried material the medullar cells are often dark in colour (fig. 332). In the main erect filaments four or less than four medullar cells are developed and in the small laterals of higher order the medulla consists of only one cell. Often one or more medullar cells reach the periphery of the filament (fig. 327, arrow). The peripheral cells are separated by walls which are more or less radial or periclinal and parallel to these radial walls. In lateral view often 3–6 longitudinal walls can be observed in large secondary segments (fig. 324; 332). Occasionally a peripheral cell is divided into an inner and an outer peripheral cell by an anticlinal wall (fig. 328). In most cases the long peripheral cells of the main filaments are subdivided into shorter ones by 1–3 transverse walls (fig. 324; 332). Occasionally secondary longitudinal walls occur in these subdivided peripheral cells. Some peripheral cells give off long unbranched appressed rhizoids (fig. 326).

The scarcely branched, often long and stiff, laterals arise in a regular or irregular pinnate pattern from superior secondary segments of the erect axes. They may be opposite (fig. 324), alternate (fig. 325), or secund. There is no difference in growth and form between axes and laterals, but the ultimate laterals have often smaller dimensions.

Hairs may arise by acrohomoblastic branching on the laterals (fig. 334), but they may be hemiblastic as well (fig. 333; 335). They are never frequent, and arise singly (fig. 333), in pairs (fig. 334; 335), or in bundles of four.

There are no propagules, but parts of the plants that break off easily form new plants that attach by newly formed basal discs.

Zoidangia occur singly or in elongated, loose racemes which arise from all parts of the filaments (fig. 336–340; 352) and occasionally also from the rhizoids (fig. 343). The main filament of a zoidangial raceme is an often slightly bent and narrow lateral (fig. 337–340) from which arise zoidangia stalks varying in number from a few to many and branched or unbranched. They are often all arranged in one plane and more or less distichous. Unilocular and plurilocular zoidangia usually occur on separate plants.

Unilocular zoidangia are ovoid or broadly ellipsoid when mature (fig. 336), more narrowly

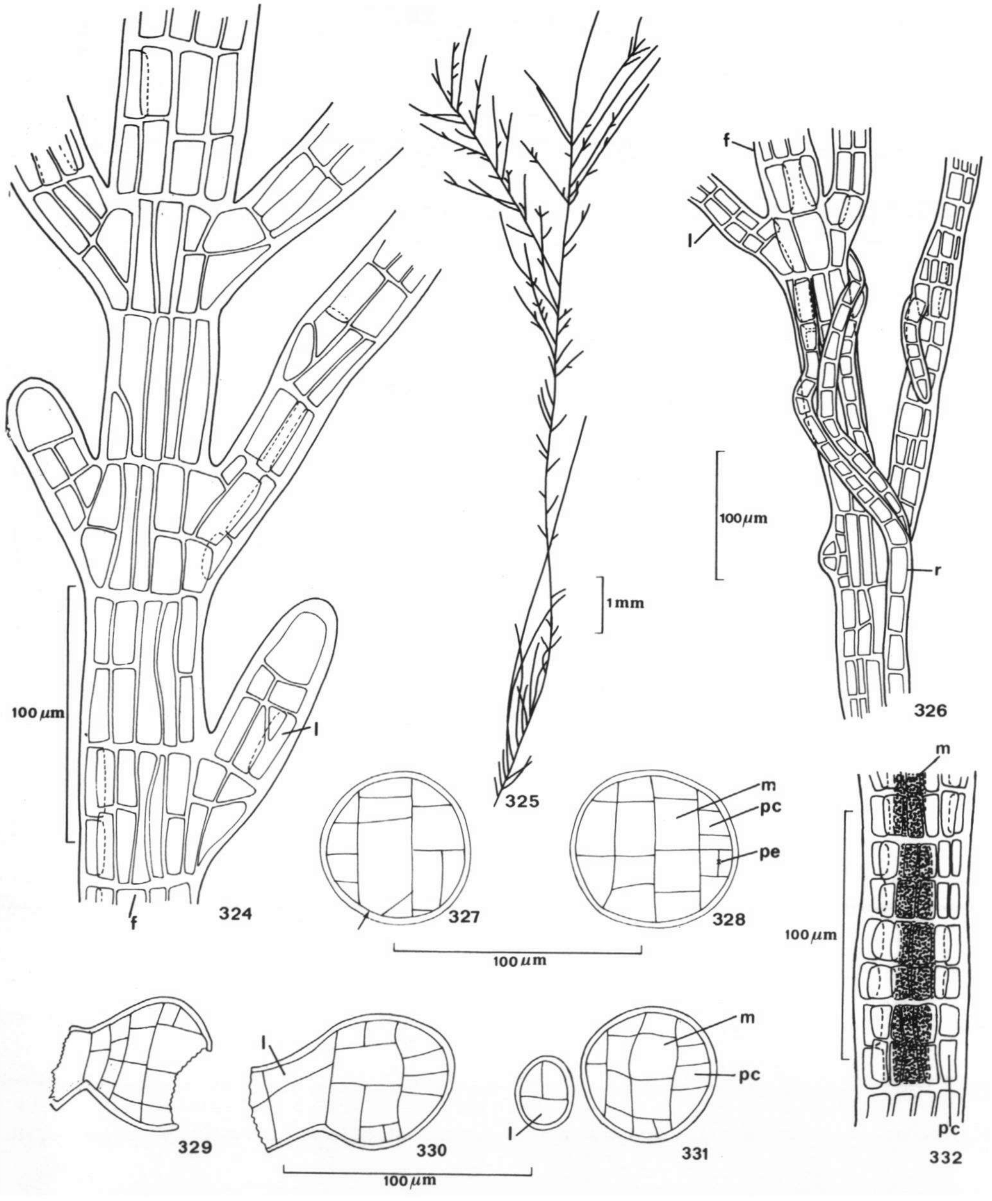


Fig. 324–332. Sphacelaria arctica. 324–326. Branching; 327–331. Cross-sections of erect filaments; 332. Part of an erect filament. f. erect filament; l. lateral; pc. peripheral cell; pe. periclinal wall; r. rhizoid. 324. Askön, *Prud'homme van Reine 67-85* (formalin); 325. Mosselbay, *Kjellman* (UPS, soaked); 326. Saltholm, *Lund 1078* (C, formalin); 327–331. Gotland, *Prud'homme van Reine 67-90* (formalin); 332. Bonden, *Kylin* (LD, soaked).

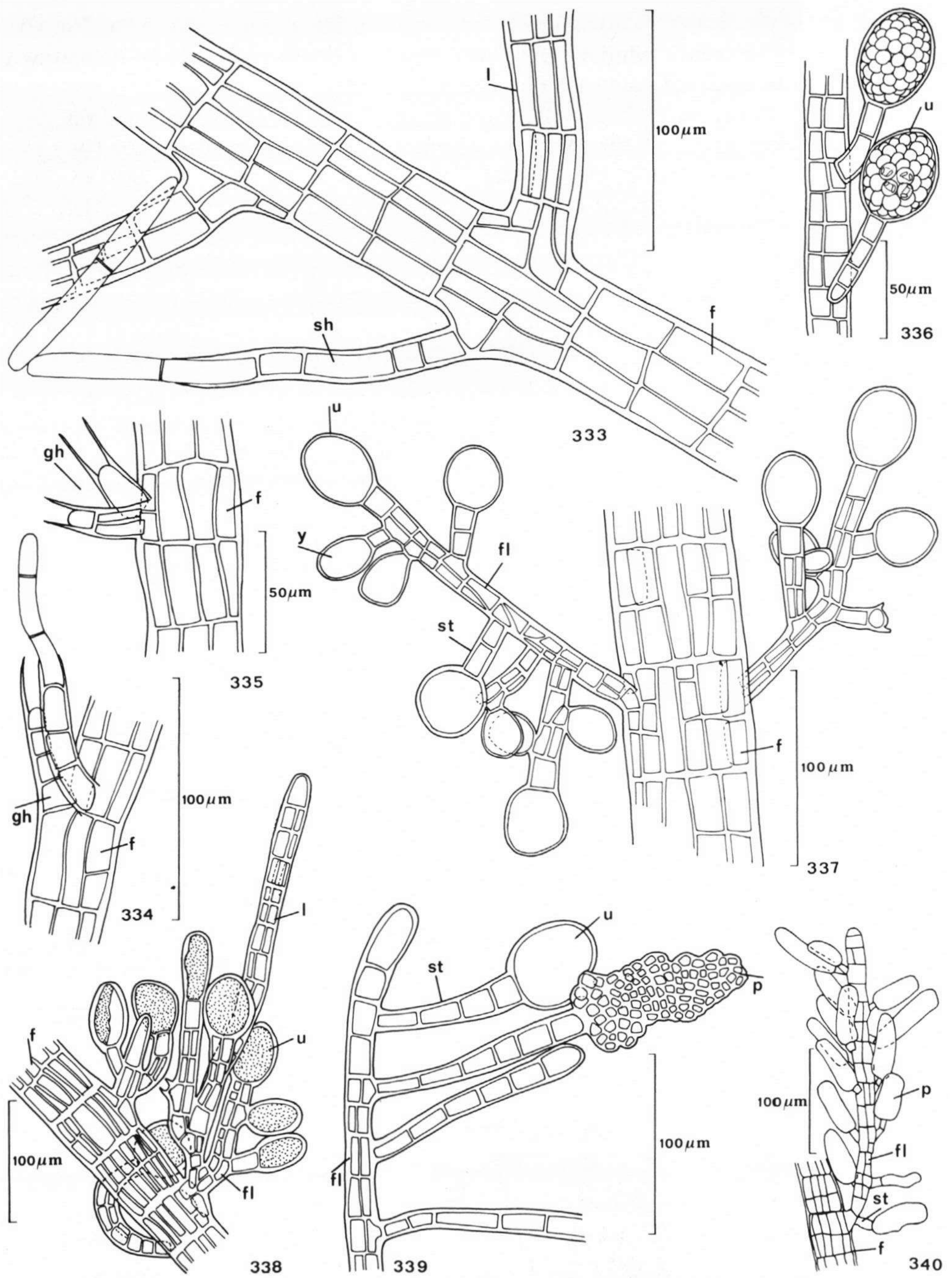


Fig. 333–340. Sphacelaria arctica. 333–335. Hairs; 336–340. Zoidangia. f. erect filament; fl. fertile lateral; gh. geminate hairs; l. lateral; p. plurilocular zoidangium; sh. solitary hair; st. stalk; u. unilocular zoidangium; y. young. 333–335. Culture 67–56; 336. Culture 67-89-3; 337. Kieler Föhrde, *Reinke* (L, soaked); 338. Saltholm, *Lund 1078* (C, formalin); 339. Culture 67-65-1; 340. East Greenland, *Lund 686a* (C, formalin).

ellipsoid when young (fig. 338). Plurilocular zoidangia are elongate and cylindrical (fig. 342), sometimes narrowly ellipsoid (fig. 344), shortly cylindrical (fig. 152), or narrowly conical (fig. 339). Zoids have not been observed.

Dimensions: Plants up to 2–8 (–10) cm high and 3–4 cm wide. Diam. basal disc 3–8 mm. Diam. of stolons 35–60 μm. Angle of ramification in regular pinnate parts (0–) 15–30°, in irregular pinnate parts 25–45 (–60)°. Diam. of main filaments (35–) 40–65 (–75) μm, but 100–130 μm when corticated. Diam. of bases of laterals 27–50 μm. Height of secondary segments 30–80 μm. Hairs 12–14 μm in diam. (without sheath) or 15–16 μm (sheath included). Rhizoids often 12–15 μm in diam. at the point where they arise. Chloroplasts 3–4 X 4–5 μm in surface view (fig. 41; 345). Zoidangial stalks 15–25 μm diam. Unilocular zoidangia (40–) 45–55 (–64) X (37–) 40–52 (–60) μm (Baltic), or 50–60 (–75) X (38–) 40–55 (–62) μm (Arctic). Plurilocular zoidangia when young 55–65 X 28–32 μm, when mature 65–200 X 25–50 (–55) μm, diam. loculi 4–9 (–12.5) μm.

Distribution. Greenland. Europe: Spitzbergen, Norway, Sweden, Finland, Arctic and Baltic coasts of the U.S.S.R., Poland, Baltic German coasts, Denmark, and the Shetlands.

The species is also known to exist in the Asian and American Arctic Ocean, the Bering Sea, the Okhotsk Sea, and the Northern American coasts of the Pacific and Atlantic Ocean.

European localities have been listed and are given in fig. 341.

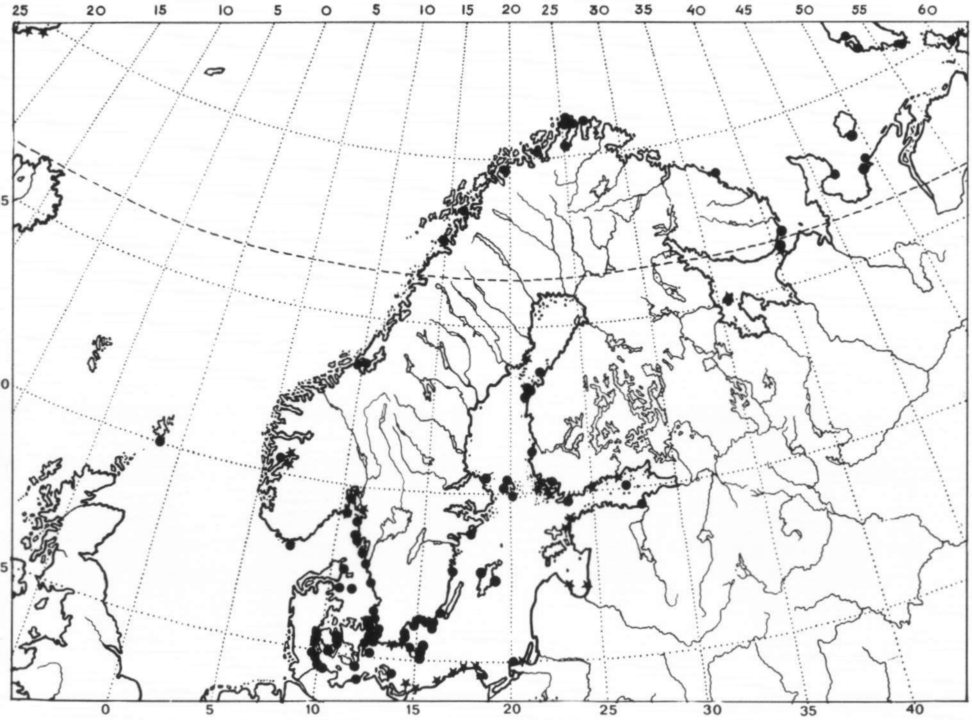


Fig. 341. Distribution of *S. arctica* in Europe

● = Material seen by author.
★ = According to literature.

For an extract of the list of collections and references see below.

GREENLAND. West coast. Seven collections/references.—East coast. More than six collections/references.

SPITZBERGEN. Many collections/references.

NORWAY. Finmarken. Eight collections/references.—Troms. Two collections.—Nordland. Four collections.—Tröndelag. Three collections/references.—Hordaland. Four collections/references.—Vest Agder. Kristiansand: Silokaia, semi-exposed, 2–4 m deep, *Åsen 179-2*, (L).—Vestfold. Tjøme: Verdens Ende, in shallow pools between rocks, together with *Zostera marina*, 0.5 m deep, *Prud'homme van Reine 67-82*, 13/6/1967 (L).—Akershus. Three collections/references. —Ostfold. Hunnebunnen (Klavestad, 1964, p. 148).

SWEDEN. Bohuslän. Seven collections/references.—Skåne (Malmöhus Län). Ten collections, amongst which Malmö: Limhamn, (as *S. radicans* forma *aegagropila*) in Hylmö Skand. Meeresalgen n. 42, 21/6/1913 (M, mainly *S. radicans* ecad *libera*, but also some *S. arctica*). *Ibidem*: (as *S. cirrhosa* var. *aegagropila*), *Hylmö 42*, 21/6/1913 (LD, mixture of *S. arctica, S. cirrosa, S. plumigera* ecad *pinnata*, and *S. radicans*).—Skåne (Kristianstad Län). Five collections/references.—Blekinge. Seven collections.—Småland (Kalmar Län). Two collections.—Gotland. Four collections.—Södermanlands Län. Trosa: Askön, several localities, 1–17 m deep, *Prud'homme van Reine*, 17–21/6/1967 (L).—Stockholms Län. Öregrund: Känningen, *Waern*, 22/7/1950 (L).—Västerbotten. Ratan (Waern, 1952, p. 104).

FINLAND. Ostrobottnia media. Nykarleby (= Uusikaarlepyy) Archipelago: Tonskär, cast ashore, *Storå*, 24/9/1953 (H, in mixture together with *S. plumigera* ecad *pinnata* and *Stypocaulon scoparium* forma *scoparioides*).—Ostrobottnia australis. More than four collections/references.—Satakunta. Rauma, several localities, 4–7 m deep: *Häyrén*, 11 & 13/7/1949 (H, in part mixed with *S. radicans* or with this species together with *Stypocaulon scoparium* forma *scoparioides*).—Regio aboensis. Five collections/references.—Alandia. Three collections.—Nylandia. Ten collections/references.—Karelia australis. Kotka (Waern, 1952, p. 104).

U.S.S.R. Western Arctic coasts. Nine collections/references.—Novaya Zemlya. More than five collections/references.—Kara Sea. Eight collections/references.—Baltic coasts. More than seven collections/references, amongst which Estonian S.S.R.: Narva, 9.5–16 m deep, Gobi in Algae rossicae exsiccatae n. 28, 6/8/1877 (C, Kiel, L).

POLAND. More than five references.

GERMANY. Baltic coasts. Eleven collections.

DENMARK. Kattegat. Three collections.—Lillebaelt. Three collections.—Sydfynske Øgaard. Aerø: Kiaerbølling (C).—Storebaelt. Three collections.—Øresund. Five collections.—Baltic Sea. Four collections.—Bornholm. Nine collections.

UNITED KINGDOM. Shetland. Mainland: Spiggie, Peerie Geo, sand covered rocks, *Irvine 12*, 16/8/1962 (D. Irvine, priv. coll.).

Notes on nomenclature. (1) Typification of *S. cirrhosa* var. *notata*. In his description C. Agardh gave as locality 'in mari Baltico'. In his herbarium six specimens are mounted on one sheet on which the name *S. cirrhosa* var. *notata* has been written in C. Agardh's hand. Of these I selected the specimen 'Agardh no. 45421, Salgö n. 84' as the lectotype, because it was the only specimen which apparently had been found growing attached on a substrate.

(2) Waern (1952, p. 96) stated that 'Gobi's (1874, p. 9) record of *S. radicans* from the Narva Bay can very well concern the real *S. radicans*' (and not *S. arctica* as is supposed by Gobi in 1878, p. 62). Gobi, however, mentioned fructification in his material in 1874, and in 1877 (p. 530) he described the racemes of unilocular zoidangia. These racemes do not occur in *S. radicans*, but are common in *S. arctica* from the Baltic. Moreover, all material from Narva in Gobi's Algae rossicae exsiccatae n. 28 and also Gobi's specimens from Narvskaya bay are *S. arctica*.

(3) Most specimens from the Baltic, found in collections as '*S. olivacea* Pringsheim *sensu* Reinke' are related to *S. arctica*. In material from the Kieler Föhrde (in HBG, KIEL, MEL, and PC) typical irregular pinnate filaments of *S. arctica* could be traced, together with

narrow filaments (20–30 μm) with some secondary transverse cell-walls. Specimens from the Strander Bucht near Kiel and from the Eckerförder Bucht (all in M) also had some typical *S. arctica*-filaments. In material from Bülk near Kiel (in M) I found only fertile narrow filaments, 20–30 μm wide and occasionally with secondary transverse cell-walls. These filaments much resemble the figures published by Lund (1950, p. 25, f. 3) as '*S. britannica*'. On the other hand some of the narrow fertile laterals of specimens from Strander Bucht also occasionally have secondary transverse walls and do not differ from the filaments of the small plants from Bülk. For that reason I suppose the small plants from Bülk are *S. arctica* too. The figure given by Reinke (1890a, fig. 1 and 1892, t. 46) as '*S. olivacea*', and copied in many handbooks, is perhaps also *S. arctica*. The suggestion made by Sauvageau (1903, p. 75 = R. 246) that this figure represents *S. racemosa* cannot be endorsed.

Notes on morphology. Reinke (1892, t. 44, f. 3–6) depicted some transverse sections of filaments of *S. arctica*. Of these, figures 4 and 5 show the periclinal type of division of secondary segments by longitudinal cell-walls as is commonly found in *S. arctica*. The figures 3 and 6, however, show the radial type of division and I have never seen this type in *S. arctica*.

In young indeterminate filaments the primary longitudinal wall in a secondary segment is often not median but periclinal (fig. 346). This wall is always perpendicular to the plane of branching in the superior secondary segments (fig. 329–331). In the inferior secondary segments the plane of the primary longitudinal cell-wall is often turned to another direction (fig. 347–349), sometimes even coinciding with the plane of branching of the filaments. The next longitudinal walls are often perpendicular to the primary wall and may be median or periclinal (fig. 346–349). Sometimes, however, these walls are parallel to the primary longitudinal wall (fig. 327; 346; 347). This is especially so in superior secondary segments from which laterals will arise in a later stage. One or both primary peripheral cells cut off by these periclinal walls may act as branch-initial.

The formation of the first longitudinal walls is succeeded by the formation of other walls, always perpendicular to one another, resulting in a 1–4-celled central medulla and many peripheral cells (fig. 327–331; 350). Transverse walls are common in the peripheral cells, but rare in the medullar cells. The pattern of branching may be quite regularly pinnate, especially in arctic specimens (see Sauvageau, 1901, f. 23A). In these cases often branching of the indeterminate laterals is in the same plane, even when the apical cell of the main erect filament dies off and the nearest distal laterals start to function as axes. In Baltic specimens, a more irregularly pinnate pattern of branching is usually found; frequently also in Arctic specimens (fig. 325). Alternate, secund, and interrupted distichous branching (fig. 324) can be found in these specimens. The laterals are often unbranched and several mm long. Growth of laterals is commonly indeterminate, but in very regularly pinnate parts the laterals sometimes become short and determinate. In some specimens branching is almost lacking (see: chapter 'Form range and cultures').

Downward growing corticating rhizoids arise at irregular intervals from peripheral cells of superior or inferior secondary segments (fig. 326). Probably every normal peripheral cell can grow into a rhizoid, but not all cells do so. In some specimens rhizoids are numerous, forming a thick layer encircling the proximal parts of the plants. In other specimens,

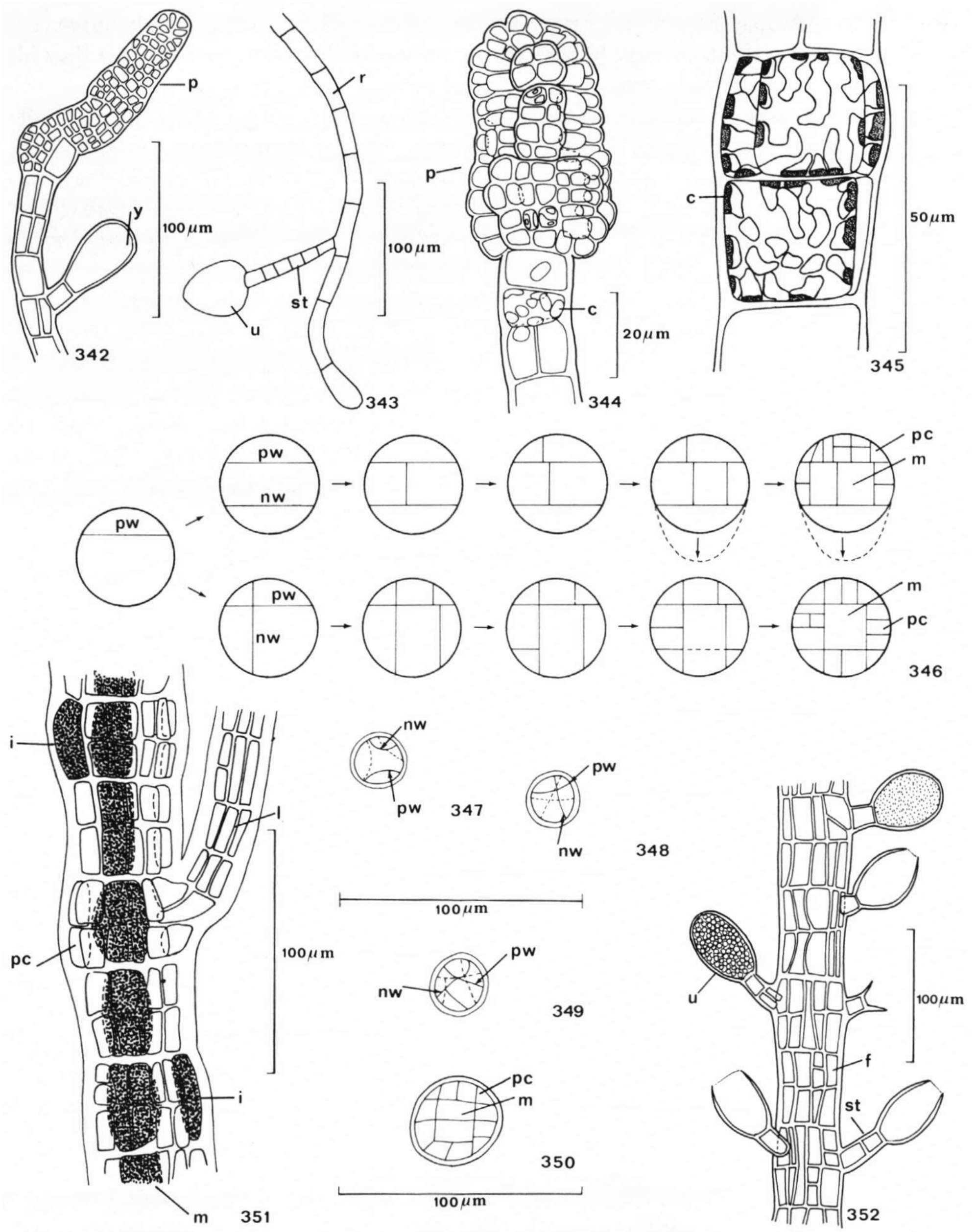


Fig. 342–352. Sphacelaria arctica. 342–344, 352. Zoidangia; 345–351. Erect filaments (347–350. Cross-sections; 346. Diagrammatic; in 347–349 the dotted lines are longitudinal walls in the superior secondary segment directly below the sectioned inferior secondary segment). c. chloroplast; i. initial; l. lateral; m. medulla; nw. new (or next) wall; p. plurilocular zoidangium; pc. peripheral cell; pw. primary wall; r. rhizoid; st. stalk; u. unilocular zoidangium; y. young. 342. Mosselbay, *Kjellman* (UPS, soaked); 343. East Greenland, *Lund 1053* (C, formalin); 344. Culture 67-82-2; 345. Culture 67-80; 347–349. Gotland, *Prud'homme van Reine 67-90* (formalin); 350, 351. Bonden, *Kylin* (LD, soaked); 352. East Greenland, *Lund 737* (C, formalin).

however, rhizoids may be rare or absent. The rhizoids are in most cases loosely appressed, but young and short rhizoids may be very closely appressed. Occasionally divaricate rhizoids occur.

Young basal discs are monostromatic (fig. 320). Further development is similar to the process described for *S. mirabilis* (p. 172 and f. 388), but the vertical cell-rows often hold few cells although branched and many-celled vertical rows also occur (fig. 322). The crusts become multi-layered when the descending rhizoids extend to the basal disc and spread over it, but also when discs or parts of discs overgrow each other (fig. 321). Discs of several specimens may together form a thick and expanded crust.

Basal discs can also originate from parts of stolons, from rhizoids in contact with a substrate or from loose fragments of erect filaments. In all these cases the cells in contact with the substrate give rise to prostrate coalescent filaments together forming a new basal disc.

In fertile specimens often narrow and slightly bent specialized laterals are formed (fig. 337–339). These laterals arise from a central cell that still maintain contact with the periphery and functions as initial. In some dried specimens these initials are as dark brown coloured as the central cell (fig. 351), but in other dried specimens they may be inconspicuous.

Notes on ecology. *Sphacelaria arctica* can be found in littoral pools, but more often it occurs in the sublittoral. In Greenland, northern Norway, and in the Öregrund Archipelago it may occur in littoral pools as well as in deep water. In other regions it usually can be found between 4 and 32 m depth. In the Baltic it sometimes can be found as deep as 40 m (Rozewie, Poland). It has been found growing on rocks, small stones, shells, wood, other algae, and sometimes unattached. These unattached specimens mostly form balls (aegagropilae) together with other members of the *Sphacelariales, viz. S. cirrosa, S. plumosa, S. plumigera* ecad *pinnata, S. radicans* ecad *libera* and *Stypocaulon scoparium* forma *scoparioides.* These aegagropilae have been found in the Kattegat, the Øresund, and the Baltic Sea.

On Arctic coasts (Greenland, Spitzbergen, northern Norway, and the Arctic coasts of the U.S.S.R.) *S. arctica* is one of the common sublittoral algae, where it is found in separate, scattered tufts. Jaasund (1965, p. 68) found *S. radicans* in northern Norway, but no *S. arctica.* It is probable that part of his material of *S. radicans* is sterile *S. arctica.* The latter species had been found on scattered localities along the coasts of western and southern Norway, often together with *S. radicans.* On a steep south-facing cliff in the Hardangerfjord near Øystese *S. arctica* formed together with *S. radicans* a broad dark-brown belt some cm below *Ascophyllum nodosum* in June 1967. In the troughs of the passing waves the upper 30 cm of this *Sphacelaria*-belt was uncovered. In this belt the gregarious *Sphacelaria* species formed an uninterrupted felty layer in which the tufts of *S. arctica* were somewhat more voluminous than those of *S. radicans. S. arctica* is often found in the sublittoral of the Danish and southwestern Swedish coasts, and it is very common in the Baltic. In the Öregrund Archipelago (Sweden) Waern (1952, p. 25) described a '*Sphacelaria arctica* belt' from the lower border of the *Fucus* belt (10–11.5 m) or the *Cladophora* belt (5–8 m), and downwards to about 22 m. In this belt *S. arctica* is often the dominating alga. Waern stated (p. 107): '*S. arctica* is the most common alga of the Öregrund Archipelago, occurring almost everywhere....'. Outside the *Sphacelaria* belt *S. arctica* has also been found in shaded habitats within the *Fucus* belt in the Öregrund Archipelago. Mathiesen (1974, p. 9) observed vigorous growth of *S. arctica* near Lågskär, Åland Archipelago, where it formed the under-vegetation at depths of 10–15 m. Many other algae, especially *S. plumigera* ecad *pinnata* and *Stypocaulon scoparium* forma *scoparioides*, may be entangled in the gregarious tufts of *S. arctica.*

Sphacelaria arctica has often been found in brackish waters. In the Bothnian Bay it has been found near Ratan and near Nykarleby, where salinity of the surface water varies between 3 and 4‰. In deeper water salinity may be some tenths of a ‰ higher. The species also occurs in brackish water with variable salinity like the inner branches of the Hardangerfjord, the landlocked bay at Hunnebunnen, and the Arctic localities, where salinity of the waters may be low due to the melting ice and snow.

Sphacelaria arctica has been found in all seasons. It is probably a perennial alga.

Form range and cultures. In *S. arctica* there is a lot of morphological variation. Waern (1945, p. 409) suggested: 'the Baltic population might possibly be considered a variety of *arctica*', but he did not return to that suggestion in his thesis (Waern, 1952).

In the Arctic population, as well as in the Baltic population, the dimensions of tufts and basal discs, the number of axes and laterals, and the diameter of these filaments show often rather large variations from one plant to another. The pattern of branching is in most cases quite regularly pinnate in Arctic specimens, and irregularly pinnate in Baltic ones. Specimens that were almost unbranched have been found in scattered localities along the middle and southern coasts of Norway, on the northern part of the Swedish west coast, and the north-eastern parts of Denmark. Many of these specimens have been identified as *S. racemosa* by Sauvageau (1903, p. 74–75 = R. 245–246), but I do not agree with him. For this reason I thoroughly studied specimens from Lyngen, Lödingen, and Røberg (Trondhjemfjord) all collected in Norway by *Foslie* and also specimens from Magerösundet (north Norway—*Kjellman*), Aalborg Bugt (Denmark—*Rosenvinge*), and Koster & Bonden (Sweden—*Kylin*). Of these, the collections from Magerösundet, Lödingen, and Koster, consisted of mixtures of *S. radicans* and small *S. arctica* plants.

On several occasions transverse sections were made to check the type of division of the filaments (periclinal in *S. racemosa* and *S. arctica*, but radial in *S. radicans*) and the number of cells in the medulla. In specimens from all localities it was possible to detect some traces of pinnate branching and/or the medulla of the main filaments contained more than one cell (fig. 350). Both characters suggest *S. arctica. S. racemosa* has not been observed by me in collections from Scandinavia.

The specimens from the Baltic identified by Reinke and Reinbold as *S. olivacea* Pringsheim, which were also regarded as *S. racemosa* by Sauvageau (1903, p. 75 = R. 246) are, according to my observations, also small plants of *S. arctica* (see Notes on nomenclature 3).

Jorde & Klavestad (1960, p. 91) observed *S. arctica* in the inner parts of the Hardangerfjord. They also described a 'large type' of *S. arctica* (p. 92 and f. 3 & 4). The specimens of this large type attained a length of 25 cm. I have not had the opportunity to study the original material, but the description and figures do not suggest *S. arctica.* The figures of the apex of a filament (f. 4b) and of the origin of laterals and rhizoids (f. 4c & d) even give the impression that they represent not a *Sphacelaria* but *Acrocytis groenlandica* Rosenvinge.

The figures given by Rosenvinge (1933, p. 9, f. 3) of his newly described species agree very well with the figures by Jorde & Klavestad. Specimens collected by me in the Oslofjord in 1967 and by *Mr. P. A. Åsen* at two localities in Vest-Agder county in 1976 are probably also *Acrocytis groenlandica.*

The pattern of branching of *S. arctica* is perhaps related to variations in salinity. It is conceivable that at low salinities with only small variations during the year, like those occurring in the Baltic, the pattern of branching becomes more irregularly pinnate. In higher salinities with more variation during the year (the Arctic) the pattern of branching might become more regularly pinnate but at high salinities and less variation branching might be almost lacking.

In culture at low salinities (6°/₀₀) in young subcultures the pattern of branching became very irregular or branching was almost lacking and the number of rhizoids and stolons increased. Sometimes thin expanded basal discs were formed, like the one figured in Reinke's descriptions of *S. olivacea.* Often the diameter of the filaments and laterals was very narrow (25–35 μm). In old cultures at these low salinities, however, typical *S. arctica* plants with irregularly pinnate branching were found. These plants were 3–3.5 years old. At higher salinities (25°/₀₀) the erect filaments of young subcultures were much better developed. The diameter of the filaments was 40–60 μm and irregularly pinnate branching occurred in all specimens. At low light intensities (88–500 Lx) sometimes parts of the filaments were quite regularly pinnate. At higher light intensities (1400–3000 Lx) the laterals, which all arose in the same plane of branching, bent into other directions. The number of rhizoids and stolons was less than in lower salinities and the basal discs, if formed, were small, thick, and polystromatic. In cultures grown at 12°C often many proliferations and short divaricate rhizoids arose, which totally changed the general appearance of the plants.

In cultures maintained in media made with natural seawater almost no branching occurred during the first months after inoculation. Large expanded thick basal crusts were formed, from which the erect filaments (diam. 30–40 μm) arose. Rarely rhizoids were formed and all specimens were sterile. In older cultures, however, irregularly pinnate plants occurred as well.

In deep water (and at low light intensities in culture) the filaments are dark brown, but in shallow water or littoral pools the plants are mostly yellowish or reddish brown or olivaceous.

Cultures have been isolated from material collected on the coasts of south Norway (Hardangerfjord-Øystese, Oslofjord-Drøbak and Tjøme) and from Baltic Sweden (Askön and Gotland). Some cultures and their subcultures have been maintained during eight years.

Sphacelaria arctica usually grew well in culture at 4°C and 12°C. There were no morphological differences in specimens growing attached or unattached in culture. In nature in the algal balls the apical parts of filaments are often broken off and in these specimens many laterals are as long as the axes. The angle of ramification is always as acute as in nature.

Hairs were rarely found in nature and culture. In one culture, growing at light intensities of 1400–2800 Lx at 4°C (short day) several solitary and geminate hemiblastic or acrohomoblastic hairs occurred.

Reproduction and life-history. Unilocular and plurilocular zoidangia are well known, but specialized propagules have never been found. Vegetative reproduction by means of detached fragments is often observed. Plurilocular zoidangia have often been observed in cultures originating from Norway (Verdens Ende and Drøbak).

These cultures were grown at 4°C, short day and low light intensities. I have never collected fertile specimens from nature, but specimens with unilocular or plurilocular zoidangia have been collected in winter and early spring at Greenland, Spitzbergen, and in the Baltic by others. Sometimes some rare zoidangia have been found in other months of the year. Unilocular and plurilocular sporangia in nature were found on separate plants, but in culture they occasionally occurred on the same plant (fig. 339).

In the Baltic zoidangia mostly occur in loose racemes which arise from all parts of the filaments and occasionally also from the rhizoids. The axis of these racemes may be short, but often this axis is relatively long (fig. 337; 338). Frequently narrow and slightly bent laterals function as the axis of a zoidangial raceme, but occasionally these laterals are not different from sterile laterals. The zoidangial stalks may be one-celled, but often these stalks are short and narrow filaments with several secondary segments. These secondary segments may have one or two longitudinal walls (fig. 338). In specimens from the Arctic the axis of the racemes is usually an ordinary lateral and the zoidangial stalks are 1–4-celled (fig. 352). Usually the zoidangial stalks arise in rows and are secund or distichous. Both unilocular and plurilocular zoidangia have been described and figured by Kjellman (1877a, p. 34 & t. 4–6) for material from the Arctic and by Reinke (1892, p. 66 & t. 45, f. 8–10) for Baltic specimens.

The unilocular zoidangia arise terminally on the zoidangial stalks (fig. 336–339; 343; 352). In Baltic specimens often lateral unilocular zoidangia arise from the same stalks and the stalk-lateral is mostly one-celled (fig. 338). A few unilocular zoidangia were found on a specimen on which many plurilocular zoidangia arose. There was no difference between the stalks of unilocular and plurilocular zoidangia on this plant, sometimes these zoidangia were found in one raceme (fig. 339).

The zoidangial stalks of the plurilocular zoidangia are rarely one-celled, more often they have 2–4 or more secondary segments (fig. 339; 340; 342; 344). From the stalks terminal and often several lateral plurilocular zoidangia arise. No zoids have been observed, but in cultures with plurilocular zoidangia germlings have been observed on several occasions. These germlings always had a small monostromatic disc and one narrow (20–30 μm) erect filament. After some time the discs became polystromatic by upward growth. Often superposed small discs were found of which the upper ones grow from and over the lower ones, forming a small crust. From these crusts at first only narrow unbranched filaments arose, but later thicker filaments were found which may show pinnate branching. No fertile plants have been grown from these germlings so far.

From the incomplete observations cited above no picture of the life-history of *S. arctica* can be obtained.

Systematic position. *Sphacelaria arctica* has been placed in the section *Racemosae* of the subgenus *Sphacelaria* together with *S. racemosa*. Reinke (1889, p. 40) suggested *S. arctica* to be a variety of *S. racemosa*. Waern (1945, p. 409 & 1952, p. 100) opposed to this view and separated *S. racemosa* and *S. arctica* again. Waern (1952, p. 103) stated that it is less difficult to distinguish *S. racemosa* from *S. arctica* than *S. racemosa* from *S. radicans*. According to Pankow (1975, p. 803) the differences between *S. arctica* and *S. racemosa* are distinct.

The main differences between *S. arctica*, *S. racemosa*, and *S. radicans* are given in table VI. The identification of presumptive *S. racemosa* plants from Scandinavia as *S. arctica* has been discussed in the above section 'Form range and cultures' of *S. arctica* (p. 157). In this section also the Baltic specimens of *S. olivacea* Pringsheim *sensu* Reinke have been discussed, as well as the 'large type' of *S. arctica* described by Jorde & Klavestad (1960, p. 92).

Pankow (1971, p. 164 and 1975, p. 803) transferred *S. plumigera* to *S. arctica*, proposing the new combination *S. arctica* forma *plumigera* for it. The main characters separating *S. plumigera* from *S. arctica* are the origin of the cortex, the pattern of branching, the formation of secondary transverse walls in the cells, and the distribution of the zoidangia. These differences are summarized in table XIII.

There is no reason to justify the combination of *S. arctica* and *S. plumigera* into one species.

Occasionally *S. arctica* forms very narrow filaments. Most specimens from the Baltic and named *S. olivacea* Pringsheim have these narrow filaments (see also Notes on nomenclature 3). For comparison of the narrow filaments of *S. arctica* and similar filaments of other *Sphacelaria* species see table X.

8. Sphacelaria racemosa Greville—Fig. 353–379

Sphacelaria racemosa Greville (1824a) t. 96 (as '*Sphacellaria*'), (1824b) 314; C. Agardh (1828) 34; Harvey (1833) 325, (1841) 39; J. Agardh (1848) 31; Kützing (1849) 466; Harvey (1851) t. 349; Johnstone & Croall (1860) 163; Holmes (1887) 80; Batters (1889) 61; Reinke (1891) 12 (*p.p.*); De Toni (1895) 505 (*p.p.*); Sauvageau (1901) 137 (= R. 99) (*p.p.*); Newton (1931) 189; Waern (1945) 410 + f. 2, (1952) 101 + f. 42; Irvine (1956) 39; Prud'homme van Reine (1974) 174; Pankow (1975) 803; Prud'homme van Reine (1978) 303.—*Sphacelaria corymbosa* Sprengel (1827) 346 (wrong citation).—Type: *Richardson s.n.* Firth of Forth, opposite Caroline Park, 4 February 1819. Growing on rocks near high water mark (BM, GL, LD).

Plants form small penicillate bushes (fig. 353) and are yellowish brown, dark brown, or olivaceous. They are solitary, gregarious or caespitose and epilithic. Sometimes they form cushion-like patches (fig. 354). Several to many sparingly branched main axes arise from one to several small basal discs (fig. 355).

In early stages the basal part is a circular basal disc with marginal growth. The young disc is monostromatic and consists of a number of radiating, branched, coalescent, creeping filaments with apical growth. In later stages the basal disc may become polystromatic by upward growth and subsequent division of the intercalary cells of the coalescent creeping filaments (fig. 357; 358). Sometimes rhizoids or creeping filaments function as stolons and form new basal discs and erect filaments (fig. 355; 356).

The erect parts of the plants are composed of several main axes and few solitary, almost unbranched, hemiblastic laterals of up to the third order. The scattered laterals are irregularly placed (never pinnate), often somewhat appressed (fig. 359; 360) and they have indeterminate growth. There is usually no difference in growth or dimensions between the axes and the laterals, but in the proximal part of the laterals the dimensions are usually

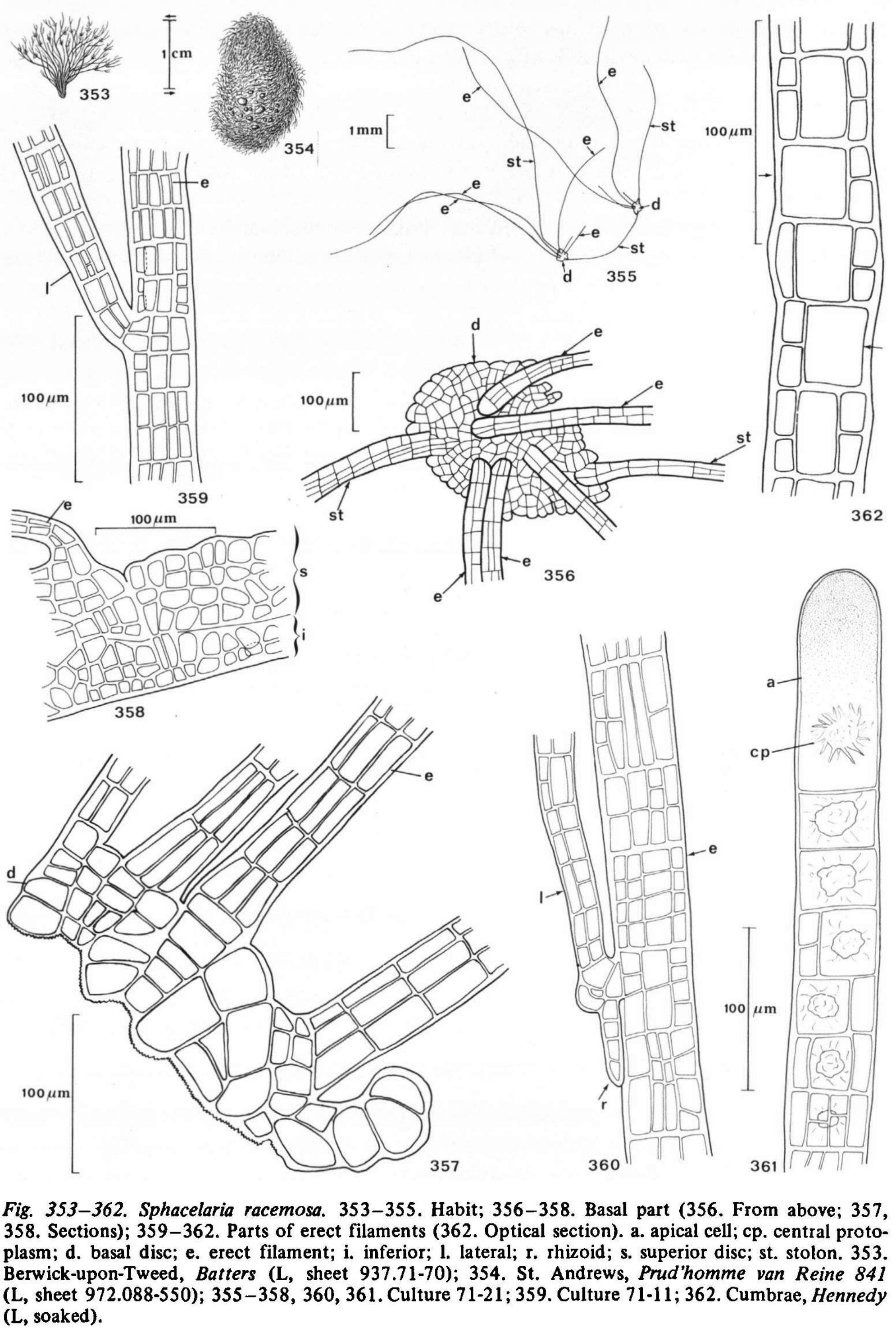


Fig. 353–362. Sphacelaria racemosa. 353–355. Habit; 356–358. Basal part (356. From above; 357, 358. Sections); 359–362. Parts of erect filaments (362. Optical section). a. apical cell; cp. central protoplasm; d. basal disc; e. erect filament; i. inferior; l. lateral; r. rhizoid; s. superior disc; st. stolon. 353. Berwick-upon-Tweed, *Batters* (L, sheet 937.71-70); 354. St. Andrews, *Prud'homme van Reine 841* (L, sheet 972.088-550); 355–358, 360, 361. Culture 71-21; 359. Culture 71-11; 362. Cumbrae, *Hennedy* (L, soaked).

smaller. Rhizoids are often lacking, but regularly a few downward growing rhizoids occur which grow from peripheral cells (fig. 360; 366; 368; 371). These divaricate or loosely appressed unbranched rhizoids never form a more or less complete cortication and they rarely reach the substrate.

The dimensions of the inferior and superior secondary segments of the erect filaments are equal to each other and they are in most cases wider than they are long (fig. 357; 359–362).

The secondary segments are subdivided by radial, periclinal, and transverse walls into a medulla and peripheral cells (fig. 363–365). In the medulla almost no transverse walls are formed (fig. 362) and in every secondary segment there is one central cell, which is quadrangular in cross-section (fig. 363). Rarely two medullar cells are formed (fig. 364). In dried material the cells of the medulla are often dark in colour. The many peripheral cells are separated by walls which are more or less radial, or anticlinal. In lateral view often 4–6 longitudinal walls can be observed in large secondary segments and the long peripheral cells are subdivided into shorter ones by 1–3 transverse walls (fig. 359; 360). Occasionally secondary longitudinal walls occur in these shorter peripheral cells (fig. 366).

Hairs are rare. They are geminate, acrohomoblastic, and short (fig. 367).

There are no propagules.

Unilocular zoidangia occur in racemes with an almost globular outline (fig. 368) which arise from all parts of the filaments. In culture solitary unilocular zoidangia with long stalks have been found (fig. 369). The racemes of plurilocular zoidangia are not globular in outline (fig. 370). From the short and narrow main filament of a raceme arise many, uniseriate, unbranched, zoidangial stalks which are unicellular or contain several cells (fig. 371; 373–375). Unilocular and plurilocular zoidangia occur presumably on separate plants. Unilocular zoidangia are ovoid or subspherical when mature (fig. 371; 372), often slightly pointed when young (fig. 373). Unizoids are pear-shaped. They have one or two brown chloroplasts and an eye-spot. Plurilocular zoidangia are elongated and cylindrical (fig. 374; 375). Plurizoids have not been observed.

Dimensions: Plants up to 2 cm high and cushion-like patches several cm in diam. Diam. basal disc 0.3–1 mm. Diam. of stolons 25–50 μm; of rhizoids 10–20 μm. Angle of ramification 0–45 (–60)°. Diam. of filaments 25–45 (–49) μm in proximal parts, (36–) 40–55 (–61) μm in distal parts. Height of secondary segments 20–65 μm. Hairs 16 μm in diam. (with sheath). Chloroplasts 2–3 X 4–5 μm in surface-view (fig. 377). Main filaments of zoidangial cluster 100–200 (–300) μm long; diam. (10–) 14–22 μm. Zoidangial stalks 10–70 X (9–) 12–19 μm. Unilocular zoidangia (48–) 54–75 (–80) X (40–) 45–70 (–75) μm. Unizoids 6.5–8 μm long. Plurilocular zoidangia 70–86 X 34–39 μm, diam. loculi 1–3.5 μm.

Distribution. Germany (Heligoland), United Kingdom.

Specimens reported from other countries are usually *S. arctica* (see p. 157).

Localities have been listed below and are given in fig. 43.

GERMANY. Heligoland. (as *S. radicans*), *Kuckuck*, 4/1/1894 (herb. Thuret in PC, mixed with *S. radicans*). W. Seite, (as *S. radicans*), *Kornmann*, microslide *193*, 25/2/1960 (HELG, mixed with *S. radicans*).

UNITED KINGDOM. Scotland. Buteshire: Cumbrae, *Hennedy* or *Arnott*, 6/5/1853 (BM, mixed with some filaments of *S. radicans*; CN, GL, PC, TCD). *Ibidem*: without collector, 2/1854 (TCD), and

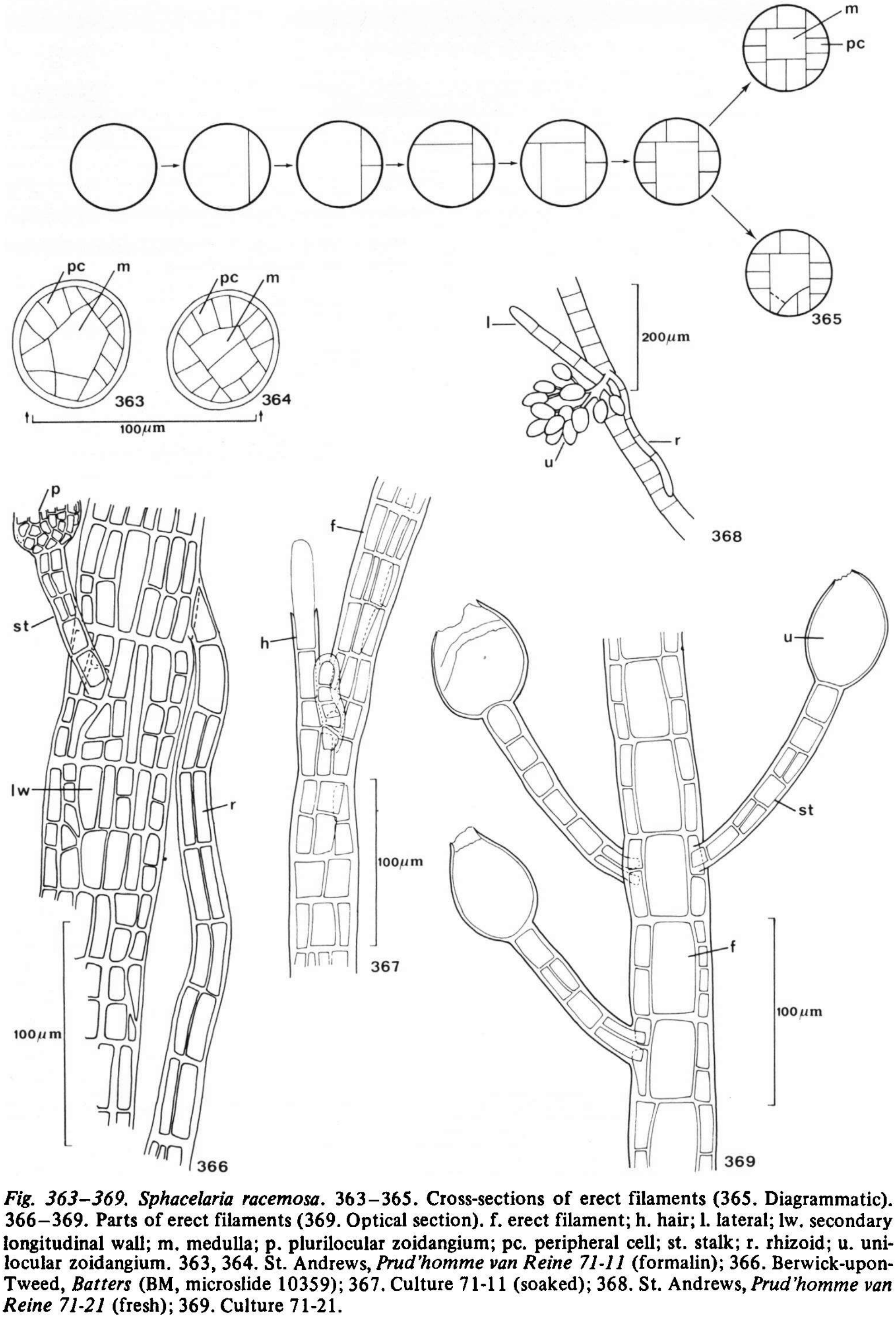


Fig. 363–369. Sphacelaria racemosa. 363–365. Cross-sections of erect filaments (365. Diagrammatic). 366–369. Parts of erect filaments (369. Optical section). f. erect filament; h. hair; l. lateral; lw. secondary longitudinal wall; m. medulla; p. plurilocular zoidangium; pc. peripheral cell; st. stalk; r. rhizoid; u. unilocular zoidangium. 363, 364. St. Andrews, *Prud'homme van Reine 71-11* (formalin); 366. Berwick-upon-Tweed, *Batters* (BM, microslide 10359); 367. Culture 71-11 (soaked); 368. St. Andrews, *Prud'homme van Reine 71-21* (fresh); 369. Culture 71-21.

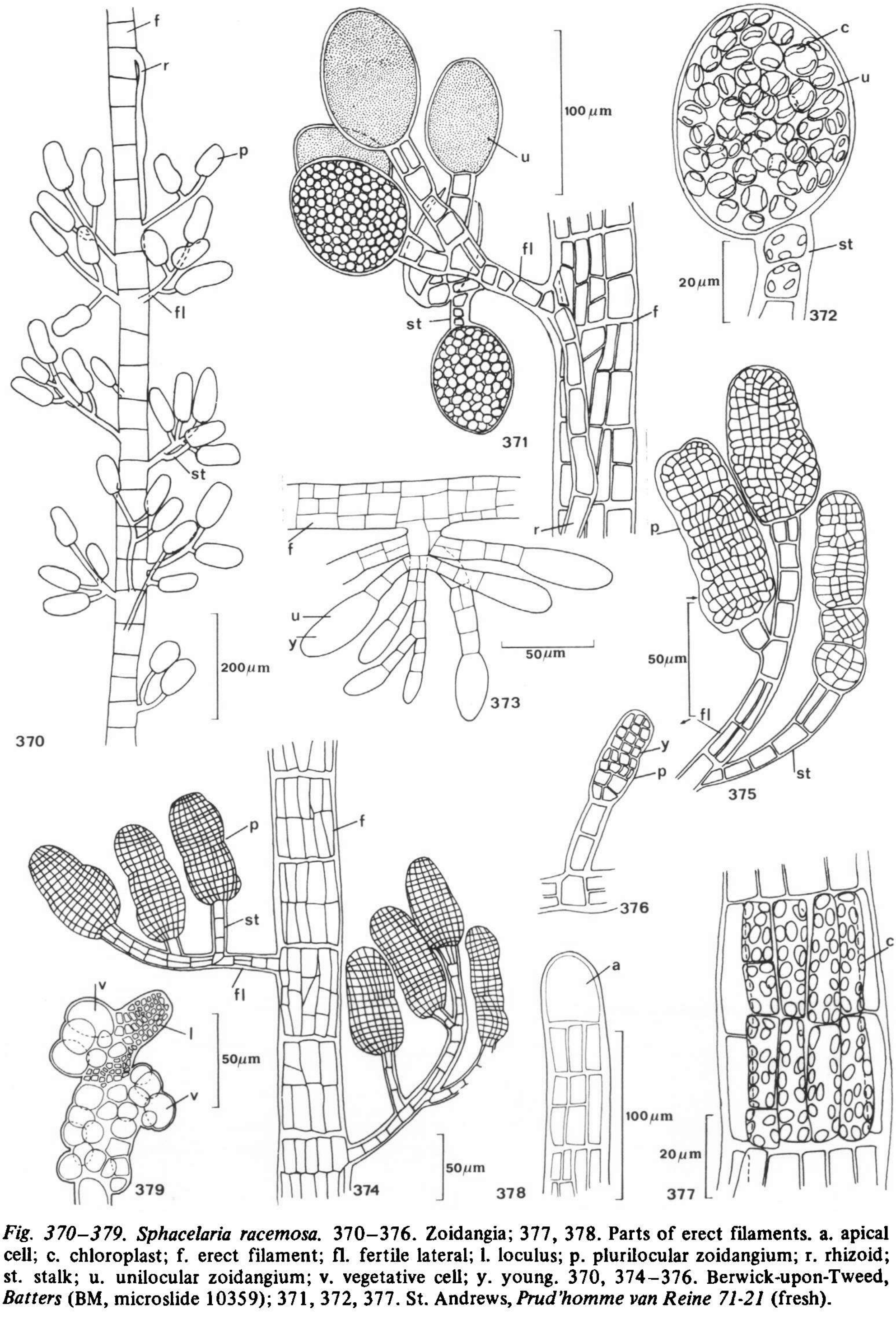


Fig. 370–379. Sphacelaria racemosa. 370–376. Zoidangia; 377, 378. Parts of erect filaments. a. apical cell; c. chloroplast; f. erect filament; fl. fertile lateral; l. loculus; p. plurilocular zoidangium; r. rhizoid; st. stalk; u. unilocular zoidangium; v. vegetative cell; y. young. 370, 374–376. Berwick-upon-Tweed, *Batters* (BM, microslide 10359); 371, 372, 377. St. Andrews, *Prud'homme van Reine 71-21* (fresh).

Batters, microslide *3360*, 1/1864 (BM). Buteshire: Arran, (Batters, 1891, p. 233). Fife: St. Andrews, Hind Rock (near the Castle), on the steep side facing to the north, *Prud'homme van Reine 841*, 10/2/1971 (L). *Ibidem*: Doo Craig (Elephant Rock), in sandy pools in *Fucus spiralis* belt, together with *S. radicans*, *Prud'homme van Reine 839*, 16/2/1971 (L, STA). Midlothian: Edinburgh, Firth of Forth opposite Caroline Park, growing on the rocks near high water mark, *Richardson*, 4/2/1819 (BM, GL, LD).—Wales. Skokholm Island (Gillham, 1954, p. 216, doubtful locality).—England. Northumberland: Berwick-upon-Tweed, *Batters*, 1/1887, in Holmes, Algae Brit. rar. exs. n. 95 (BM, BR, KIEL, LIVU, OXF, PC). *Ibidem*: *Batters*, 10/1888 (PC, probably wrong date); 1/1887 (PC, KIEL); 1/1888 (BM, L); 2/1889 (BM).

Notes on morphology. The apical cells of the filaments are often quite short (fig. 378) but in fast growing filaments the apical cells are often longer (fig. 361). In young filaments the primary longitudinal wall in a secondary segment is often not median but periclinal (fig. 365). The next longitudinal walls are often periclinal and perpendicular to the primary wall, rarely they are radial (fig. 365). Later longitudinal walls are anticlinal, and mostly perpendicular to the earlier walls. Usually the planes of the primary longitudinal walls in two succeeding secondary segments are turned into different directions.

Occasionally the medullar cell of a secondary segment is not totally surrounded by peripheral cells and is still in contact with the periphery (fig. 362, arrows; 365). These medullar cells are initials from which the scarce laterals may arise. The first longitudinal wall in a segment bearing a lateral is often perpendicular to the plane through axis and lateral, rarely parallel to that plane.

In his description of the transverse section of filaments of *S. radicans* Sauvageau (1901, p. 31 = R. 60) used a mixture of filaments of *S. radicans* and *S. racemosa*. At that moment he did not recognize the filaments of *S. racemosa* as belonging to another species. Later he (Sauvageau 1903, p. 75 = R. 246) corrected his view for a part of the material from Heligoland. All cross-sections in his figure 15 K represent *S. racemosa* and not *S. radicans*.

The scattered laterals arise in different planes and branching is never pinnate. Usually the angle of branching is quite small, but occasionally larger angles can be found (especially in cultures). In material from nature often appressed and seemingly dichotomous filaments arise, which are already mentioned in the descriptions of Greville, Harvey, etc. Waern (1952, p. 102, f. 42) also mentioned this kind of branching. These appressed dichotomous filaments arise when the apical cell of a filament is damaged and killed. From the primary segment or superior secondary segment directly below, one or more new apical cells grow into the cavity of the dead cell. The number of new apical cells depends on the degree of division of the segment below the apical part that has to be replaced. In *S. racemosa* this meristematic segment was often not yet divided (as in the filament marked xx in Waern's figure 42, giving a single new filament still bearing a collar formed by the remaining wall of the dead cell) or divided by the primary longitudinal wall only (giving two appressed and seemingly dichotomous filaments). This kind of branching can be found in many *Sphacelariales* and is not specific for *S. racemosa*. It is, however, often more conspicuous in *S. racemosa* than in other *Sphacelaria* species.

Rhizoids rarely arise spontaneously (fig. 366), but may be formed near to an injury of the filament, or near to the point where a lateral (fertile or sterile) arises (fig. 360; 368). These rhizoids are usually firmly appressed over a small distance when they are young and short (fig. 360; 368; 371). Longer and older rhizoids may be loosely appressed. Sometimes they encircle the filaments but usually they are more or less straight and grow downwards (fig. 366). These straight rhizoids (and rarely also the encircling ones) may become divaricate. Usually no rhizoids reach the substrate, but rarely a rhizoid may become a stolon. These stolons are similar to erect filaments, but usually twisted (fig. 356). New erect filaments may arise perpendicularly from these stolons. Stolons may also form new small basal discs, from which many erect filaments may arise.

Young basal discs are monostromatic. Further development is similar to the process described for *S. mirabilis* (p. 172 and fig. 388), but the upright files of cells often remain short, almost unbranched, and few-celled (fig. 357). Overgrowing of discs by other discs occurs and polystromatic crusts have been observed. These crusts are never very thick or very extensive (fig. 358).

Notes on ecology. *Sphacelaria racemosa* has always been found in sandy littoral pools. Often *S. radicans* is also growing in these pools and sometimes the plants of both species grow in mixed stands. In some cases the pools with *S. racemosa* are high in the littoral, in the *Fucus spiralis* belt.

In southwestern Scandinavia small plants of *S. arctica* have also been found in the littoral and together with *S. radicans.*

S. racemosa is probably a rare alga and in nature it is not different in habit from *S. radicans.* Sterile filaments of *S. racemosa* can only be distinguished from those of *S. radicans* by careful microscopic observations. For this reason it is possible that sterile filaments of *S. racemosa* have been reported as *S. radicans.* However, of the many herbarium specimens from many collections, all named *S. radicans*, only specimens from Cumbrae and Heligoland (fig. 373) could be identified as *S. racemosa*, and some others as *S. arctica.*

Form range and cultures. In the few specimens of *S. racemosa* that are known there is not much morphological variation. The small tufts may form cushion-like patches. According to Batters (1889, p. 61) these patches loosen into separate tufts when detached from the rock. He noted: 'So far as I have observed, the plants have not the least tendency to become bound together by the rhizoidal filaments, which, although present, are not numerous.' Batters also stated that the cushion-like patches are formed when 'many plants grow side by side and get buried in the sand which binds them together....'. The cushions I found at Hind Rock, St. Andrews in 1971 were not bound together by sand and the number of laterals, stolons, and rhizoids was enough to keep the cushions intact after being detached from the rocks. Perhaps the many other intermixed filamentous algae also helped to keep the cushions intact.

Cultures have been isolated from material collected in Scotland (St. Andrews). These cultures and their subcultures have been maintained for five or six years.

Sphacelaria racemosa usually grew well in culture at 4°C and 12°C. No cultures have been started at 20°C.

There were no morphological differences in specimens growing attached or unattached in culture. The angle of ramification was often acute as usual in nature, but laterals with a larger angle of ramification occurred also. The differences between material grown in culture-medium (Erdschreiber) made with natural seawater or with artificial seawater were conspicuous.

In the former medium the plants were dark-brown, compact, and much branched (more laterals than in nature), in the latter medium plants were light-brown, and scarcely branched. In both culture media proliferations, rhizoids, and nodules have been observed. Specimens in both culture media were fertile at the same date.

Hairs were rarely found. In one culture, grown at light intensities of 175–700 Lx at 12°C (long day) one pair of acrohomoblastic hairs was observed (fig. 367).

Reproduction and life-history. Unilocular zoidangia are well known, but plurilocular zoidangia and propagules have not been described. In a microslide (*n. 10359*) in the British Museum of Natural History, prepared by *E.A.L. Batters* and named *S. racemosa* by him, I observed many plurilocular zoidangia (fig. 370; 374; 375). The specimen had been collected at Berwick-upon-Tweed in February 1889, but Batters never published anything on it. The material was too sparse to be sure about the identity of the species (*S. arctica* or *S. racemosa*), but the locality strongly suggested *S. racemosa*. Many young (fig. 374; 375) and mature (fig. 376) plurilocular zoidangia were observed.

The loculi of the mature plurilocular zoidangia were very small (1–3.5 µm) and their arrangement was quite irregular (fig. 375). Arrangement and dimensions of loculi can be affected by shrinkage in the desiccated microslide.

In an old culture, kept at 4°C and low light intensity (88–500 Lx) after 5.5 years of culture many unilocular zoidangia were found. Usually these unilocular zoidangia occurred in globular racemes, but solitary unilocular zoidangia were also found (fig. 369). Many young plants, probably germlings from unizoids, were found on the walls of the culture-tubes. On only one of these germlings a few remnants of plurilocular zoidangia were observed. Most loculi were empty and from the remaining loculi the contents had grown into young vegetative cells (fig. 379).

Unilocular zoidangia have been observed in January, February, and May. In the racemes of plants collected in winter more zoidangia have been found than in those from Cumbrae, collected in May. I collected fertile specimens with numerous racemes of unilocular zoidangia in February, but I did not succeed in observing their unizoids. In cultures isolated from sterile filaments of these fertile specimens, I observed unilocular zoidangia after three years of culture at 88–500 Lx, 4°C and short-day conditions. Discharge of unizoids was observed at one occasion and this took place in the same way as described for *S. radicans* (p. 78). The zoids moved quite quickly and no sign of clumping or copulation was observed. I did not succeed in growing germlings from these unizoids.

The main axes of the racemes of zoidangia and the stalks of solitary zoidangia (fertile laterals) arise form the peripheral cells of the filaments (fig. 369; 371; 373; 374). Sauvageau (1901, p. 139 = R. 101) also mentioned fertile laterals arising from divaricate rhizoids, but I have not seen this. The racemes are usually located in the distal part of the filaments and may be very numerous. Sometimes several racemes arise from one secondary segment (fig. 370).

The fertile laterals are usually short and narrow. In their secondary segment 0–2 longitudinal cell-walls can be observed. Some of these determinate fertile laterals may become indeterminate laterals at a later stage of growth. Usually the narrow attachment of these new indeterminate laterals can easily be observed (Waern, 1945, f. 1).

Systematic position. The main differences between *S. racemosa*, *S. arctica*, and *S. radicans* are given in table VI. In sterile living filaments the conspicuous sun-like central protoplasm (probably including the nucleus) is present in the apical cell of all three species. In *S. racemosa* this central protoplasm is also quite conspicuous in the medullar cells of secondary segments and can easily be observed inside the filaments though covered by the peripheral cells (fig. 361). In *S. arctica* the central protoplasm of the medullar cells of secondary segments is not so conspicuous. The medullar cells of *S. arctica* are divided by longitudinal walls and after each division the central protoplasm becomes smaller. In *S. radicans* the central protoplasm disappears after the subdivision of the secondary segments by longitudinal walls and thus the filaments of this species can be easily distinguished from the filaments of the species of the section *Racemosae.*

In *S. plumigera*, *S. plumosa*, and *Cladostephus spongiosus* the central protoplasm of the medullar cells can often be observed in many secondary segments of the filaments. The thick basal holdfasts and characteristic branched filaments of these species exclude confusion with *S. racemosa.* The identity of presumptive *S. racemosa*-plants from Scandinavia is discussed in the chapter 'form range and cultures' of *S. arctica* (p. 157). Pankow (1975, p. 803) discussed the relations between *S. arctica, S. racemosa,* and *S. plumigera.* For this discussion see also the section 'Systematic position' of *S. arctica* (p. 159).

The racemes of zoidangia and the occasional rhizoids arising without order are the characters used to place *S. racemosa* and *S. arctica* in the section *Racemosae.*

III. Subgenus Battersia (Reinke *ex* Batters) Prud'homme van Reine, *nov. subgenus*

Battersia Reinke *ex* Batters (1889) 59; Reinke (1890a) 205, (1891), 4; De Toni (1895) 499; Sauvageau (1900) 224 (= R. 12), (1903) 79 (= R. 249); Newton (1931) 191 (all as genus).—Type species: *Battersia mirabilis* Reinke *ex* Batters.

The encrusting thallus is very similar in habit to *Ralfsia.* The structure of the polystromatic crusts much resembles the basal parts of many *Sphacelariaceae.* Zoidangia occur in sori and are borne at the apices of simple or branched erect filaments arising from the upper cell-layers of the crusts. Hairs and propagules are absent.

9. Sphacelaria mirabilis (Reinke *ex* Batters) Prud'homme van Reine *nov. comb.*—Fig. 380–421, plate 2a–c

Battersia mirabilis Reinke *ex* Batters (1889) 59, t. 9, f. 1–4; Reinke (1890a) 205, f. 2, (1891) 4, t. 1, f. 1–6; De Toni (1895) 499; Sauvageau (1900) 224, f. 1 & 2 (= R. 12), (1903) 79 (= R. 249); Printz (1926) 163; Newton (1931) 191, f. 119; Prud'homme van Reine (1974) 170; Russell & Fletcher (1975) 766; Wilce & Grocki (1977) 292; Prud'homme van Reine (1978) 302.—*Sphacelaria mirabilis* (*nom. inval.*) Sauvageau (1903) 80 (= R. 251).—Type: *Batters s.n.*, Berwick-on-Tweed, Northumberland, 1/1888, as '*Sphacelaria*' ? on *Ralfsia* (KIEL).—See notes on nomenclature 1 & 2.

Plants form hard, flat, thick, dark brown or black, polystromatic epilithic crusts, often growing over each other (fig. 380–383). In early stages the circular basal disc with marginal growth is monostromatic and consists of a number of radiating, branched, coalescent, creeping filaments with apical growth (fig. 384–386). Upward growth of the intercalary cells of the coalescent creeping filaments results in the formation of a polystromatic disc. The cells of the upper layers of the polystromatic disc are much smaller than the cells of the lower layers (fig. 381; 382; 387; 388) and they are very dark in colour. Several of these polystromatic

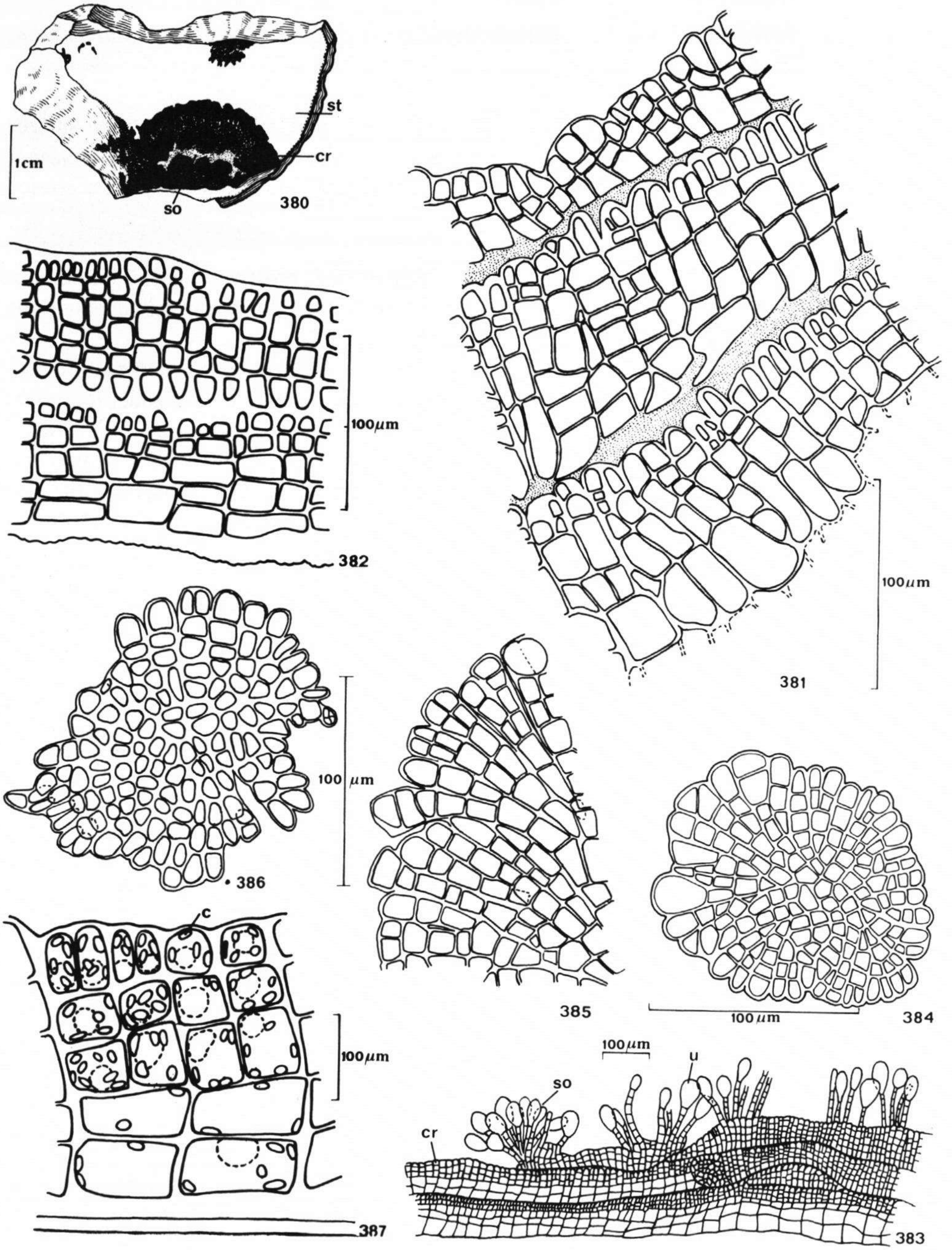


Fig. 380–387. Sphacelaria mirabilis. 380. Habit; 381–387. Basal parts (381–383, 387. Sections; 384. Monostromatic disc; 385, 386. Polystromatic discs; 385. From below; 386. From above). c. chloroplast; cr. basal crust; so. sorus; st. stone; u. unilocular zoidangium. 380. St. Andrews, *Prud'homme van Reine 664* (L, dried); 381, 383. Berwick-upon-Tweed, *Batters* (BM, microslide 7190); 382, 387. St. Andrews, *Prud'homme van Reine 71-17* (fresh); 384. Culture 71-17-3A; 385, 386. Spittal, *Batters* (BM, microslide 7187).

discs are superposed to form a thick polystromatic crust (fig. 381–383). In culture stolons are often formed (fig. 389).

There are no erect axes.

All cells of the crust contain many disc-like and mostly parietal chloroplasts. In surface view they are rounded, oval, or more or less irregular in shape. In the apical and adjacent cells the many chloroplasts are crowded together, in the large lower cells they are scattered (fig. 387).

There are no propagules.

Zoidangia are formed on small, branched or unbranched, mostly monosiphonous, but sometimes polysiphonous, erect stalks. These stalks arise from the upper cell-layers of the crusts and form yellowish-brown sori (fig. 383; 390).

Unilocular zoidangia are spherical or somewhat ellipsoid or obovoid when mature (fig. 383; 390; 391); more or less clavate when young. After discharge of the zoids the upper stalk-cell may form a new zoidangium inside the empty zoidangium-wall, and with or without a few-celled stalk. The wall of the old zoidangium remains as a small collar around the new zoidangium. Sometimes several of these collars are formed, which may envelop the new zoidangia (fig. 390; 392). Zoids of the unilocular zoidangium are of the normal phaeophycean type; they are pear-shaped, with one parietal chloroplast which is often curved (fig. 393). The red eye-spot is located on the chloroplast adjacent to the point of attachment of the flagella.

Plurilocular zoidangia are long-cylindrical or conical (fig. 389; 394). Loculi are not very regularly arranged (fig. 394). Zoids of the plurilocular zoidangia have not been seen. Each loculus contains one parietal and curved chloroplast with an eye-spot.

Dimensions: Crusts 2–4 mm thick, up to 40 mm in diam. Marginal apical cells, length × width × height = 10–30 × 7–30 × 10–25 µm. Apical cells in the upper layers, length × width × height = 2–15 × 2–15 × 5–17 µm. Large cells of the lower layers, length × width × height = 30–60 × 20–40 × 5–40 µm. Diam. of stolons 13–22 µm. Chloroplasts 2–3 × 3–4 (–5) µm in surface-view. Sporangial stalks 15–25 µm diam., till 325 µm long. Unilocular zoidangia 44–60 × 40–52 µm; zoids 6–9.5 × 3.5–6.5 µm. Plurilocular zoidangia 40–65 × 20–30 µm; diam. of loculi 6–7 µm.

Distribution. Norway, southwest Sweden (doubtful), and the northern part of the United Kingdom. The species has also been found in the Gulf of Maine, U.S.A. European localities have been listed below and are given in fig. 43.

NORWAY. Tröndelag. Ladehammaren: Trondhjemsfjord (Printz, 1926, p. 163).

SWEDEN. Bohuslän. Gåsö: on shell bottoms (?, Waern, 1958, p. 333).

UNITED KINGDOM. Shetland. Dales Voe: 2–3 m deep, *Fletcher*, 8-1973 (pers. comm. Dr. R. L. Fletcher).—Scotland. Fife: St. Andrews, Witch lake, shallow shaded pools in the lower littoral, *Prud'homme van Reine 664*, 11/2/1971 (L, STA).—England. Northumberland: Berwick-upon-Tweed, *Batters*, 1/1888 (KIEL, lectotype). *Ibidem: Batters*, div. data (BM, HBG, KIEL). *Ibidem*: in Holmes, Algae Brit. rar. exs. n. 105 (BM and several other herbaria). *Ibidem*: *Fletcher*, 1971 (pers. comm.). *Ibidem*: Spittal, *Batters*, 2/1888 (BM).

Notes on nomenclature. (1) Batters sent his material for identification to Reinke. Reinke described it as the sole species in a new genus. He sent his description to Batters who

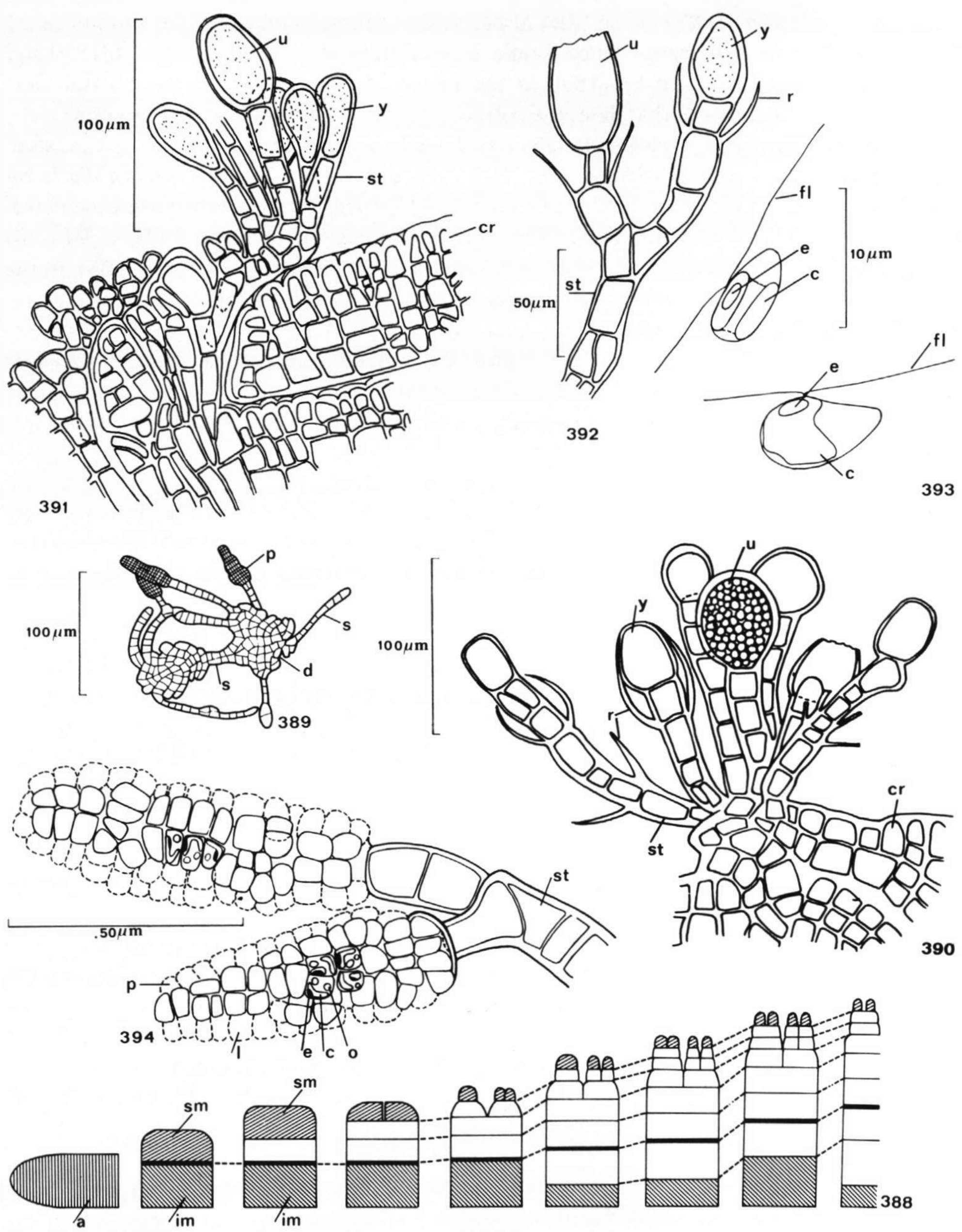


Fig. 388–394. Sphacelaria mirabilis. 388–391. Basal parts (388. Sections, diagrammatic); 389–392, 394. Zoidangia; 393. Unizoids. a. apical cell = marginal meristem; c. chloroplast; d. basal disc; e. eye-spot; fl. flagellum; im. inferior meristematic cell; l. loculus; o. oil-like drop; p. plurilocular zoidangium; r. remnants of wall of zoidangium; s. stolon; sm. superior meristematic cell; u. unilocular zoidangium; y. young. 389, 393, 394. Culture 71-17-3A; 390. St. Andrews, *Prud'homme van Reine 71-17* (fresh); 391. Berwick-upon-Tweed, *Batters* (BM, microslide 7190); 392. Berwick-upon-Tweed, *Batters* (BM, microslide 7192).

published it (Batters, 1889) giving 'Rke Mscr.' as the author. Reinke (1890a) also published a description of his new genus. Since Reinke's description was published on 22/8/1890 and Batters' list was received on 5/3/1890 in the British Museum (Natural History) and must have been published before that date, the correct citation of authors has to be as given.

(2) Sauvageau (1903, p. 80 = R. 251) suggested to consider *B. mirabilis* as the basal, creeping part of a species of *Sphacelaria.* He proposed, however, to use the name '*Battersia mirabilis*' as long as the erect part of the hypothetic *Sphacelaria* species had not been detected. The author used the notations: '*Sphacelaria mirabilis?*' (Sauvageau 1903, p. 94 = R. 264), '*Sphacelaria ? mirabilis*' (1904, p. 385), and '*Battersia mirabilis*' (1914, p. 506). In the index of Sauvageau's collected papers on *Sphacelariales* '*Battersia mirabilis*' is printed on p. 613 in heavy type and '*Sphacelaria ? mirabilis*' on p. 623 in normal type. All this information together demonstrates that Sauvageau did not fully accept the name *Sphacelaria mirabilis* and, according to article 34.1 of the International Code of Botanical Nomenclature (Stafleu *et al.* 1978) this name is not validly published. Article 34.2 is irrelevant to the case under consideration.

Notes on morphology. Soon after the germination of the spores monostromatic discs are formed, consisting of a layer of radially arranged, creeping, coalescent filaments (fig. 384). All these filaments grow apically, and this results in marginal growth of the disc.

The prostrate filaments show pseudodichotomous branching, and sometimes in the cells longitudinal walls occur perpendicular to the substrate. Starting in the centre of the young disc, and proceeding towards the periphery, all cells formed by the original apical cells of the creeping filaments are cut into an inferior and a superior one by a median wall in a plane parallel to the substrate. The superior cells become apical cells of vertical files that form the polystromatic disc. Branching of these vertical cell-rows is dichotomous or pseudodichotomous and the cells above the point of branching have to be narrower by lack of space (fig. 381; 382; 388). These narrow apical cells terminate the vertical files which are laterals of determinate growth. Owing to crowding of the small apical cells of the vertical files, the structure of the disc when seen from above is much less regular than when seen from below (fig. 385; 386).

The inferior cells formed by horizontal division of the cells of the originally monostromatic disc also contribute to the vertical growth. These cells elongate vertically and cut off cells by horizontal cross-walls. After each division the inferior cell elongates again and repeats its meristematic activity. Thus these inferior cells function in a similar way as the upper apical cells, but in opposite direction (fig. 388, see also Sauvageau, 1901, f. 1 & 2).

All cells that are cut off by one of the meristematic cells in the discs are homologous to primary segments, but most of them never divide into secondary segments. In the polystromatic discs the marginal cells remain meristematic (fig. 395).

Sphacelaria mirabilis crusts are in most cases composed of several superposed polystromatic discs (fig. 381–383). Mostly an upper disc starts its growth from a lower one when an arc of superficial cells of the lower disc resumes growth and develops a new marginal meristem (fig. 396; 397). More rarely neighbouring discs overlap each other, or young germlings attach to older ones. Stiff mucilaginous layers of varying thickness are generally interposed between the polystromatic discs forming the crust. Quite often also specimens of other algae can be found between the superposed discs.

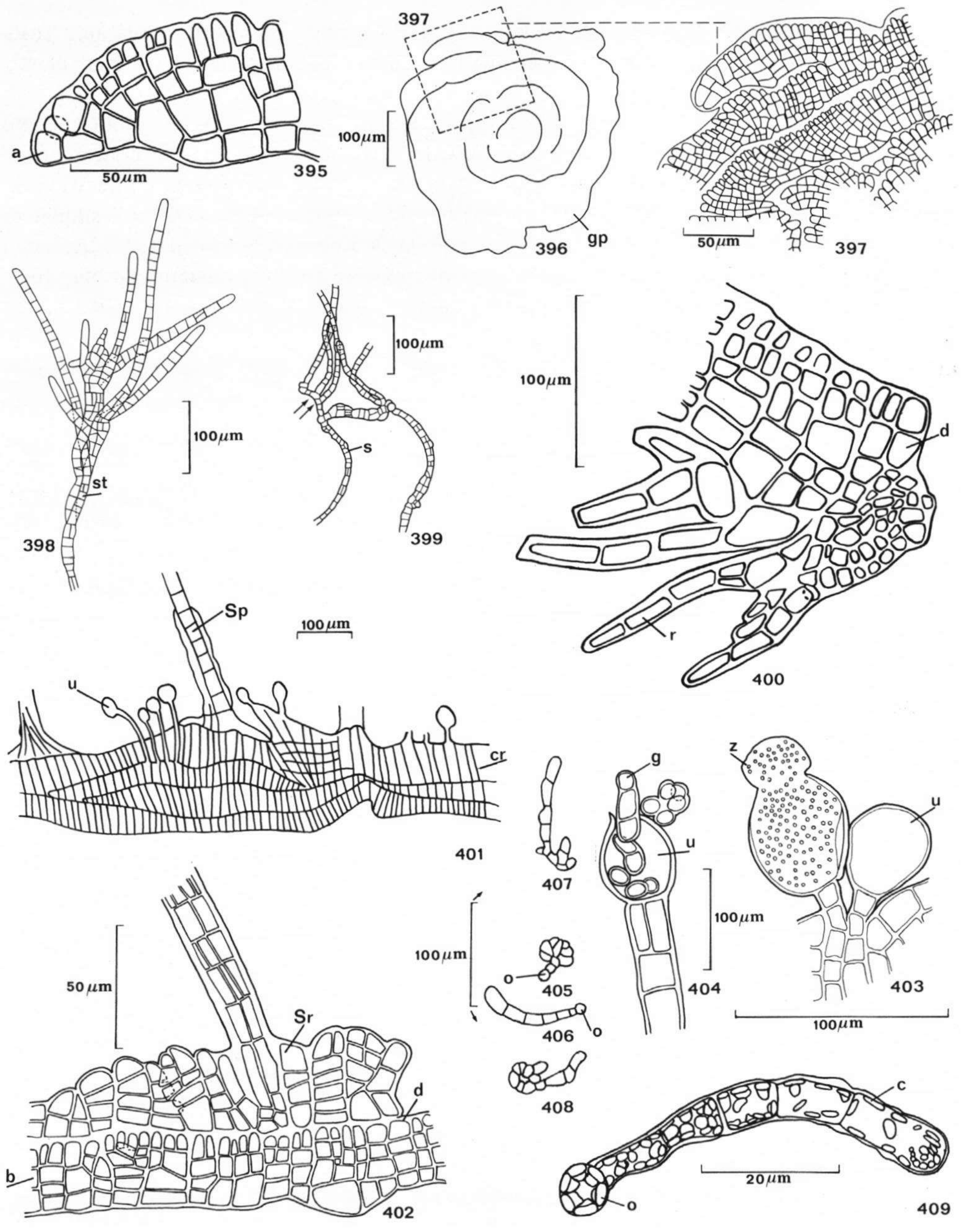


Fig. 395–409. Sphacelaria mirabilis. 395–402. Basal parts (395–397; 400–402. Sections); 403, 404. Unilocular zoidangia; 405–409. Germlings from unizoids. a. apical cell = marginal meristem; cr. basal crust; d. basal disc; g. germling; gp. globular plant; o. original spore; r. rhizoid; s. stolon; Sp. *Sphacelaria plumigera*; Sr. *Sphacelaria radicans*; u. unilocular zoidangium; z. zoids in a common mucilage-envelope. 395. Berwick-upon-Tweed, *Batters* (BM, microslide 7192); 396, 397, 404. Culture 71-17-3A; 398. Culture 71-17-5; 399. Culture 71-17-3H-2A; 400–403. St. Andrews, *Prud'homme van Reine 71-17* (fresh; 403. Microslide coloured with acetocarmine); 405–409. Culture 71-17-3.

In cultures stolons have often been observed (fig. 389; 398). These stolons originate from marginal cells. The stolons are narrow creeping filaments (13–22 μm diam.) which are mostly monosiphonous. In some portions of the stolons segments may be divided into at most two cells by one longitudinal wall (fig. 389; 398). Branching of the stolons is hemiblastic and often difficult to observe (fig. 399, arrow). New discs can be formed by proliferation of the stolons (fig. 389). Several successive secondary segments form two prostrate laterals each, which coalesce into a monostromatic disc. Further development of these discs is similar to the growth of discs as described above. In some cases stolons start as more or less erect filaments, but after a while these filaments bend backward to the substrate and may form new discs. The only genuine erect filaments are the sporangial stalks as described in the section on reproduction and life-history.

Specimens from St. Andrews bore rhizoid-like structures (fig. 400). These monosiphonous filaments may have the function of fastening the crusts to an irregular substrate. Rhizoids have not been observed in cultures.

Notes on ecology. *Sphacelaria mirabilis* has been found in very few localities. In St. Andrews I found the species growing in large quantities in small shallow pools (10–25 cm deep) situated at the foot of high, steep, north facing cliffs. Because of these cliffs no direct sunlight reached the plants. In February very few other species of algae grew in these pools, but in most cases many specimens of each species could be found. *Sphacelaria plumigera* and *S. radicans* especially were frequent in the pools and they grew often on the crusts of *S. mirabilis* (fig. 401; 402). According to Dr. R. L. Fletcher (pers. comm.) in Berwick-upon-Tweed *S. mirabilis* grew in a similar habitat. Printz (1926) did not give much information about the locality where he found this alga in Norway, but he mentioned a north facing coast (p. 36). Dr. Fletcher (pers. comm.) recently collected the species at a depth of 2–3 m in the Shetland Archipelago. In the U.S.A. it has also been found in the sublittoral.

The crusts of *S. mirabilis* are probably perennial and they seem to grow very slowly. Sometimes other algae may be found between the superposed discs. *Sphacelaria mirabilis* is supposed to be a sublittoral species capable of surviving in lower littoral pools where no direct sunlight penetrates. It looks very much like *Ralfsia*, so it may quite often have been overlooked when sterile.

Form range and cultures; reproduction and life-history. Morphological variation in *S. mirabilis* is not very striking. The dimensions of the crusts, the branching of the fertile erect filaments and the occurrence of stolons are the most variable features.

The unilocular zoidangia, arising from branched or unbranched stalks, have been figured by Batters (1889, Pl. IX, fig. 2–4), Kuckuck (in Reinke, 1891, Taf. I, fig. 5 & 6), and Newton (1931, p. 191). The fertile filaments are mostly extensions of the vertical files of cells of young discs, more rarely of the horizontal filaments forming the basal layer of a disc (Sauvageau, 1901, fig. 2H). Often the fertile discs sprout from discs deeper in the polystromatic crust (fig. 391). The branching of the sporangial stalks seems to be hemiblastic (fig. 392). At maturity the contents of the unilocular zoidangia escape through an apical aperture (fig. 403). The zoids are enclosed in a common mucilage-envelope; their release through the apical aperture takes less than one minute at 12°C and within 10–40 seconds the zoids separate from one another. The zoids move quite slowly and no sign of clumping or copulation has been observed. Sometimes the zoids germinate inside the zoidangium (fig. 404).

Cultures have been started from unizoids and from fragments of material collected in St. Andrews. These cultures have been maintained for more than three years.

Hanging drops of Erdschreiber-medium, containing fragments of fertile specimens with unilocular zoidangia were kept at 4°C (short day) and 12°C (long day). Some time after discharge of the zoids small germlings could be observed in culture (fig. 405–408). Germination at 12°C was much more abundant than at 4°C. At both temperatures two types of germlings could be observed (fig. 405–408). The majority of the germlings formed small monostromatic discs, in which the original spore was often found as a marginal cell. These discoid germlings grew out radially and became polystromatic as described in the section 'Notes on morphology' (fig. 381–386; 388). Several other spores (sometimes up to 50% of the total number) gave rise to creeping filaments (fig. 409). In later stages these filaments formed many coalescent laterals which together formed a new disc.

The primary stages of the filamentous type, and even more so the young discoid germlings, may contain very small cells which are often less than 5 μm in diameter. These dimensions are extremely small for vegetative cells in the *Sphacelariales.*

When young germlings were placed in separate culture-dishes and grown under identical conditions, after some months no differences could be observed between plants originating from the two types of germlings. When many germlings together were cultured for several months in a culture-tube, differences between young plants occurred and three types of plants could be distinguished (fig. 399; 410–413).

In the lower parts of the culture-tube discoid plants often appeared (fig. 413). These polystromatic discs were in most cases well attached to the wall of the culture-tube.

Another type of young plant, viz. small, irregular, hard, balls were particularly found on parts of the wall of the culture-tube where during some time the boundary between culture-fluid and the air had been located (fig. 413).

In the third type the plants were composed of branched, creeping, filaments, growing in the direction of the lower parts of the culture-tube. This direction probably resulted from negative phototropism (fig. 399; 413). Intermediate stages between the three types of young plants were often found (fig. 399; 410–412). Discoid plants detached from the substrate never became attached again, but formed irregular, hard globules.

After one year in culture most plants (no matter if they started as discs, filaments, or globules) had grown into these black, irregular, hard globules. After sectioning these globular plants appeared to consist of many superposed discs (fig. 396; 397). Growth of the globules is very slow. Maximum growth occurred at 4°C at light intensities of 1400–2800 Lx resulting in an approximate average growth of less than 100 μm per month.

In culture zoidangia were formed on the polystromatic globules but rarely on filaments or discs. Detached discs transformed into globules often became fertile after a few weeks (fig. 414; 415). Unilocular zoidangia were formed at 4°C, low light intensities and short-day conditions. These unilocular zoidangia were observed 16 months after germination of the unizoids of material from St. Andrews (fig. 416). Later, at the higher light intensities of 1400–2800 Lx, 4°C, and short-day conditions, unilocular zoidangia were also formed.

Plurilocular zoidangia only appear at low light intensities at 4°C in my cultures. At first these plurilocular zoidangia were only found on small germlings grown from unizoids (fig.

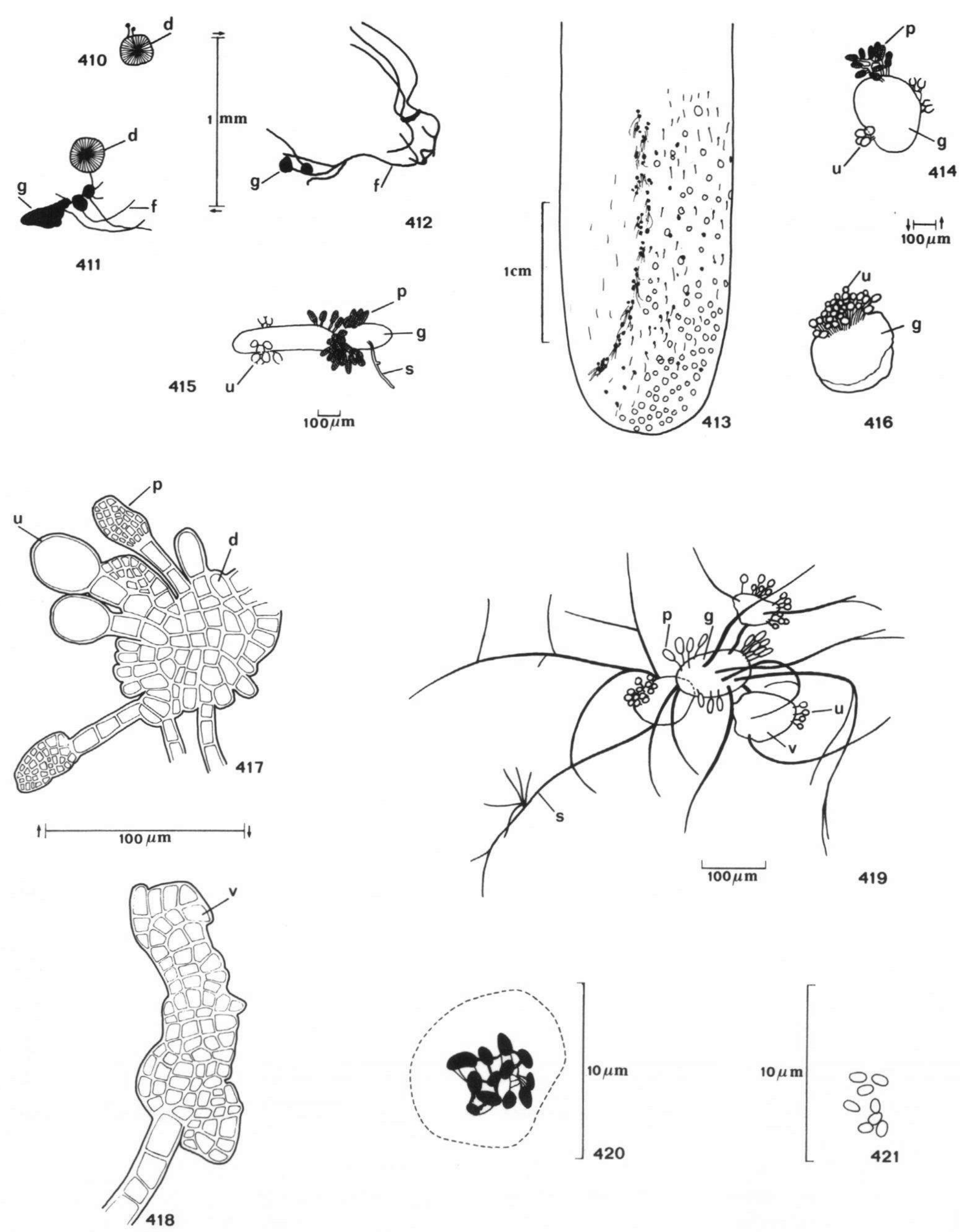


Fig. 410–421. Sphacelaria mirabilis. 410–417, 419. Germlings (413 in culture-tube); 418. Plurilocular zoidangium grown into vegetative cells; 420, 421. Chromosome figures (420. In initial of a unilocular zoidangium—diakinesis?; 421. In unilocular zoidangium—mitosis-metaphase or early anaphase). d. disc or discoid germling; f. filamentous germling; g. globular germling or plant; p. plurilocular zoidangium; s. stolon; u. unilocular zoidangium; v. vegetative tissue originating from plurilocular zoidangium. 410–413. Culture 71-17-3H-2A; 414, 415. Culture 71-17-3H-2B; 416, 418. Culture 71-17-3A; 417. Culture 71-17-3E; 419. Culture 71-17-3H; 420, 421. St. Andrews, *Prud'homme van Reine 71-17* (microslides, coloured with acetocarmine).

389). These plurilocular zoidangia were formed on small discoid plants (diameter of plants less than 500 μm) which often had many branched or unbranched stolons resulting in the development of very complex systems of small, branched, irregular, fertile crusts at 4°C and low light intensities (fig. 389, 394). In most cases the stalks of the plurilocular zoidangia were uniseriate (diam. 15–18 μm, consisting of 3–5 cells). Occasionally the stalks were much longer and even branched (fig. 394). The stalks arose in most cases from the discoid parts of the plants, but sometimes also from the stolons.

Later plurilocular zoidangia appeared also on small, irregular globules; occasionally even on those globules on which unilocular zoidangia also occurred. In these cases the small sori of unilocular or plurilocular zoidangia grew side by side (fig. 414; 415; 417).

No discharge of the zoids of the plurilocular zoidangia has been observed but occasionally germlings occurred in the culture-dishes. Often the cells of the plurilocular zoidangia grew directly into vegetative tissue (fig. 418). Sometimes new plurilocular zoidangia developed from these newly formed vegetative parts of the thallus, but more often unilocular zoidangia arose from these transformed plurilocs (fig. 419).

In unilocular zoidangia the chromosomes could be observed by using an acetocarmine technique. In a very young unilocular zoidangium a division figure was observed that could be interpreted as diakinesis (fig. 420; plate 2b). The chromosomes were counted in metaphases and early anaphases in polar view, giving a count of 8 chromosomes (fig. 421; plate 2a). In maturing unilocular zoidangia all nuclei were in simultaneous mitotic division (plate 2c).

The available data do not permit any conclusion with regard to the life-history model which could possibly be applied to *S. mirabilis.*

Systematic position. Batters discovered fertile specimens of *S. mirabilis* in Berwick-upon-Tweed. He supposed that the unilocular zoidangia together with the erect filaments bearing them were parts of a minute alga parasitizing the crusts of a *Ralfsia* species (Batters, 1889, p. 59). Reinke, however, described the material as a new species in the new genus *Battersia*, which he correctly described as a crust-forming brown alga with sori of unilocular zoidangia on the upper surface of the crusts (Reinke, 1890a, p. 205).

Reinke placed '*Battersia*' in the *Sphacelariaceae s.l.* (in a special group, the *Sphacelariaceae crustaceae*) mainly on the basis of the blackening of the cell walls when treated with bleaching liquid. The structure of the basal disc and sporangial stalks, the apical growth of these stalks, and the number of small discoid chloroplasts per cell are in agreement with his ideas. The structure of the basal disc and the supposed hemiblastic branching of the sporangial stalks of '*Battersia*' are very similar to these structures in some species of *Sphacelaria*. For these reasons, in modern taxonomy '*Battersia*' is placed in the *Sphacelariaceae s.s.*

Sauvageau, who discovered that *Sphaceloderma helgolandica* (another crust-forming member of the *Sphacelariaceae*) is the basal part of a *Sphacelaria* species, doubted the validity of *Battersia* as a genus.

At St. Andrews *S. mirabilis* is often found together with *S. plumigera* and *S. radicans.* These two species often grow over the crusts of *S. mirabilis*, and sometimes it is almost impossible to separate the basal parts of these specimens from the crusts (fig. 401; 402). Since unilocular zoidangia of *S. plumigera* (fig. 304; 305) are quite similar in structure to these of *S. mirabilis*, some relationship between the two species seemed obvious. However, detailed study of the basal parts of *S. plumigera* from Vlissingen (The Netherlands), and culture studies, showed many differences between the two species. Especially the morphology of the germlings and the structure of the basal parts is quite different (table VII).

In earlier stages of this study I assumed *S. mirabilis* had to be united with *S. caespitula*. The latter species often develops a large and complex basal part (fig. 120). Detailed studies of living material in St. Andrews, however, invalidated this suggestion. Both the structure of the basal part and the form and arrangement of the unilocular zoidangia are quite different (table VII).

In cultures of *S. mirabilis* erect filaments, apart from the sporangial stalks and initial parts of some stolons, have never been observed. For that reason I prefer to consider *Battersia* as a separate subgenus in the genus *Sphacelaria*. The subgenus *Battersia* seems to be quite closely related to the species of *Sphacelaria* subgenus *Pseudochaetopteris*. The *Sphacelaria* crusts with racemes of plurilocular zoidangia mentioned by Waern (1958, p. 333) may be very closely related to *S. mirabilis*, if not the same species.

IV. Subgenus Propagulifera Prud'homme van Reine *nov. subgenus*

Sphacelaria subgenus *Propagulifera* Prud'homme van Reine (1978) 309, 310 & 312 (*nom. inval.*).— Type species: *S. cirrosa* (Roth) C. A. Agardh.

Thalli parvi (breviores quam 2 cm) vel modice grandes (ad 4 cm alti) disco basali unistratoso vel pluristratoso vel filamentis repentibus brevibus praediti. Filamenta lateralia hemiblastica determinata vel indeterminata, pauca vel multa a filamentis erectis emersa. Interdum parietes transversales et longitudinales paucae vel plures figuram radialem formantes in segmentis secundariis filamentorum principalium. Pili saepe presentes, semper solitarii. Propagula plerumque praesentia.

Plants are small (less than 2 cm high) or of moderate size (up to 4 cm high), attached by a monostromatic or polystromatic basal disc or by short creeping filaments. A varying number of determinate or indeterminate hemiblastic laterals arise from the erect filaments. The secondary segments of the main filaments contain only occasional transverse walls and a varying number of longitudinal walls, which arise in a radial pattern. Hairs are often present and always solitary. Propagules are usually present.

IVa. Section Tribuloides Prud'homme van Reine *nov. sect.*

Sphacelaria groupe *tribuloides* Sauvageau (1901) 233 (= R. 123). *Sphacelaria* sect. *Tribuloides* Prud'homme van Reine (1978) 312 (*nom. inval.*).—Type species: *S. tribuloides* Meneghini.

Sauvageau (*l.c.*) described this group extensively, but he did not include *S. plumula*. Later (1903, p. 72–73 = R. 243–244) he discussed the relationship between *S. plumula* and the '*tribuloides*-groupe', but without reaching a final conclusion.

Filamenta lateralia indeterminata, filamentis principalibus similia, irregulariter spiraliter disposita, vel determinata, distincte diversa a filamentis principalibus, regulariter pinnatim disposita. Propagula tribuliformia, pilis nullis.

Laterals are indeterminate, not different from the main filaments and arranged in an irregular helicoid pattern or laterals are determinate, distinctly different from the main filaments and arranged in a regular pinnate pattern. Propagules are tribuliform, without terminal hairs.

10. Sphacelaria tribuloides Meneghini—Fig. 422–454

Sphacelaria tribuloides Meneghini (1840a) 2, (1840b) 512; J. Agardh (1842) 28 ('*Sphacellaria*'); Meneghini (1843) 336; Kützing (1845) 239; J. Agardh (1848) 31; Kützing (1849) 464, (1855) 26, t. 89, f. 2; Geyler (1866) 516, t. 36, f. 12–17; Zanardini (1873) t. 90B; Pringsheim (1874) 166, t. 8, f. 7–23; Hauck (1878) 291, (1885) 342, f. 144; Ardissone (1886) 88; Reinke (1891) 8; Vinassa (1891) 246; De Toni (1895) 502; Sauvageau (1901) 233 (= R. 123), f. 28 & 29, (1903) 53 (= R. 237), f. 47; Funk (1927) 353; Newton (1931) 189; Schmidt (1931) 24, f. 30; Hamel (1938) 253, f. 47.10–47.12; Lund (1950) 42, f. 8; Irvine (1956) 36; Taylor (1960) 211, t. 29, f. 6; Lindauer, Chapman & Aiken (1961) 158, f. 15; Rodrigues (1963) 34, t. 1, f. j; Joly (1965) 77, f. 129, 158 & 180; Misra (1966) 127, f. 64; Jaasund (1969) 262–263, f. 9; John & Lawson (1972) 824, f. 4; De Rios (1972) 246, f. 27; Tsuda (1972) 93, t. 1, f. 6–9; t. 2, f. 4; Acleto (1973) 12, f. 17–21; Prud'homme van Reine (1974) 173; Richardson (1975) 99, f. 16–27; Russell & Fletcher (1975) 766; Schnetter (1976) 52, t. 2, f. F; Coppejans (1977) f. 78 & 79; Galatis, Katsaros & Mitrakos (1977) 139; Prud'homme van Reine (1978) 303.—Type: *Meneghini s.n.*, Spezia (L, sheet 937.71-699, lecto; isotypes in LD and PC).—See notes on nomenclature 1.

Sphacelaria cervicornis auct. non C. Agardh: Schimper (1837) Unio itiner 1835, Exs. n. 476; Decaisne (1841) 127. (Both authors added a question-mark to the name).

Ceramium fulvum Bertoloni in Kützing (1843) 292 (*pro syn.*)—*Sphacelaria fulva* Kützing (1843) 292, (1849) 464, (1855) 27, t. 91, f. 1.—Type: *Bertoloni 13*, Spezia (L, sheet 937.71-687, holo; isotype in FI).

Sphacelaria tribuloides var. *radicata* DeNotaris (1846) 69, t. 1; Ardissone (1886) 89.—Isotypes *DeNotaris s.n.*, Genua, 1845 (BR, FI, HBG).

Sphacelaria rigida Hering *in* Krauss (1846) 213; Kützing (1855) 26, t. 90, f. 1; Zanardini (1858) 252; Trono (1969) 27, t. 1, f. 7 & 8.—Type: *Krauss s.n.*, Port Natal (FI, KIEL, M).

Sphacelaria caespitula auct. non Lyngbye: Kjellman (1890) 67.—See also notes on nomenclature 2.

Plants forming small, dense, hemispherical cushions (fig. 422; 423) or irregular, erect, penicillate bushes (fig. 424). They are reddish-brown, dark-brown, or olivaceous; solitary or gregarious, and epilithic or epiphytic (fig. 424). Many erect filaments arise from the basal creeping parts (fig. 423). The basal parts consist of small, irregular, monostromatic discs and several creeping stolons (fig. 426).

The erect parts of the plants are composed of many stiff erect filaments (fig. 423) which are unbranched or provided with scarcely branched laterals of up to the fourth order (fig. 427). The divaricate to somewhat appressed laterals with indeterminate growth are scattered, rarely opposite (fig. 427, arrow) and never distichous. They are crowded in the distal half of the erect main filaments. Often all main filaments and laterals grow to an equal height (fig. 422; 423).

There is usually no difference in growth or dimension of axes and mature laterals, but in the proximal part of these laterals the dimensions are usually smaller. Rhizoids do not arise from the erect filaments; they have only been found growing from the small basal discs in specimens epiphytic on *Codium bursa* (fig. 425; 433–435). These rhizoids grow deeply in between the utriculi of the *Codium*.

The dimensions of the usually elongate apical cells of the erect filaments (fig. 432; 436) and of the secondary segments are quite variable. The secondary segments are often longer than they are wide (fig. 428; 442) but in old filaments or in laterals secondary segments are occasionally shorter than wide (fig. 429; 447). Dimensions of superior and inferior secondary segments are equal.

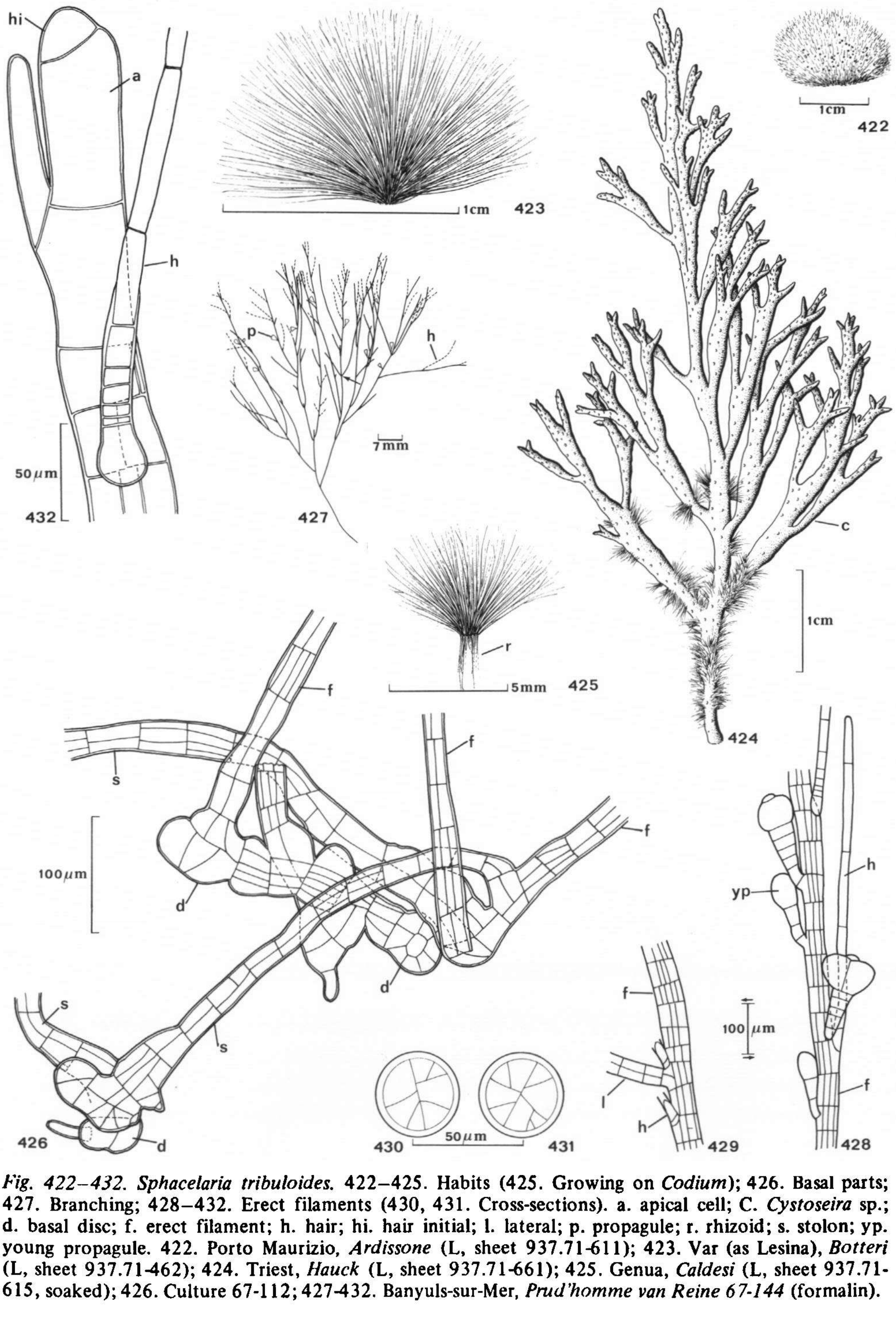


Fig. 422–432. Sphacelaria tribuloides. 422–425. Habits (425. Growing on *Codium*); 426. Basal parts; 427. Branching; 428–432. Erect filaments (430, 431. Cross-sections). a. apical cell; C. *Cystoseira* sp.; d. basal disc; f. erect filament; h. hair; hi. hair initial; l. lateral; p. propagule; r. rhizoid; s. stolon; yp. young propagule. 422. Porto Maurizio, *Ardissone* (L, sheet 937.71-611); 423. Var (as Lesina), *Botteri* (L, sheet 937.71-462); 424. Triest, *Hauck* (L, sheet 937.71-661); 425. Genua, *Caldesi* (L, sheet 937.71-615, soaked); 426. Culture 67-112; 427-432. Banyuls-sur-Mer, *Prud'homme van Reine 67-144* (formalin).

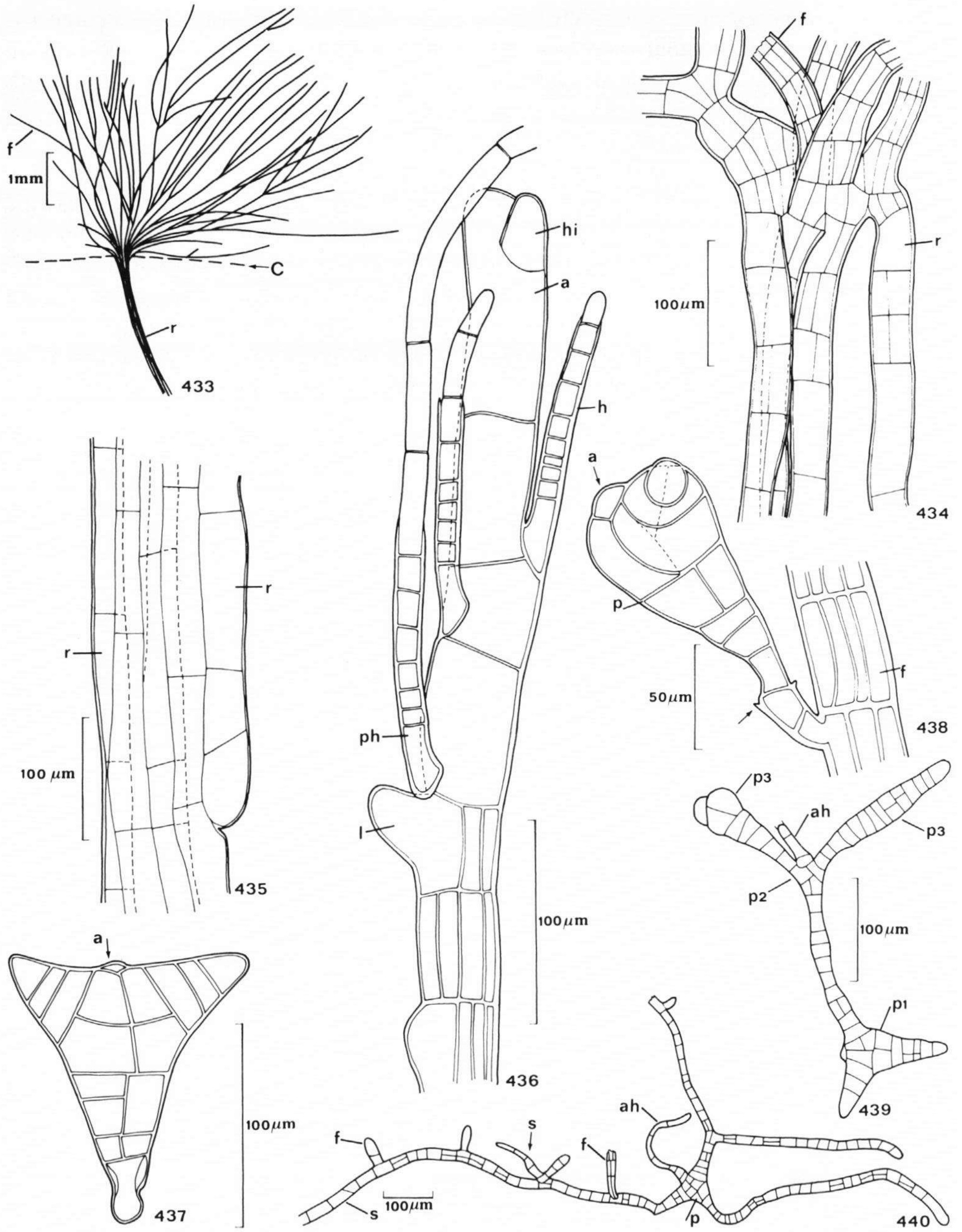


Fig. 433–440. Sphacelaria tribuloides. 433. Habit, growing on *Codium bursa*; 434, 435. Endophytic rhizoids in *Codium bursa*; 436. Part of an erect filament; 437–440. Propagules (439, 440. Germinating). a. apical cell; ah. apical hair; C. *Codium bursa*; f. erect filament; h. hair; hi. hair initial; p. propagule; p2–3. propagules formed by germinating propagule pl; ph. pseudo-axillary hair; r. rhizoid, s. stolon. 433–435. Rovinj, *Liechtenstern* (O, soaked); 436. Banyuls-sur-Mer, *Prud'homme van Reine 67-144* (formalin); 437, 438. Collioure, *Prud'homme van Reine 785* (soaked); 439, 440. Culture 67-112.

The secondary segments are subdivided by radial and semi-radial walls into a parenchymatous tissue without subdivision into medullar and peripheral cells (fig. 430; 431). In lateral view (0–) 1–4 longitudinal walls can be observed in secondary segments. In the cells transverse walls occur rarely.

Solitary hairs are usually frequent (fig. 427; 428; 432; 436).

Propagules are frequent on the distal parts of the erect filaments in specimens collected in summer in Western Europe (all the year round in the Mediterranean). Mature propagules are triangular with one angle attached to the narrow, straight, cylindrical, monosiphonous, 1–3-celled stalk and the other two angles rounded or extended into short horns (fig. 437; 438). Between these two angles or horns, opposite the stalk, a small lenticular cell is situated (fig. 437; 438) which rarely grows into a hair (fig. 439; 440). Occasionally the terminal cell of a horn forms a new propagule (fig. 439; 441). The basal cell of a propagule persists on the filament as a unicellular stalk after the propagule has been shed. It often forms new propagules (fig. 438, arrow, also 442b).

The rare unilocular zoidangia are clavate or ellipsoid when young; mature ones are globular according to Sauvageau (1903, p. 53 = R. 237, f. 47).

The equally rare plurilocular zoidangia are ellipsoid or cylindrical when mature (fig. 443–445), ellipsoid when young. Plurilocular zoidangia with small and with large loculi have been found on different plants.

Dimensions: Plants 5–20 (–30) mm high. Diam. of basal discs 90–125 µm. Stolons 40–100 µm in diam., rhizoids in *Codium bursa* 40–70 µm in diam. Angle of ramification (15–) 25–45 (–60)°. Diam. of erect filaments (20–) 23–50 (–70) µm. Height of secondary segments 30–70 (–75) µm. Diam. of hairs 14.5–16 µm (with sheath) or 11–12.5 µm (without sheath). Chloroplasts 3–5 µm in diam. when seen in surface-view (fig. 446). Stalk of propagules 30–40 X 18–20 µm, body 80–110 X 90–120 (–150) µm. Unilocular zoidangia 65–80 µm according to Sauvageau (*l.c.*). Plurilocular zoidangia 55–100 X (29–) 36–55 µm with loculi of (5–) 6–7.5 (–9) µm or (34–) 44–59 (–64) X 24–32 µm with loculi of 3–4 µm.

Distribution. Europe: Denmark, United Kingdom, France (Atlantic and Mediterranean coasts), Spain, Portugal, Italy, Yugoslavia, Greece, Bulgaria. Also on the Mediterranean coasts of Syria, Israel, Tunisia, Algeria, and Morocco, on the Atlantic coasts of Morocco, on the Azores, Madeira, and the Canary Islands.

The species is also mentioned from many localities in Africa, America (North, Middle, and South), Asia (Red Sea, Persian Gulf, Indian Ocean, South China Sea, Japan, Australasian Archipelago), Australia, New Zealand, and from several of the islands in the Pacific Ocean.

European localities (and some localities on the coasts of western Asia and northern Africa) have been listed and are given in fig. 454.

For an extract of the list of collections and references see below.

DENMARK. Kattegat. Hulsig Stene, *Rosenvinge 11272*, 25/7/1933 (C).

UNITED KINGDOM. Scotland. Three collections, amongst which Holmes in: Algae Brit. rar. exs. n. 309, 8/1895 (BR, KIEL, M, OXF).—England. Northumberland: Berwick-upon-Tweed, *Batters 34*, 10/1884 (herb. Thuret in PC). Devon: Salcombe, N. Sando, *Parke*, 12/7/1941 (D. Irvine, priv. coll.). Dorset: Swanage (partly as *S. furcigera* var. *saxatilis*), *Holmes*, 26/6/1885 (BM).

FRANCE. Atlantic coasts. Charente Maritime: Ile-de-Ré, Ars-en-Ré, *Sauvageau*, 7/6/1902 (PC). Pyrénées Atlantiques: Guéthary, *Sauvageau*, 10/7–30/8/1896 & 21/9/1898 (PC).—Mediterranean coasts. Pyrénées Orientales: more than six collections. Bouches du Rhône: Marseille, Cap

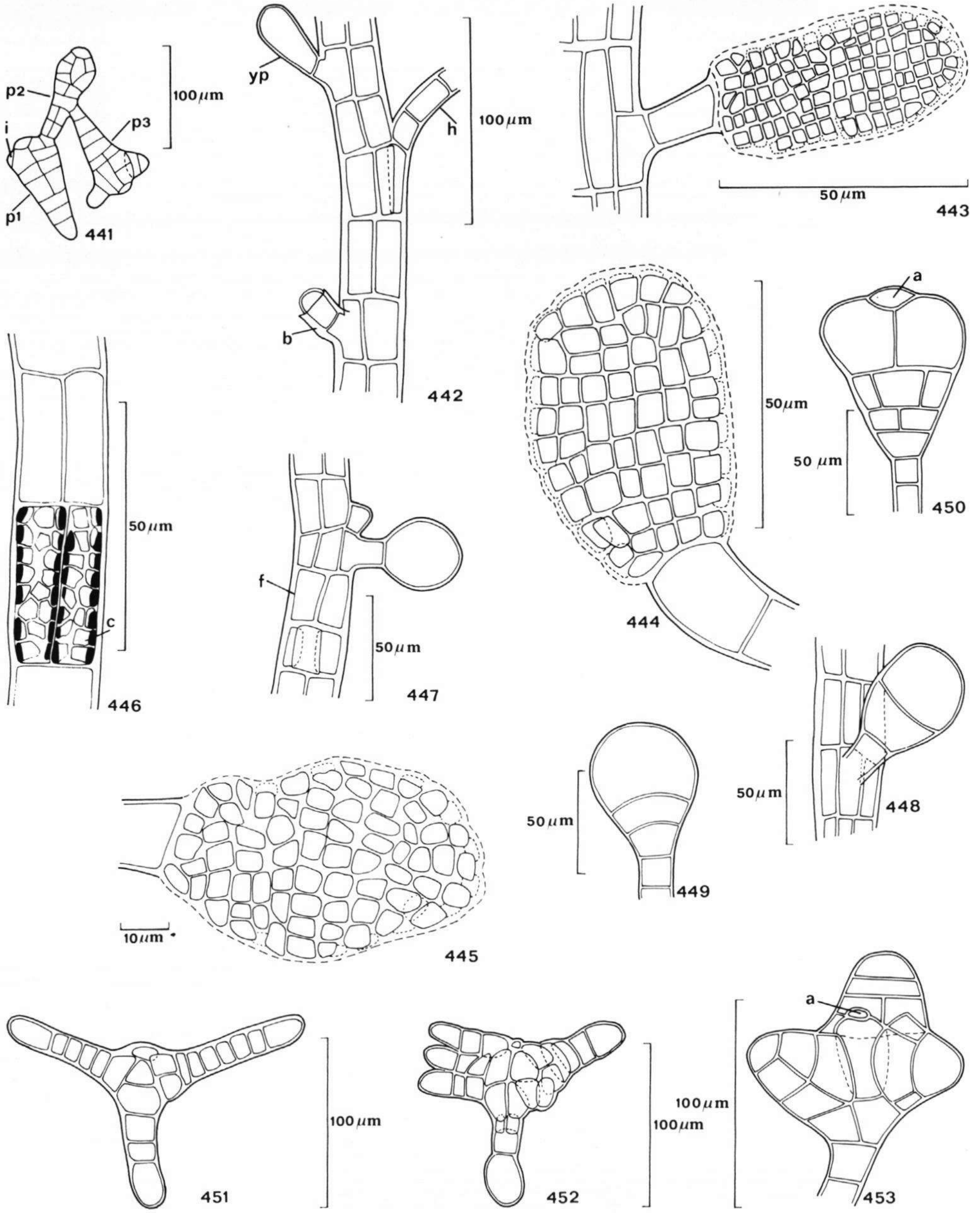


Fig. 441–453. Sphacelaria tribuloides. 441. Germinating propagule; 442, 446. Part of an erect filament; 443–445. Plurilocular zoidangia (443, Micro; 444. Macro, and 455. Intermediate loculi); 447–450. Subsequent stages in the development of propagules; 451–453. Aberrant propagules. a. apical cell; b. basal cell of a shed propagule; c. chloroplast; f. erect filament; h. hair; p2–3. propagules formed by germinating propagule pl; yp. young propagule. 441, 446, 451, & 452. Culture 67–112; 442, 447–450. Port Vendres, *Lokhorst & Prud'homme van Reine 318* (soaked); 443. Vis (as Veglia), Schiffner, Exsicc. n. 146 (UPS, soaked); 444. Krk (as Lissa), Schiffner, Exsicc. n. 655 (UPS, soaked); 445. Rovinj (as Rovigno), Schiffner, Exsicc. n. 146 (BM, soaked); 453. Culture 67–122.

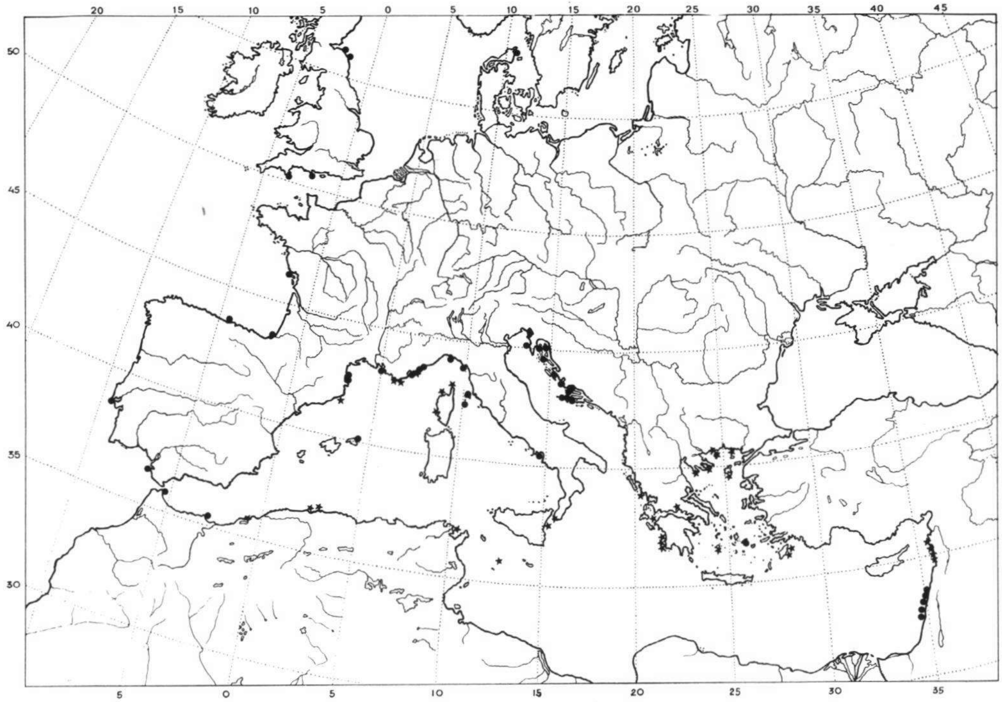


Fig. 454. Distribution of *S. tribuloides*, mainly in Europe.

● = Specimens seen by the author. ★ = Data from literature.

Pinède, *Thuret*, 30/10/1854 (KIEL, L, M, PC, UPS). Var: seven collections/references. Alpes Maritimes: two collections. Corse: four collections/references, amongst which: Without exact locality, Debeaux in: Algues de la Corse n. 23 (CN, PC).

SPAIN. Atlantic coasts. Three collections.—Mediterranean coasts. Two collections/ references.—Moroccan side of the Mediterranean. Two collections.

PORTUGAL. Estremadura: Tago Salso: Trafaria, on *Mytilus edulis, Welwitsch*, 27/1/1852 (LISU).

ITALY. Ligurian coasts. Ten collections, amongst which Cornegliano, *Dufour* in: Erb. critt. Ital. ser. 1, n. 132 (FI, L, PC, WU). *Ibidem*: S. Nazaro, (as *S. tribuloides* var. *radicata*), *Dufour* in: Erb. critt. Ital. ser. 2, n. 70 (BM, E, FI, L, PC, WU). Without exact locality: *Dufour* in: Rabenhorst, Algen Sachs. n. 913 (in L and many other herbaria).—Tyrrhenian coasts. Four collections.—Sicilia. Two references.—Ionian coasts. Reggio di Calabria (Giaccone, 1969, p. 499).—Adriatic coasts. Two collections.

YUGOSLAVIA. Many collections/references, amongst which Rovinj (as Rovigno). Val di Bora, 2 m deep, on *Codium bursa*, Schiffner in: Algae mar. exs. n. 146 (BM, W, WU). Krk (as Veglia): *Lusina* in: Schiffner, Algae mar. exs. n. 146 (UPS). Lošing: Mali Lošing (as Lussinpiccolo), *Schiller* in Krypt. exs. Mus. Palat. Vindob. n. 1944 (in L and many other herbaria). Solta: Maslinica, on rocks, 10 m deep, Schiffner in: Algae mar. exs. n. 922 (BM, WU). Vis (as Lissa): 1–2 m deep, *Schiller* in: Schiffner, Algae mar. exs. n. 655 (BM, UPS, WU).

GREECE. Many collections/references.

BULGARIA. Without exact locality (A. Zinova, 1967, p. 150).

SYRIA. Seven references.

ISRAEL. Five collections.

TUNISIA. Carthago (Hamel, 1938, p. 254).

ALGERIA. Three references.

MOROCCO. (For Mediterranean coasts see Spain). Atlantic coasts. Agadir (Dangeard, 1949, p. 123).

AZORES. Without exact locality: Q.M.C. expedition, 1952 (BM).

MADEIRA. Several localities (Levring, 1974, p. 28). Selvagem Grande (Levring, *l.c.*).
CANARY ISLANDS. Hierro: Faro de Orchilla, 18–23 m deep, CANCAP 476, 7/9/1977 (L). Tenerife: two collections. Gran Canaria: Guia, Punta Ancha, rockpools, CANCAP 1605, 9/11/1978 (L).

Notes on nomenclature. (1) Meneghini's 'lettera al Dottore Jacob Corinaldi' (Meneghini, 1840a) is a printed brochure of three pages. I have seen it in the phycological library of the Laboratoire de Cryptogamie of the Muséum National d'Histoire Naturelle in Paris. The description of *S. tribuloides* is literally repeated in Flora (Meneghini, 1840b).

(2) *Sphacelaria minuta* C. Agardh was given as a probable synonym of *S. tribuloides* by De Toni (1895, p. 503). The holotype of *S. minuta* (*Gaudichaud 1016*, Sandwich Isles, herb. Agardh 45325 in LD) is a minute tuft of a sterile *Sphacelaria* (fig. 455; 456) which is perhaps *S. tribuloides*. It is also possible, however, that it is a *S. rigidula*. The material being undeterminable, it cannot serve as type. If it could be identified, the name *S. minuta* should have priority over both the name *S. tribuloides* and the name *S. rigidula*, because of the date it was published (C. Agardh, 1824, p. 164).

Notes on morphology. In the secondary segments of *S. tribuloides* usually only a few longitudinal walls are formed. All walls are more or less radial, never periclinal. The sequence of the formation of the longitudinal walls, as can be observed in cross-sections, has been described and figured by Geyler (1866, p. 516, t. 36, f. 12) and Pringsheim (1874, p. 176, t. 8, f. 7–9). Their figures agree with my figures 430; 431.

Primary laterals are formed by hemiblastic branching of young superior secondary segments (fig. 436). These segments carry one somewhat protruding cell, containing a large nucleus and dense protoplasm. These cells grow into the primary laterals without much delay. Pringsheim (*l.c.*) called these initials 'Brutzellen', a term he also used for the pericysts of *S. radicans*. The branch-initials of *S. tribuloides*, however, are inconspicuous and not comparable to the marked pericysts as described for *S. radicans*. All mature cells of the filaments are peripheral and in consequence they all can function as branch-initials. Usually only cells of superior secondary segments form laterals.

Laterals of the second and third order may arise in a later stage of growth. They are always scarce and are formed without order (fig. 427). All laterals show indeterminate growth, but the branching system as a whole is determinate. The main filaments and laterals grow until they have reached a common height, resulting in a semi-globular outline of the cushions (fig. 422). The angle of ramification is quite variable, but usually the laterals are spreading with sharp angles (fig. 427). Usually the erect parts of the plants are more prominent than the creeping parts, but occasionally the creeping parts are more conspicuous. Most erect filaments are straight and show only small gradual changes in diameter. Stolons, however, may be twisted and the diameter of their secondary segments often varies considerably (fig. 426).

Basal discs of *S. tribuloides* are usually small and monostromatic (fig. 426). They are often formed by lateral proliferation of stolons which happen to meet a suitable substrate. When growing on *Codium bursa S. tribuloides* forms long rhizoids (fig. 425; 433–435). DeNotaris (1846, p. 69) described a new variety *radicata* for these plants. Other species of *Sphacelaria*, however, form similar rhizoids when growing on *Codium* (compare *S. cirrosa* fig. 638, *S. plumula* fig. 480 & 505). The presence or absence of long rhizoids cannot be used as a character of taxonomic importance in these species.

Hairs in *S. tribuloides* are acroheteroblastic or terminal and always solitary (fig. 427; 428; 432; 436), but occasionally they are arranged in short secund series (fig. 436). Quite often a lateral will be formed from the secondary segment just below a hair, resulting in a lateral with a pseudo-axillary hair (fig. 429; 436).

For a discussion about this pseudo-axillary position see Sauvageau (1903, p. 84 = R. 255) and the section 'Notes on morphology' of *S. cirrosa* (p. 242).

Notes on ecology. *Sphacelaria tribuloides* can be found on rocks and on other algae in many localities all over the world. In Europe it is not common outside the Mediterranean. In the Mediterranean it occurs in rock-pools as well as in deep water. In rock-pools it usually grows in isolated cushions on rocks or on calcareous algae. It has been collected in rather deep water (4–30 m) (as an epiphyte on *Cystoseira spp.*, on Gorgonids, and on *Codium bursa*) and even once from very deep water (85 m) by dredging between the Islands Pianosa and Montecristo in the Toscane Archipelago, Italy.

Sphacelaria tribuloides has not been found intertidally outside rock pools and does not occur in brackish waters.

Form range and cultures. Morphological variation in *S. tribuloides* is not very conspicuous. The habit of subglobular plants growing in tidal pools is quite characteristic (fig. 422), but on *Cystoseira spp.* (fig. 424) or on *Codium bursa* (fig. 425; 433) it forms small, stiff, irregular, penicillate bushes. The stiff, scarcely branched, erect filaments are quite characteristic, but the form of the propagules is the most important character discriminating it from all other species of *Sphacelaria*.

Cultures have been isolated from material collected along the Mediterranean coasts of France (Banyuls-sur-Mer, Port Vendres, and Collioure). One of these cultures and its subcultures have been maintained for more than twelve years. These cultures died within a week when kept at 4°C, but at 12°C and 20°C they grew well and formed many hairs and propagules. When grown from propagules the plants which grew attached to the glass walls of the culture-vessels formed stolons and small basal discs (fig. 426). Plants grown from fragments never attached secondarily, but formed globular free-floating plants. Morphology of the filaments of these unattached plants was not different from the morphology of plants collected from nature.

Reproduction and life-history. The life-history of *S. tribuloides* has never been described, but the propagules and the rare zoidangia have been described by several authors. In my cultures I only observed propagules.

Meneghini (1840a) mistook the propagules for sporangia, but J. Agardh (1842) introduced the name propagule for them. Kützing (1855) figured propagules of *S. tribuloides* (t. 89, f. 2) and of its synonym *S. rigida* (t. 90, f. 1). The former figure is correct, the latter incorrect. The development of the propagules has been described in detail by Geyler (1866, p. 518, t. 36, f. 15–17), Pringsheim (1874, p. 174, t. 8, f. 15–18), and Sauvageau (1901, p. 238 = R. 128, f. 29E–J) (see also my fig. 447–450). Zimmerman & Heller (1956, p. 299) classified the development of the propagules of *S. tribuloides* as belonging to the '*Plumula*-type'. Sauvageau (*l.c.*) also stressed the similarity in development of propagules in both species. Young stages of propagules are very reminiscent of the unilocular zoidangia of other

Sphacelaria species (fig. 447), but their contents are usually less dense and less granular than those of unilocular zoidangia. In the young propagules the sub-apical cell (just below the small lenticular apical cell) is a primary segment which directly forms the horns (fig. 450). Both horns arise simultaneously. The number of segments in the body is 2–3 (–4). In the horns this number is quite variable, and the horns can be prominent (fig. 437; 451) as well as almost inconspicuous (fig. 441).

In European Atlantic localities propagules of *S. tribuloides* have been found in summer and autumn, in the Mediterranean they occur in all seasons, but less frequently in winter. In most collections germination of propagules can be observed (fig. 439; 440). Usually the apical cells of the horns as well as the lowermost secondary segment of the stalk can grow into a filament which usually functions as a stolon. From this young stolon erect filaments as well as small basal discs and new stolons may arise (fig. 440). Occasionally new propagules are formed from germinating horns (fig. 439; 441). Rarely also other peripheral cells of propagules proliferate (fig. 441; 452). In culture many aberrant propagules occurred (fig. 439; 441; 452; 453).

Unilocular zoidangia have been observed very rarely (Sauvageau, 1903, material from Rovinj in the Adriatic; Jaasund, 1969, Tanzania), and plurilocular ones rarely (Hauck, 1878; Sauvageau, 1901; this study, herbarium specimens collected along the Adriatic coast in the months 1, 2, 4, 5, 7, and 12). Mostly the plurilocular zoidangia on one plant can be either considered plurilocular macrozoidangia, or plurilocular microzoidangia (see description), but one collection (fig. 445) contains zoidangia with loculi of intermediate size (5–6 µm); these zoidangia are possibly asexual. In specimens with many plurilocular zoidangia and occasional propagules the filaments were only 20–24 µm broad; filaments of specimens with only propagules in the same collections were 24–32 µm broad.

The above incomplete observations do not present a reasonably complete picture of the life-history of *S. tribuloides*. When compared to the observations of Van den Hoek & Flinterman (1968) on *S. rigidula* (as *S. furcigera*), a hypothetical life-history may be drafted. The data are not incompatible with the image of an isomorphic or slightly anisomorphic diplohaplontic life-history with plurilocular microgametangia and macrogametangia, unilocular zoidangia, many propagules, and perhaps also plurilocular asexual zoidangia.

Systematic position. The form of the propagules is a characteristic feature for *S. tribuloides*. The only other species in Europe with comparable propagules are the rare *S. brachygonia* and the more common, but pinnate *S. plumula*. For differences between these taxa see table XIV.

Of the extra-European *Sphacelaria* species in section *Tribuloides* the names *S. brevicornis* Setchell & Gardner, *S. taitensis* Setchell, and *S. mexicana* Taylor are very probably synonymous with *S. tribuloides*. The propagules in type-specimens of *S. taitensis* and *S. mexicana* do not differ from those of *S. tribuloides*. The type (and only collection) of *S. brevicornis* is probably lost (Silva, pers. comm.) but Setchell & Gardner's description and figures (1924, p. 725, f. 59) suggest synonymy to *S. tribuloides*. However, instead of triangular propagules they picture tetrahedral ones. Tetrahedral propagules occasionally occurred in my cultures (fig. 453).

Sterile filaments of *S. tribuloides* are often almost indistinguishable from sterile filaments of *S. rigidula* and *S. nana*. In most cases, however, at least young propagules can be found

TABLE XIV. Comparison of the species of the section Tribuloides found in Europe

(all dimensions in µm)

	S. tribuloides	S. plumula	S. brachygonia
tufts	dense cushions	open, occasionally	dense cushions
basal parts	usually small, monostromatic	few short creeping filaments	quite extensive polystromatic structures
branching of erect filaments	unbranched or with scattered branches	pinnate	irregular helicoid pattern
diameter of main filaments	(20–)23–50(–70)	(53–)65–150(–200)	(40–)48–80
longitudinal walls in segments	(0–)1–4	4–8(–10)	4–8
propagules	solitary, tribuliform, or obtriangular	solitary, tribuliform, or obtriangular	geminate, transverse ellipsoid, or transverse fusiform
uniloc. zoidangia dimensions	very rare 65–80	very rare 55–80	only in culture unknown
pluriloc. zoidangia	(34–)44–100 x 24–55	not known	not known

on filaments of *S. tribuloides*, often after a prolonged search. Occasionally, especially when growing on *Codium bursa*, irregular erect penicillate *Sphacelaria* tufts cannot properly be assigned to a species. See also table XI.

11. **Sphacelaria brachygonia** Montagne—Fig. 457–472

Sphacelaria brachygonia Montagne (1843) 305; Kützing (1849) 464, (1855) 26, t. 88, f. I; Montagne (1856) 400; Sauvageau (1901) 244 (= R. 134), f. 32; Hamel (1938) 254; Rodrigues (1963) 27, t. 1, f. i; Joly (1965) 76, f. 121–127; John (1972) 3, f. 1–2; Prud'homme van Reine (1974) 173; John & De Graft-Johnson (1975) 751; Prud'homme van Reine (1978) 303.—*Sphacelaria tribuloides* var. *crassa* Reinke (1891) 9.—Type: *Ins. Divae Catharinae, ad Brasiliam, Col. Gaudichaud*, 2e Itinaire (Lectotype in PC, herb. Montagne; isotypes in L, PC, TCD).

Sphacelaria fasciculata Schousboe *ex* Sauvageau (1902) p. 400 (= R. 212), *pro syn.*—Type: *probably lost.*

Sphacelaria elliptica Dickinson (1952) 41, f. 1.—Lectotype: *Lawson 211* (*A. 71* acc. to John (1972) 2), Ghana Teshi, 2/1951 (K, now in BM).

Plants forming dense, hemispherical cushions (fig. 457) or thick mats (fig. 458). They are dark-brown or olivaceous, solitary or matted, and epilithic.

Many erect filaments arise from the basal creeping parts (fig. 459). The basal parts consist of quite extensive polystromatic basal holdfasts and many small, irregular, creeping stolons (fig. 460–462). A varying number of divaricate rhizoids arise from the stolons and from the erect filaments (fig. 460; 462; 463).

The erect parts of the plants are composed of many stiff, erect filaments with a varying number of laterals of up to the second or third order (fig. 459; 460). The acutely divaricate to somewhat appressed laterals with indeterminate growth occur in an irregular helicoid pattern, rarely opposite or secund (fig. 464). Usually filaments and laterals grow to an equal height and this results in a hemispherical outline.

There is usually no difference in growth or dimensions of axes and mature laterals, but in the proximal parts these laterals are usually narrower.

The dimensions of the short apical cells of the erect filaments (fig. 465) and of the

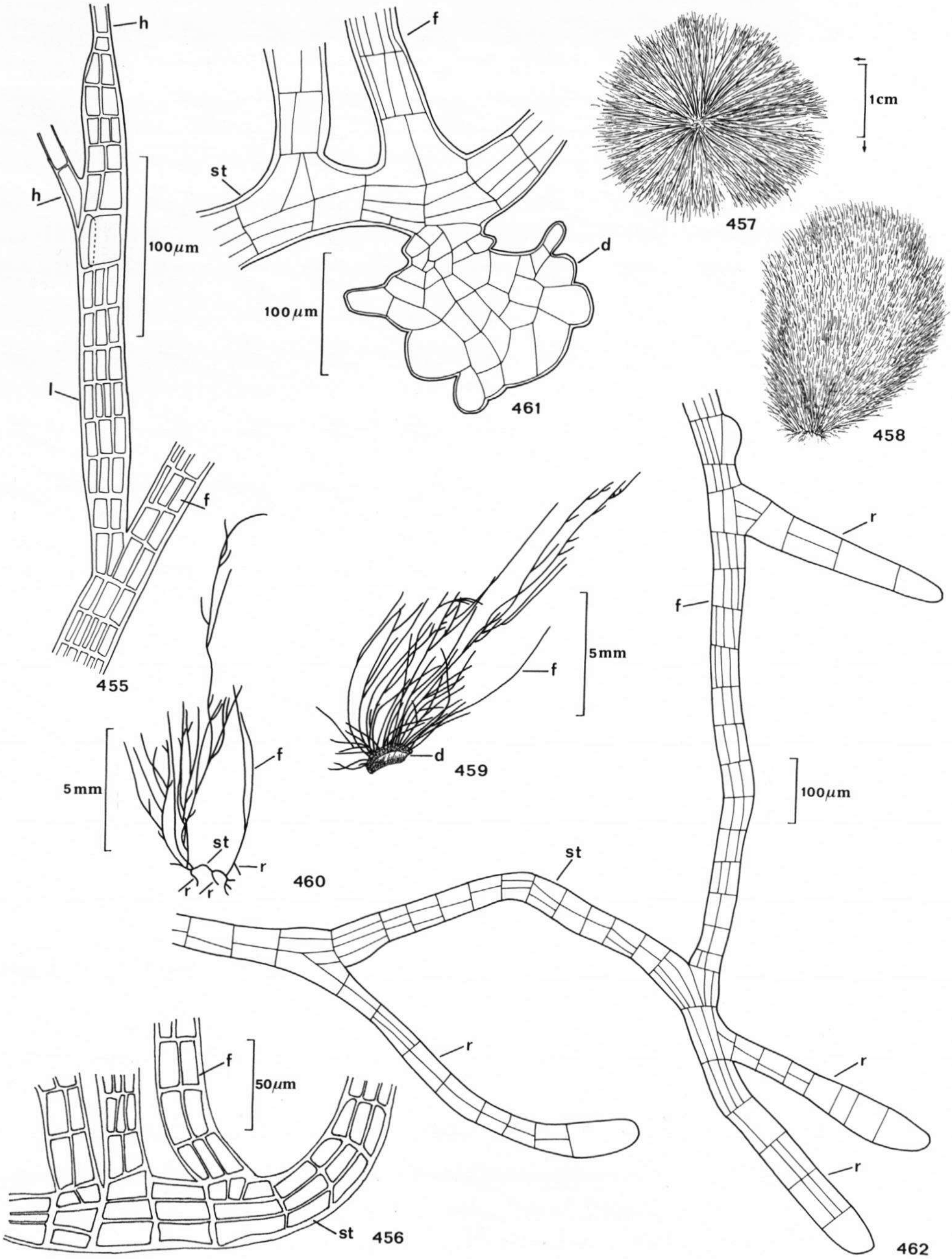


Fig. 455, 456. Sphacelaria minuta. 455. Part of an erect filament; 456. Basal parts; Fig. 457–462. *S. brachygonia.* 457–460. Habits; 461, 462. Basal parts. d. basal disc; f. erect filament; h. hair; l. lateral; r. rhizoid; st. stolon. 455, 456. Sandwich Isles, *Gaudichaud 1016* (LD, soaked); 457. Winneba, *Lawson A1081* (L, sheet 962.66-380); 458–462. Teshi, *Lawson A 1851* (L, soaked).

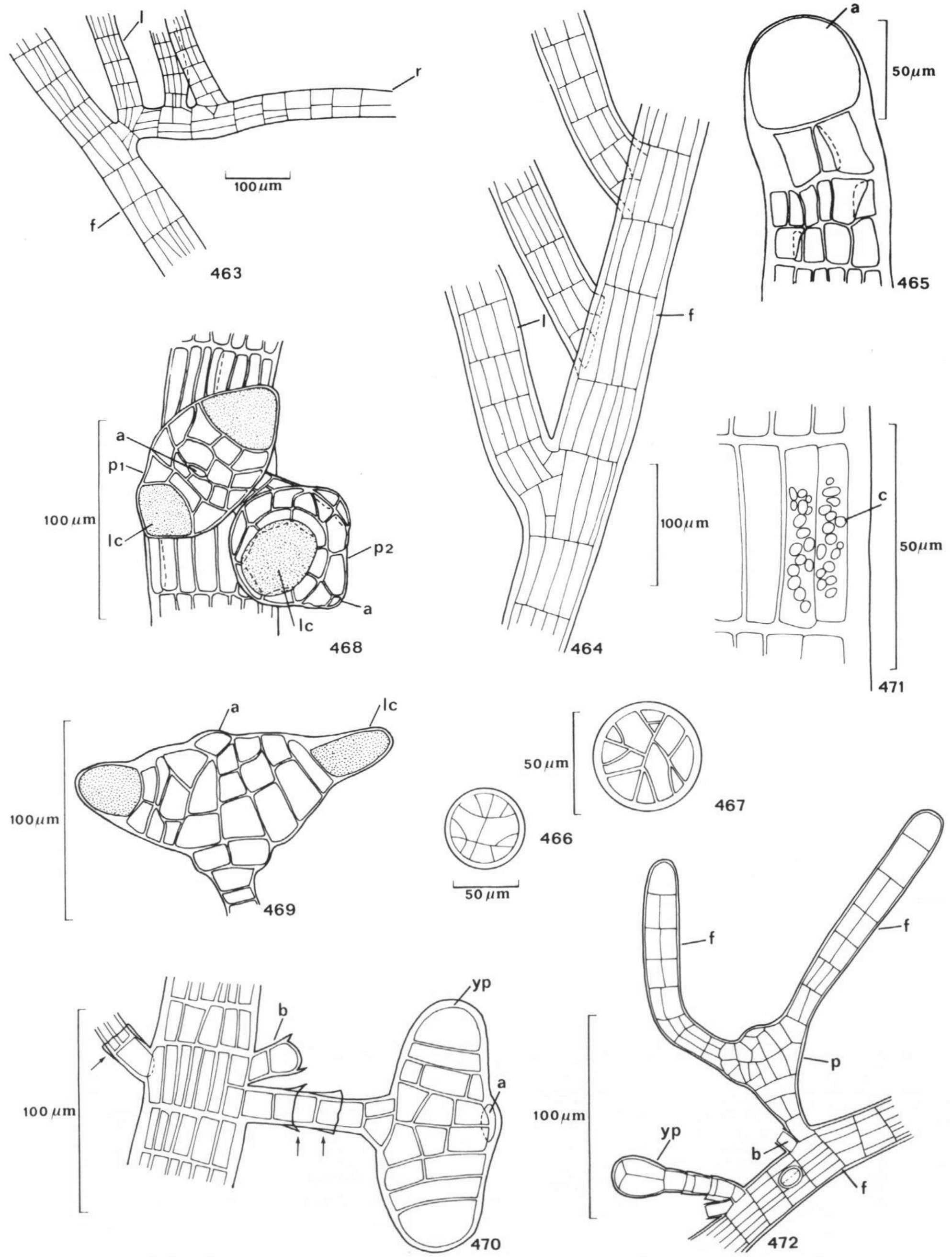


Fig. 463–472. Sphacelaria brachygonia. 463–467, 471. Parts of erect filaments (467, 468. Cross-sections); 468–470, 472. Propagules. a. apical cell; b. basal cell of a shed propagule; c. chloroplast; f. erect filament; l. lateral; lc. lateral cell; p. propagule; yp. young propagule. 463, 464, 466, 467, & 471. Teshi, *Lawson A 1851* (L, soaked); 465, 468, 469. Parede, *Welwitsch* (LISU P 46259, soaked); 470, 472. Wineba, *Lawson A 1818* (L, soaked).

usually short secondary segments (fig. 462–465) are quite variable. Dimensions of superior and inferior secondary segments are equal.

The secondary segments are subdivided by radial and semi-radial walls into a parenchymatic tissue, without subdivision into medullar and peripheral cells (fig. 466; 467). In lateral view 4–8 longitudinal walls can be observed in mature secondary segments. In the cells transverse walls rarely occur.

Colourless hairs with basal sheaths do occur sparsely, according to John (1972) and John & De Graft-Johnson (1975).

Propagules are usually frequent on the distal parts of the erect filaments. Mature propagules consist of a narrow, straight, monosiphonous, 2–4 celled cylindrical stalk bearing a transversely ellipsoid to spindle-shaped body with two large lateral cells and a small lenticular terminal cell (fig. 468–470). The stalks are often geminate (fig. 468; 470). The basal part of the stalk of a propagule persists on the erect filament as an unicellular or bicellular lateral after the propagule has been shed (fig. 470, arrows). It usually forms new propagules, which as a result get fairly long stalks with one or several collared cells (fig. 470). The number of cells in the bodies is quite variable (fig. 469; 472).

Unilocular zoidangia have been mentioned but not described by John & De Graft-Johnson (1975). Plurilocular zoidangia are not known.

Dimensions: Plants 6–20 (–25) mm high. Diam. of basal holdfasts 6–8 mm. Mats over 30 cm in diam. Stolons 50–60 μm in diam. Rhizoids 20–60 μm in diam. Angle of ramification (15–) 25–45°. Diam. of erect filaments (40–) 48–80 μm. Height of secondary segments (15–) 26–60 (–76) μm. Diam. of chloroplasts 3–7 μm in surface-view (in soaked specimens) (fig. 471). Stalk of propagules 25–75 (–125) X 18–23 μm, body (50–) 60–76 X (100–) 120–150 (–200) μm.

Distribution: Europe: Portugal, Gibraltar. Also in Tangier and on the coasts of Senegal and Ghana.

The species is also known to occur in several localities in Brazil, in southern Australia, and in southern Africa.

European localities (and some localities of the coasts of Africa) have been listed below and are in part given in fig. 43.

PORTUGAL. Estremadura: Praia de Pasedes, *Welwitsch*, 28/1/1853 (LISU; P 46259).

GIBRALTAR. (As *S. fasciculata*), *Schousboe* (Sauvageau, 1902, p. 400 = R. 213).

MOROCCO. Tangier (as *S. fasciculata*), *Schousboe* (Sauvageau, *l.c.*).

SENEGAL. Dakar (Sourie, 1954, p. 178 & 195).

GHANA. Teshi: (as *S. elliptica*), *Lawson 211* or *A71*, 2/1951 (K in BM); *Ibidem*: (as *S. elliptica*), on moderately exposed rocks, *Lawson A1851*, 23/1/1962 (GC, L). Botianaw (as Bortianor): (as *S. elliptica*), on very exposed rocks in the lower eulittoral, *John 6268*, 11/11/1969 (GC, L). Kokrobite (John & De Graft-Johnson, 1975, p. 752). Winneba (as *S. elliptica*), *Lawson A1081*, 27/2/1956 (GC, L), and *Lawson A1818*, 7/1/1962 (GC, L). Apam (John, 1972, p. 2).

Notes on morphology. Sparse hairs are recorded by John (1972) in material from nature (Ghana) and by John & De Graft-Johnson (1975) in culture material. I did not succeed in retracing hairs in John's material.

Notes on ecology. *Sphacelaria brachygonia* has been collected from the lower eulittoral of exposed to moderately exposed rocky coasts in Portugal, Ghana, and Brazil.

Form range and cultures. There is very little variation in the few specimens of *S. brachygonia* I have seen. The habit of the dark subglobular plants is quite characteristic. The dimensions of the tufts, mats, and basal holdfasts are variable.

I have never seen living specimens, but John & De Graft-Johnson (1975) described some experiments performed with *S. brachygonia* in culture. They found a high optimum temperature (20.5–27.5°C) for the growth of this alga in culture and concluded that *S. brachygonia* can be considered to be a genuine warm water species. They observed the multicellular hairs (see also the notes on morphology overhead) occurring in very large numbers in those cultures showing particularly good growth. The best growth observed was at the highest light intensities in the used light intensity gradient (2850–4946 Lx in a gradient running from 720–4946 Lx).

Reproduction and life-history. The development of the propagules which were detected by Reinke (1891, p. 9) has been described and figured by Sauvageau (1901, p. 247 = R. 136, f. 32C–32K) and (much less extensively) by Dickinson (1953), Joly (1965), and John (1972). Cultured *S. brachygonia* from Ghana produced propagules as well as unilocular zoidangia under widely varying culture conditions: long day ($16.\overline{8}$) and short day ($8.\overline{16}$) conditions, between approximately 20–28°C, and varying light intensities. Unilocular zoidangia were also produced at lower temperatures (11.5°C) and long day conditions, but propagules were not (John & De Graft-Johnson, 1975).

Usually only the large lateral cells of the propagule grow into filaments when germinating (fig. 472), but occasionally also its stalk (see Dickinson, 1953, f. 1C).

Systematic position. The form of the propagules of *S. brachygonia* is characteristic and relates this species to other species with tribuloid propagules (section *Tribuloides*). For differences between the three species of this section found in Europe, see table XIV.

12. Sphacelaria plumula Zanardini—Fig. 473–507, plate 5

Sphacelaria plumula Zanardini (1865) 139, t. 33; Hauck (1885) 345; Reinke (1891) 10, (1892) 67, t. 48, f. 1–7; Kuckuck (1894) 229; De Toni (1895) 503; Sauvageau (1901) 107 (= R 90), f. 18–20; Funk (1927) 353; Hamel (1938) 251, f. 47; Lund (1950) 44, f. 9; Irvine (1956) 37; Prud'homme van Reine (1974) 173; Russell & Fletcher (1975) 766; Prud'homme van Reine (1978) 303.—*Sphacelaria plumosa auct. non* Lyngbye: Meneghini (1843) 351, (1846) 353 (*p.p., excl. syn.*).—Lectotype: *Vidovich s.n.*, Dalmazia, *sub nomine Sphacellaria plumosa* Ag. (WU).—See notes on nomenclature 1.

Sphacelaria pseudoplumosa Crouan (1867) 164, t. 25, f. 161.—*Chaetopteris plumosa auct. non* (Lyngbye) Kütz.: Crouan (1852) Exsicc. n. 42 (*excl. syn.*).—Type: Crouan Exsicc. n. 42 (CONC, L, M, PC).

Sphacelaria pectinata Reinsch (1875) 102, t. 36.—Lectotype: *Reinsch* Prep. Micr. Alg. 236, Mediterranean, 1874 (BM).

Sphacelaria plumula var. *cervicornis* Sauvageau (1901) 109 (= R. 92).—Type: Porto Maurizio, Straforello in Erb. critt. Ital. ser. 2, n. 1439 (as *Sphacelaria cervicornis*) (PC, in herb, Thuret).—See notes on nomenclature 2.

Sphacelaria plumula var. *patentissima* Sauvageau (1903) 49 (= R. 233); Hamel (1938) 253.—Type: *Lebel s.n.*, Normandy (probably Carteret); 1867 (PC, in herb. Thuret).—See also notes on nomenclature 1.

Plants forming small erect tufts, sometimes complanate, when all axes and main branches are arranged in one plane. They are light to dark brown; solitary or rarely gregarious and epilithic or epiphytic (fig. 473; 474). One to many branched main axes with large apical cells arise from a few irregular tuberculous creeping filaments, which may be covered by rhizoids (fig. 475).

The erect parts of the plants are composed of one or more main axes and hemiblastic laterals of up to the third order. The distal parts of the main filaments are pinnate and clothed with opposite, determinate, hemiblastic laterals (fig. 473–480; 505; plate 5). These ultimate pinnate parts have a narrowly lanceolate or slightly triangular outline.

The dimensions of the inferior and superior secondary segments of the main filaments are usually equal, but in some specimens the superior secondary segments are somewhat longer than the inferior ones.

The proximal parts of the main axes are usually narrower than the younger distal parts and the secondary segments are often longer than they are wide. In the distal parts of the indeterminate filaments the secondary segments are as long as they are wide or much shorter, sometimes half as long as wide (fig. 477; 478; 481; 482).

The secondary segments are subdivided by radial and semi-radial walls into 1–4 large central cells and many smaller peripheral cells but without a distinct separation into medullar and peripheral cells (fig. 483–487). Transverse walls are rarely formed and exclusively in the proximal parts of the main filaments. In lateral view 4–8 (–10) longitudinal walls can be observed in large secondary segments (fig. 477; 478; 481).

The opposite, determinate, unbranched laterals arise from the superior secondary segments of all axes and indeterminate laterals (fig. 481), occasionally also from the inferior secondary segments (fig. 479, arrow). These determinate laterals are mostly tapering towards their apex and several of their terminal segments may be monosiphonous (fig. 488). Usually a few of the laterals show a less determinate or even an indeterminate growth. These indeterminate laterals of the first order often form laterals of the second order (fig. 488).

A varying number of rhizoids are formed from peripheral cells of the erect filaments. They are closely appressed and grow downward (fig. 489). New determinate laterals may arise from these rhizoids (fig. 490). Occasionally the apical cells of determinate or indeterminate filaments (even main axes) in contact with the substrate may be transformed into long creeping rhizoids.

Hairs are quite rare, but they may arise solitary by acrohomoblastic branching on the ultimate and penultimate filaments (fig. 488).

Mature propagules are triangular (fig. 491–494), but young ones are globular or club-shaped and often quite similar to unilocular zoidangia. They are borne on the laterals and rarely on the axes. The basal cell of the propagule persists on the lateral as a unicellular stalk after the propagule has been shed. It often forms new propagules (fig. 481).

Unilocular zoidangia are very rare. They have occasionally been found by Sauvageau, on specimens also bearing propagules or sometimes on separate plants (Sauvageau, 1901, p. 106 = R. 89). The zoidangia are borne on unicellular stalks scattered on the laterals. Plurilocular zoidangia are not known.

Dimensions: Plants up to 1–2 (–4) cm high. Width of distal pinnate parts 1–4 mm. Diam. basal holdfast 100–200 μm. Diam. of rhizoids 20–32 μm. Angle of ramification (35–) 50–80 (–90)°, in loose-lying plants more often 90°. Diam. main filaments (53–) 65–150 (–200) μm, in the proximal parts (40–) 50–74 (–100) μm. Diam. determinate laterals adaxial 29–40 μm, apex 7.5–25 μm. Height of secondary segments of main fila-

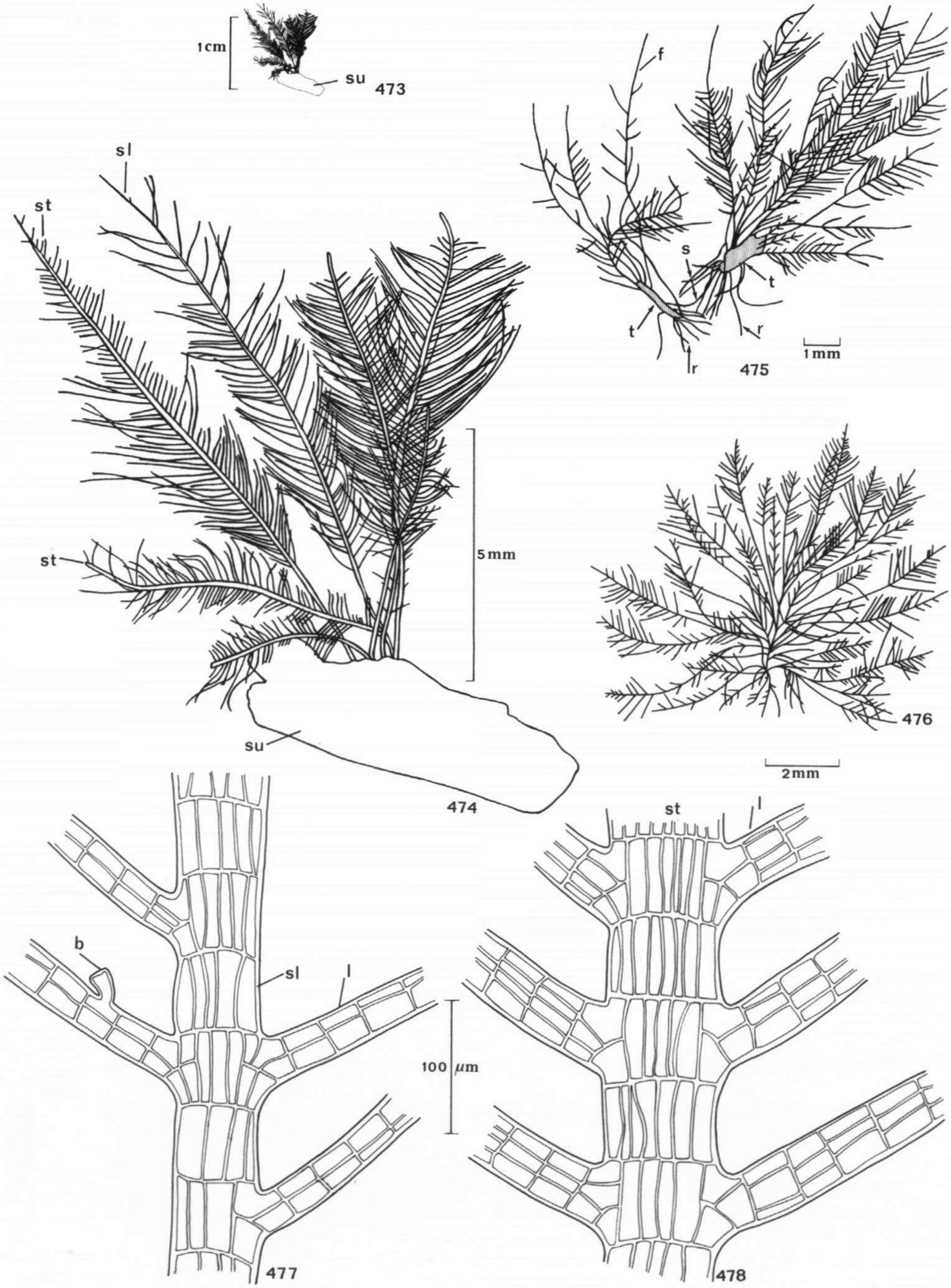


Fig. 473–478. ***Sphacelaria plumula.*** **473–476. Habits; 477, 478. Parts of erect filaments. b. basal cell of shed propagule; f. erect filament; l. lateral; r. rhizoid; s. stolon; sl. slender main filament; st. stout main filament; su. substrate; t. tuberculous basal part. 473, 474, 477, 478. Dalmatia,** ***Vidovich*** **(W. 14029, soaked); 475. Rovigno,** ***Liechtenstern*** **(W, soaked); 476. Culture 68-25-2.**

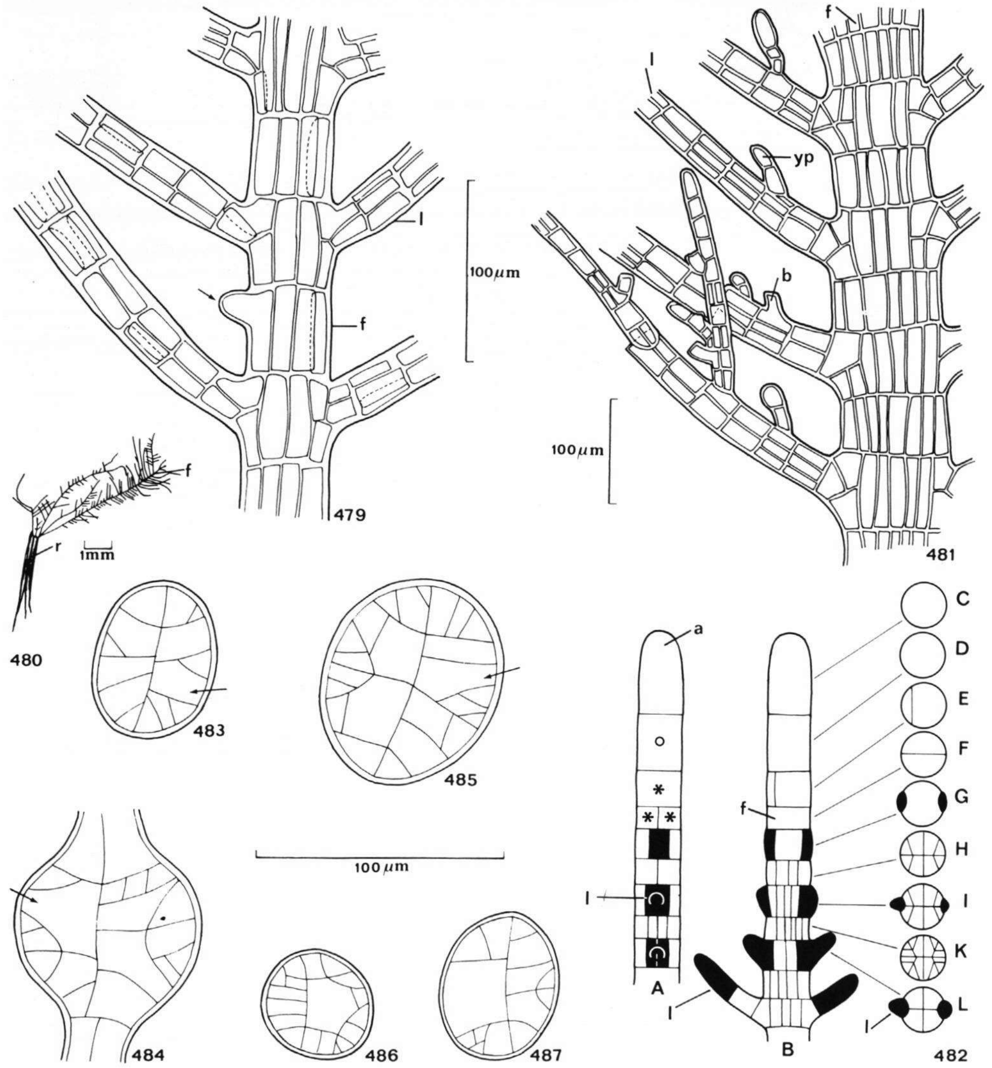


Fig. 479–487. Sphacelaria plumula. 479, 481–487. Parts of erect filaments. 482. Diagrammatic, filament seen from two perpendicular directions (A, B), and cross-sections of subsequent segments (C–L); 483–487. Cross-sections (483–485. Indeterminate filaments; 486, 487. Determinate laterals); 480. Habit of a plant epiphytic on *Codium bursa.* a. apical cell; b. basal cell of shed propagule; f. erect filament; l. lateral; r. rhizoids; yp. young propagule. 479. Culture 68-25-2; 480. Port Vendres, *Prud'homme van Reine 67-121* (formalin); 481. Rovigno, *Liechtenstern* (W, soaked); 483–487. Banyuls-sur-Mer, *Prud'homme van Reine 67-134* (microslides).

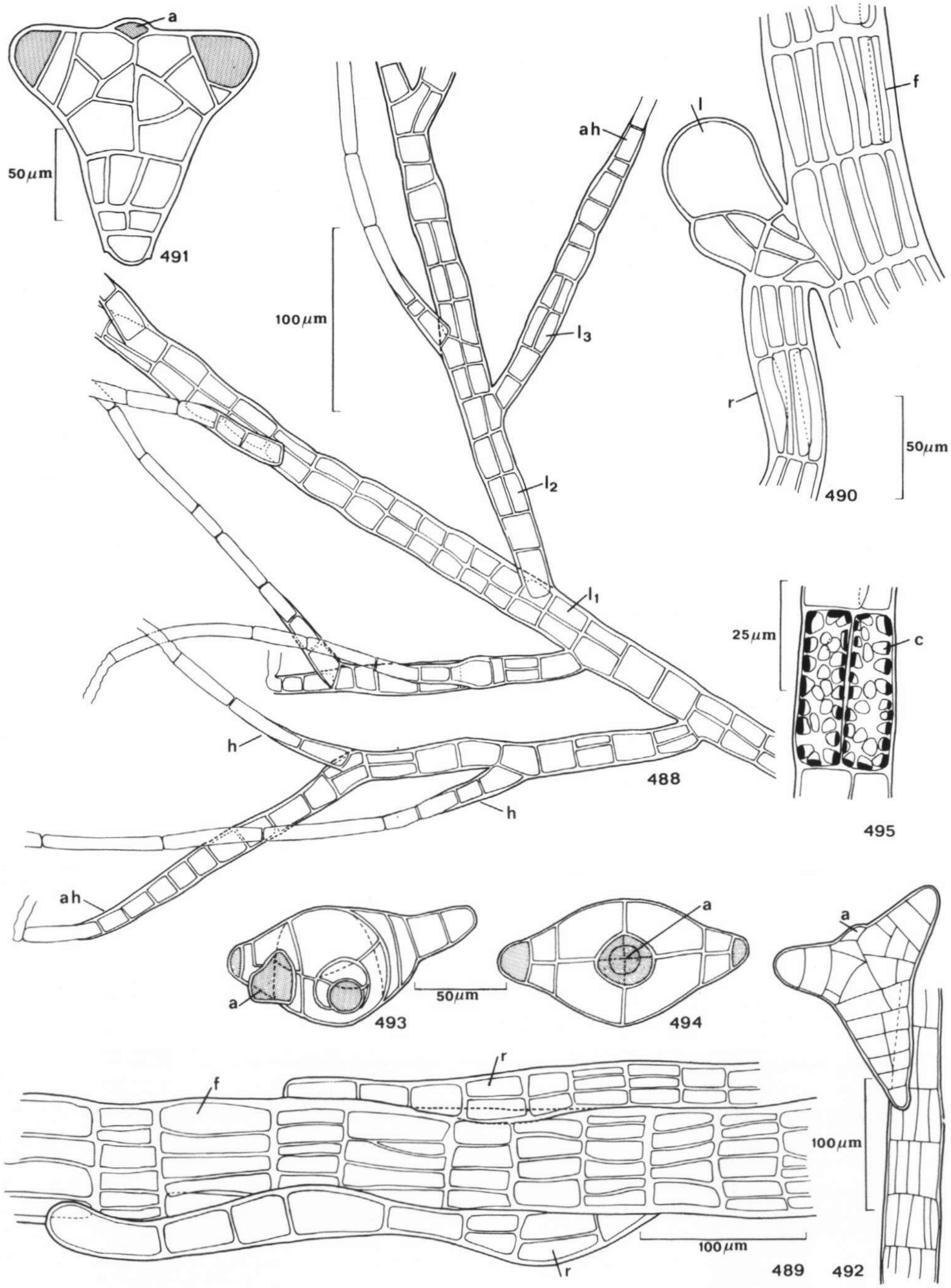


Fig. 488–495. Sphacelaria plumula. 488–490, 495. Parts of erect filaments and laterals; 491–494. Propagules (491–493. Lateral view, 493. Perpendicular to the others; 494. Apical view). ah. apical hair; c. chloroplast; f. erect filament; h. hair; l. lateral; l1, 2, 3. laterals of the first, second, and third order; r. rhizoid. 488, 493–495. Culture 68-25-2; 489. Rovigno, *Liechtenstern* (W, soaked); 490. Roscoff, *Prud'homme van Reine 66-95* (formalin); 492. Dalmatia, *Vidovich* (W, soaked).

ments (30–) 40–100 (–150) µm. Hairs 5–12.5 µm in diam. (without sheath) or 10–17 µm (sheath included). Chloroplasts 3–4 X 3–5 µm in surface-view (fig. 495). Length of propagules 100–150 µm, maximum width (60–) 80–140 µm. Diam. unilocular zoidangia 55–80 µm according to Sauvageau.

Distribution. SW. Norway, W. Sweden, Denmark, Heligoland, United Kingdom, Eire, France (Atlantic and Mediterranean coasts), Spain, Portugal, Italy, Yugoslavia, and Greece. The species has also been observed in Syria and from eastern Canada. A closely related taxon: *S. plumula* var. *californica* Setchell & Gardner (1925) 395, has been found in California, U.S.A.

European localities and the localities in Syria have been listed and are given in Fig. 496.

For an extract of the list of collections and references see below.

NORWAY. Sör Tröndelag. Hirta: Dolmöy, on empty shells, 10–15 m deep, *Sivertsen*, 31/7/1977 (L, O).—Hordaland. Three references.—Rogaland. Espevaer (north of Haugesund): on mussel shells, 3–5 m deep (Printz, 1952, p. 136).

SWEDEN. Bohuslän. Three references.

DENMARK. Skagerrak. Mellemgrund off Lönstrup: 8–10 m deep, on *Buccinum* shells, (as *S. olivacea*), *Rosenvinge 7545*, 2/8/1904 (C, mixed with *S. caespitula*).—Kattegat. Nordre Rønner: 11–14 m deep, on stones (Lund, 1950, p. 46).

GERMANY. Heligoland. Several collections.

THE NETHERLANDS. Huisduinen (near Den Helder): on a stone, washed up, *Swennen & Louwrier*, 24/9/1950 (L).

UNITED KINGDOM. Shetland. Two collections.—Scotland. St. Kilda: Village Bay, dredged (Watling, Irvine & Norton, 1970, p. 38). Ross & Cromarty: Summer Isles, Taner Mhor, 12/6/1971 & 10/9/1972, *Farnham* (priv. coll.). Hebrides: Colonsay, 6–12 m deep (Norton *et al.*, 1969, p. 130). Arran: Lamlash Bay, *Batters*, 28/8/1891 (BM).—Isle of Man. Port Erin Bay: cast ashore (Parke, 1935, p. 30).—England. Durham: South Shields, in deep, shady, eulittoral pools (Edwards, 1975, p. 292). Cornwall: two collections/references. Devon: four collections. Dorset: two collections/references, amongst which Weymouth, Holmes, Algae Brit. rar. exs. n. 24, 8/1882 (BM, KIEL, LD, NMW, OXF). Sussex: two collections.—Channel Islands. Guernsey: dredged (Lyle, 1920, p. 9).

EIRE. Two collections/references.

FRANCE. Atlantic coasts. Manche: two collections/references. Ille-et-Vilaine: two collections. Finistère: eight collections, amongst which Brest: Crouan, Algues mar. Finist. 42 (CO, L, M, PC). Basses Pyrénées: three collections/references.—Mediterranean coasts. Pyrénées Orientales: eight collections. Bouches-du-Rhône: Marseille (Bellan-Santini, 1969, p. 60). Var: Iles d'Hyères (Belsher *et al.*, 1976, p. 72).

SPAIN. Northwest coast. Lanzada (south of Ria de Arosa): in shadowed littoral pools, *Donze M. 349 & M. 363*, 10 & 11/8/1964 (L).—Baleares. Two collections.

PORTUGAL. Arrabida (south of Lisboa) (Ginsburg-André, 1963, p. 376).

ITALY. Ligurian coasts. Three collections/references, amongst which Porto Maurizio: (as *S. cervicornis*), *Strafforello* in Erb. critt. Ital. ser. 2, n. 1439, autumn 1840 (PC; FI, mixed with *S. cirrosa*).—Tyrrhenian coasts. Two collections/references.—Sicily. Seven references.—Adriatic coast. Three collections/references.

YUGOSLAVIA. More than six collections/references.

GREECE. Twelve references.

SYRIA. Two references.

Notes on nomenclature. (1) Zanardini (1865, p. 140) mentioned 'Dalmazia—Sebenico, *Vidovich*' as locality and collector. The specimens were mixed between *Halopteris filicina*. The author cited also Meneghini's description of *S. plumosa* adding '*non Ag. quoad specim. adr.*' and on p. 141 he stated that he studied the material from Meneghini's herbarium. According to De Toni & Levi (1888, p. 130) there is no material of *S. plumula* left in

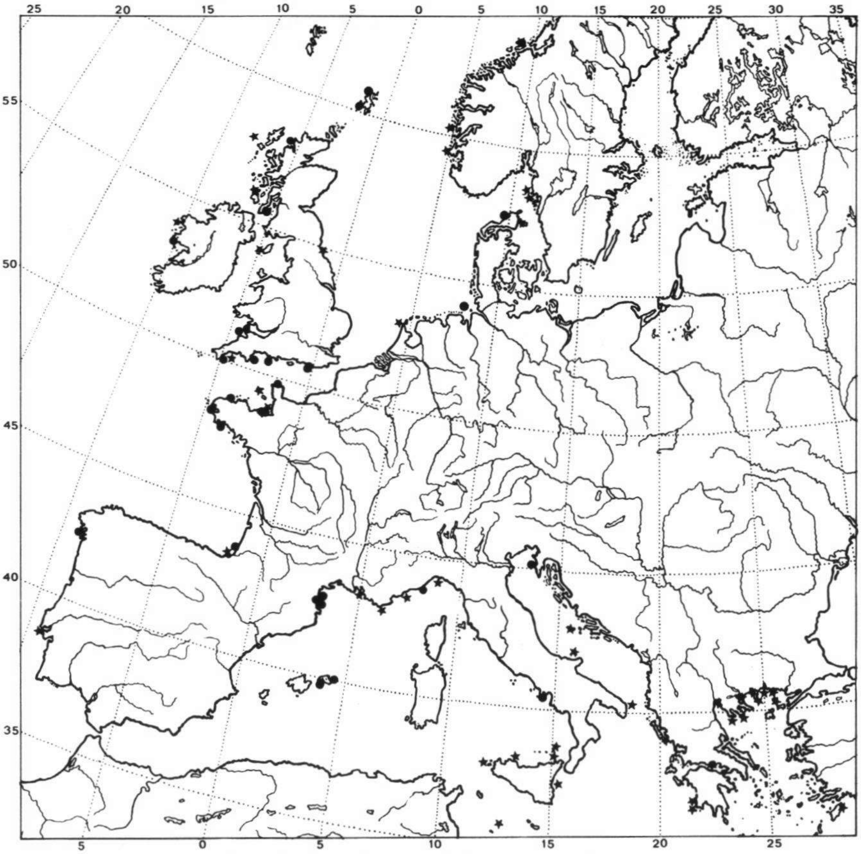


Fig. 496. Distribution of *S. plumula* in Europe.

● = Material seen by the author.
★ = According to literature.

the herbarium of Zanardini. Three collections could be located that may be related to type material. Of these collections material from Vienna (W), collected by *Vidovich* and mixed with *Halopteris filicina* seems to be closest to the specimens described by Meneghini and Zanardini (fig. 350; 352; 358; 363). The other two collections, one labelled '*Sphacelaria plumula* Zanard.—*rarissime*—*mar. adr.*—herb. Zanardini' in MEL, and the other '*Sphacelaria plumula* Zanard.—*Mar. adr.*—*raro*—leg. Zanardini' in HBG may have been collected after the date of publication of the new species by Zanardini. According to Sauvageau (1903, p. 49 = R. 233) the plant figured by Zanardini (1865, t. 33) belongs to his new var. *patentissima*, but this drawing is also the figure of the type material of the species. If the variety should be maintained, this would complicate nomenclature. Later it will be explained that there is no reason to maintain the variety as a separate taxon.

(2) Not all exsiccata of the Erbario crittogamico Italiano series 2, n. 1439 (as *S. cervicornis*) contain specimens of *S. plumula* var. *cervicornis* Sauv. In FI most specimens of *Sphacelaria* of this number are *S. plumula*, but some plants of *S. cirrosa* can be found amongst them. In M and W all *Sphacelaria* specimens of this number proved to be *S. cirrosa*.

Notes on morphology. The prominent elongate apical cells of the indeterminate filaments are very large and often wider than the primary segments (see plate 5, and fig. 482). The apical cells are very delicate and vulnerable and they are often damaged and killed (fig. 498). In these cases new indeterminate filaments will be formed, (see also the thorough description by Sauvageau, 1901, 96–101 = R. 80–85). In most cases the planes of branching of these substitute axes differ from the plane of branching of the original axis. If determinate laterals spontaneously change into indeterminate laterals they usually branch in the same plane as the original axis.

The sequence and pattern of division within the secondary segments is as follows. Young superior secondary segments at first form two parallel periclinal walls, perpendicular to the plane of branching (fig. 482G). These periclinal walls cut off two peripheral cells which become the initials of the laterals (dark cells in fig. 482). After these parallel periclinal walls a median wall will be formed in the plane of branching, followed by radial walls perpendicular to the plane of branching (fig. 482L). Later longitudinal walls are radial or have acute angles with the ones formed before (fig. 482I; 484). As in other *Sphacelaria* species showing a radial pattern of segmentation of the secondary segments, some of the central cells may still reach the periphery of the filaments (fig. 483–485, arrows).

In the inferior secondary segments the first two parallel periclinal walls are lacking (fig. 482F) and the other walls are formed in a similar sequence as in the superior secondary segments (fig. 482H), resulting in a more regular radial pattern (fig. 482K; 485).

In indeterminate laterals, and even more in determinate ones, the regular radial pattern is often disturbed. There the first longitudinal wall often is not radial but periclinal, resulting in one large central cell surrounded by some smaller peripheral cells (fig. 486; 487).

In older filaments a central cell of a superior or inferior secondary segment that still maintained contact with the periphery may grow out and form an appressed rhizoid (fig. 489). These rhizoids are rarely branched (hemiblastic). Sometimes the first superior secondary segment of a rhizoid will form an erect filament again, which is in most cases not in the plane of branching of the main filament (fig. 490). Later these adventitious filaments are like other indeterminate laterals, but provided with several basal rhizoids (fig. 499). Rhizoids occasionally function as very short stolons, creeping over the substrate and forming one or two erect filaments or some new rhizoids (fig. 500).

The basal holdfast of the thalli is in most cases composed of few irregular, somewhat swollen, short, creeping filaments, and some rhizoids (fig. 497; 501). In older thalli rhizoids may cover these basal filaments and together with new erect filaments arising from stolon-like rhizoids complex tuberculous structures can be formed (fig. 502; 503). Rarely rhizoids or erect filaments form small few-celled monostromatic discs (fig. 504). If *S. plumula* grows on a soft substrate like *Codium bursa* many very long, straight, unbranched rhizoids can be formed which grow deep into the thallus of the *Codium* (fig. 480; 500; 505). In a large ball of *Codium bursa*, dredged from 20 m depth near Cap Béar, Pyrenées Orientales, France, on which many small specimens (2–5 mm high) of *S. plumula* were growing, the rhizoids were 1–3 mm long and their diameter was 40–45 µm (fig. 480; 505). The transparent segments of these rhizoids were 1.5–2 × as long as wide. In some cases the rhizoids were united into two or three clusters. In other specimens growing on *Codium bursa* (from Brighton and Caen) similar rhizoids have been observed.

Hairs of *S. plumula* are always solitary and acrohomobastic; they are not very frequent.

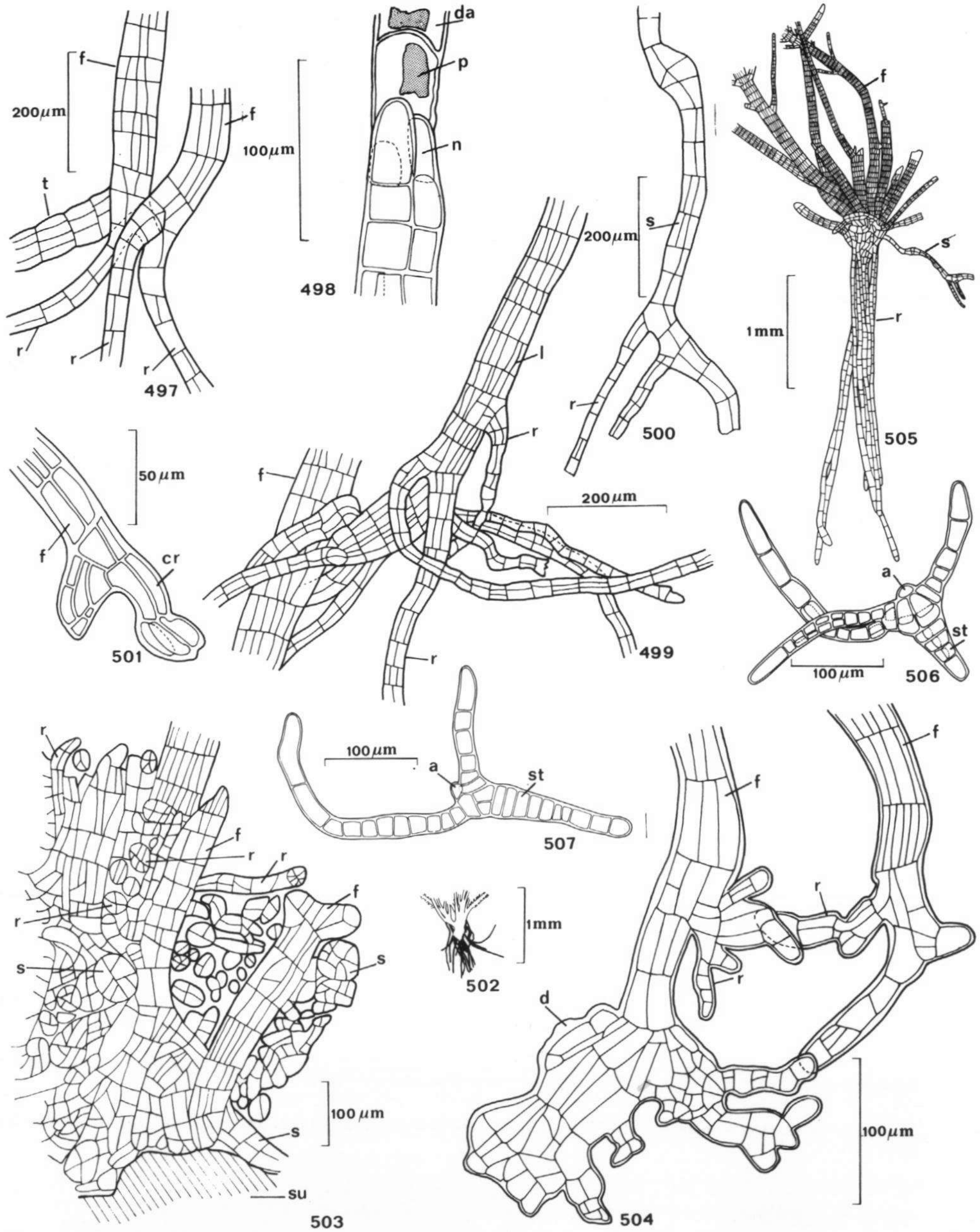


Fig. 497–507. Sphacelaria plumula. 497, 500–505. Basal parts (503. Longitudinal section of a complex basal holdfast; 505. Epiphyte on *Codium bursa*); 498, 499. Parts of erect filaments; 506, 507. Germinating propagules. a. apical cell; cr. short creeping filament; d. basal disc; da. damaged apical cell; f. erect filament; l. lateral; n. new apical cell; p. primary segment (dead); r. rhizoid; s. stolon; st. stalk; su. substrate; t. tuberculous basal holdfast; 497. Dalmatia, *Vidovich* (W, soaked); 498, 506, 507. Culture 68-25-2; 499, 501, 503. Roscoff, *Prud'homme van Reine 66-95* (formalin); 500, 505. Port Vendres, *Prud'homme van Reine* 67-121 (formalin); 502, 504. Rovigno, *Liechtenstern* (W, soaked).

In most cases they arise near the apex of determinate laterals (h in fig. 488), rarely also from axes of which the apical cells ceased to function, and occasionally as apical hairs (t in fig. 488). The hairs are often very short and reduced but in some cases longer hairs have been found (fig. 488).

Notes on ecology. *Sphacelaria plumula* is a sublittoral, permanently submerged species. It is an inhabitant of deeper water. On the atlantic European coasts it has been found between 1 m depth (Heligoland) and 27 m depth (Shetland). Occasionally it has been found in permanent, deep, shaded pools in the eulittoral (Durham; Ria de Arosa). In the Mediterranean it is found at greater depths (95–100 m, Baleares and Gulf of Naples; see also Funk, 1927, p. 425 & 454), but also in marine caves and permanent, shaded, eulittoral pools.

Sphacelaria plumula grows on several kinds of substrates like rocks, gravel, shells, wood, seagrasses, and other algae. It is common on the 'fond coralligène' in the Mediterranean and has been found on several occasions growing on *Codium bursa*. The plants are solitary, never forming dense carpets. They often grow together with *Halopteris filicina*. In some cases unattached specimens have been found, often among sea-grasses, especially *Zostera marina*. *S. plumula* is a marine species that never penetrates into brackish areas. The species has been found in all seasons, but most frequently in summer and autumn. It is not possible to tell whether *S. plumula* is a perennial species, or whether several generations occur during a year.

Form range and cultures. Sauvageau (1901, p. 95 = R. 79) described two forms 'reliées par d'insensibles transitions', a stout form and a slender one. Later (Sauvageau 1903, p. 49 = R. 333) he included the slender form into his *S. plumula* var. *patentissima*. In many cases, however, stout and slender thalli can be found growing from one basal part (fig. 474; 477; 478), so there is no reason to keep them as separate taxa.

In unattached specimens from *Zostera marina* beds the laterals are often perpendicular to the axes (var. *patentissima*). These specimens are mostly sterile and lack rhizoids. In culture no differences with originally attached specimens could be found (see fig. 476; 479; 488 of culture 68–25, originating from specimens found loose between *Zostera* near Roscoff).

The longest specimens have been found in the Mediterranean (3–4 cm); along the atlantic coasts of Europe the specimens rarely reach 1 cm in length. No seasonal variation in growth has been observed.

Cultures have been made from material collected on the Atlantic coasts (Roscoff, St. Lunaire) and on the Mediterranean coasts (Banyuls, Collioure, Port Vendres) of France. In only six of the eleven series of cultures some growth occurred, and in three cultures (at 12°C and light intensity of 175–950 Lx) pinnate thalli and propagules have been observed. At higher light intensities (2800–3000 Lx) at 12°C *S. plumula* became very pale and died within one month. At 20°C at 185–500 Lx the algae often showed many proliferations and rhizoidal growth, but at *c.* 1400 Lx they sometimes formed normal thalli (fig. 476) and at 4°C there was no growth at all. The pinnate thalli in culture were never as regular as thalli found in nature, but in other respects they did not differ.

Reproduction and life-history. The propagules of *S. plumula* seem to be the most important reproductive organs. Unilocular zoidangia have only been observed in one collection (Concarneau, april 1900, see Sauvageau, 1901, p. 106 = R. 89 + fig. 20, N–R). The present author did not succeed in tracing these specimens in the Sauvageau collection at PC. The propagules arise in the plane of branching and from the laterals of the first order (fig. 477; 481). According to Sauvageau the unilocular zoidangia are similarly arranged. Recently Coppejans (1977) depicted unilocular zoidangia of a *S. plumula* he found in Port Cros. They are arranged similar to the observations of Sauvageau, but the largest unilocular zoidangia Coppejans depicted were only 41 μm in diameter.

In most cases the first propagule on a lateral is adaxial and grows from the second superior secondary segment of this lateral (fig. 477). If a second propagule is formed on the same lateral, it is often also adaxial and grows from the third superior secondary segment of the lateral. Further propagules arise irregularly but often adaxially and from superior secondary segments. Rarely propagules are formed from inferior secondary segments of the laterals (fig. 481). Propagules may also arise from laterals of the second or third order and also, but rarely, from axes. In the latter case they are always substituting for a lateral.

Propagules are very common in summer and early autumn; in other seasons they seem to occur less regularly.

Zanardini (1865, p. 139 + fig. 33) in his description of *S. plumula* already correctly described and figured young and mature propagules. The brothers Crouan (1867, p. 164 + fig. 161) described the propagules as spores that become multicellular when still fixed on the plants.

Sauvageau (*l.c.*, p. 105 = R. 88–89 + fig. 20A–H) thoroughly described the formation and growth of propagules. He did not mention, however, that the plane in which the arms (or horns) are formed is in most cases perpendicular to the plane of branching of the thalli. In many cases the formation of primary and secondary segments in the basal parts of the propagules is less regular than Suavageau supposed, resulting in more (fig. 492) or less (fig. 491) than five transverse divisions.

When a propagule is shed, its basal cell remains on the plant and can form some successive propagules (fig. 481b). When germinating, the lateral horns of the propagule each can form a filament (rarely more than one, see fig. 506), while often the lowermost cell of the stalk also will form a filament (fig. 507). The small lenticular apical cell remains as such.

Systematic position. *Sphacelaria plumula* is the only European regularly pinnate species in the subgenus *Propagulifera.* It differs from pinnate species in the subgenus *Pseudochaetopteris* in having almost no transverse walls in the secondary segments. The tribuliform propagules are very much like those of *S. tribuloides.* For comparison with the other European species in the section *Tribuloides* see table XIV. The unattached forms, named *S. plumula* var. *patentissima* by Sauvageau, in culture became attached again and were not different from normal specimens. So this variety cannot be maintained as a separate taxon.

IVb. Section Furcigerae Prud'homme van Reine *nov. sect.*

Sphacelaria sect. *Furcigera* Prud'homme van Reine (1978) 312 (*nom. inval.*).—Type species: *Sphacelaria rigidula* Kützing.

Filamenta lateralia indeterminata, filamentis principalibus similia, irregulariter spiraliter disposita. Propagula ramulis longis cylindricis praedita, pilis nullis.

Laterals are indeterminate, not different from the main filaments and arranged in an irregular helicoid pattern. Propagules have long, cylindrical arms and are without a terminal hair.

13. Sphacelaria rigidula Kützing—Fig. 508–554

Sphacelaria rigidula Kützing (1843) 292, (1849) 463, (1855) 25, t. 86, f. I.—Type: *Schimper s.n.*, Red Sea, on *Cystoseira triquetra* (L, sheet 937.117-229, holo; W. isotype, Grunow 19682).
Sphacelaria furcigera Kützing (1855) 27, t. 90, f. II; Askenasy (1888) 21; Reinke (1890a) 208, (1891) 14, t. 4, f. 5–13 (*p.p.*), see notes on nomenclature 2; Kuckuck (1894) 229; De Toni (1895) 506; Sauvageau (1900) 221 (= R. 7), (1901) 379 (= R. 156), f. 35; Setchell & Gardner (1925) 396, t. 37, f. 29; Hamel (1938) 255; Lund (1950) 29, f. 5; Irvine (1956) 28; Taylor (1960) 210, t. 29, f. 5; Van den Hoek & Flinterman (1968) 193; Jaasund (1969) 261, f. 8; Colijn & Van den Hoek (1971) 899; Goodband (1971) 957; Prud'homme van Reine (1974) 174; Kornmann & Sahling (1977) 153, f. 82; Prud'homme van Reine (1978) 303.—Type: *Lenormand 314*, Island Karak (= Khärk), Persian Gulf (L, sheet 937.714-72, holo; CN, PC).
Sphacelaria cirrhosa minima Figari & De Notaris (1851) 167.—Type: Red Sea, on *Dilophus fasciola.* Not seen, probably lost.
Sphacelaria olivacea var. *solitaria* Pringsheim (1874) 166, t. X, f. 1, 11–13.—*Sphacelaria solitaria* Kylin (1947) 28.—No type-specimen known.
Sphacelaria racemosa auct. non Greville: Reinsch (1874) 22, t. 29.—Type: Trieste (Tergeste). Probably lost.
Sphacelaria furcigera var. *saxatilis* Kuckuck (1897) 373, f. 1, K, N, O (*p.p.*, only Büscheln); Newton (1931) 189 (*p.p.*); Waern (1945) 401 (*p.p.*).—Type: *Kuckuck s.n.*, Oldehovenbrunnen, Heligoland, 27/9/1893 (HELG).
Sphacelaria fusca auct. non (Hudson) S. F. Gray: Zimmerman (1923) 113, (1925) 17, t. 1, f. 6; Zimmerman & Heller (1956) 290, f. 2B, 3, 4A & 6; Gayral (1958) 201, (1961) 8; De Haas-Niekerk (1964) 148. f. 1–33 (*p.p.*); Goodband (1971) 957 (*p.p.*); Russell & Fletcher (1975) 766 (*p.p.*).—*Sphacelaria cirrhosa* var. *fusca* Crouan (1852) Exsicc. n. 35 (*p.p.*), see Sauvageau (1902) 394 (= R. 207); Knight & Parke (1931) 66 & 111.—*Sphacelaria cirrhosa* forma *fusca* Holmes & Batters (1891) 81 (*p.p.*).—*Sphacelaria pennata* var. *fusca* Irvine (1956) 32 (*p.p.*); Blackler (1956) 66; Gayral (1966) 235.—See notes on nomenclature 1 and 2.

Plants are usually very dense, forming small, erect penicillate bushes (fig. 508; 509), felty cushions (fig. 510), or confluent mats (fig. 511). They are reddish-brown or dark-brown; solitary, gregarious or caespitose; epilithic, or occur occasionally on sediment-bottoms, or are epiphytic and sometimes partly endophytic. Many branched erect filaments arise from the basal creeping parts.

The basal parts consist of small monostromatic or polystromatic discs (fig. 512–516), and many creeping stolons and rhizoids (fig. 514; 516).

The erect parts of the plants are composed of many main axes and a varying number of laterals of up to the second or third order (fig. 517–519). The sharply divaricate or somewhat appressed laterals with indeterminate growth arise in an irregularly helicoid pattern.

There is usually no difference in growth or dimensions of axes and mature laterals of the first order, but in the proximal part of these laterals the dimensions are usually

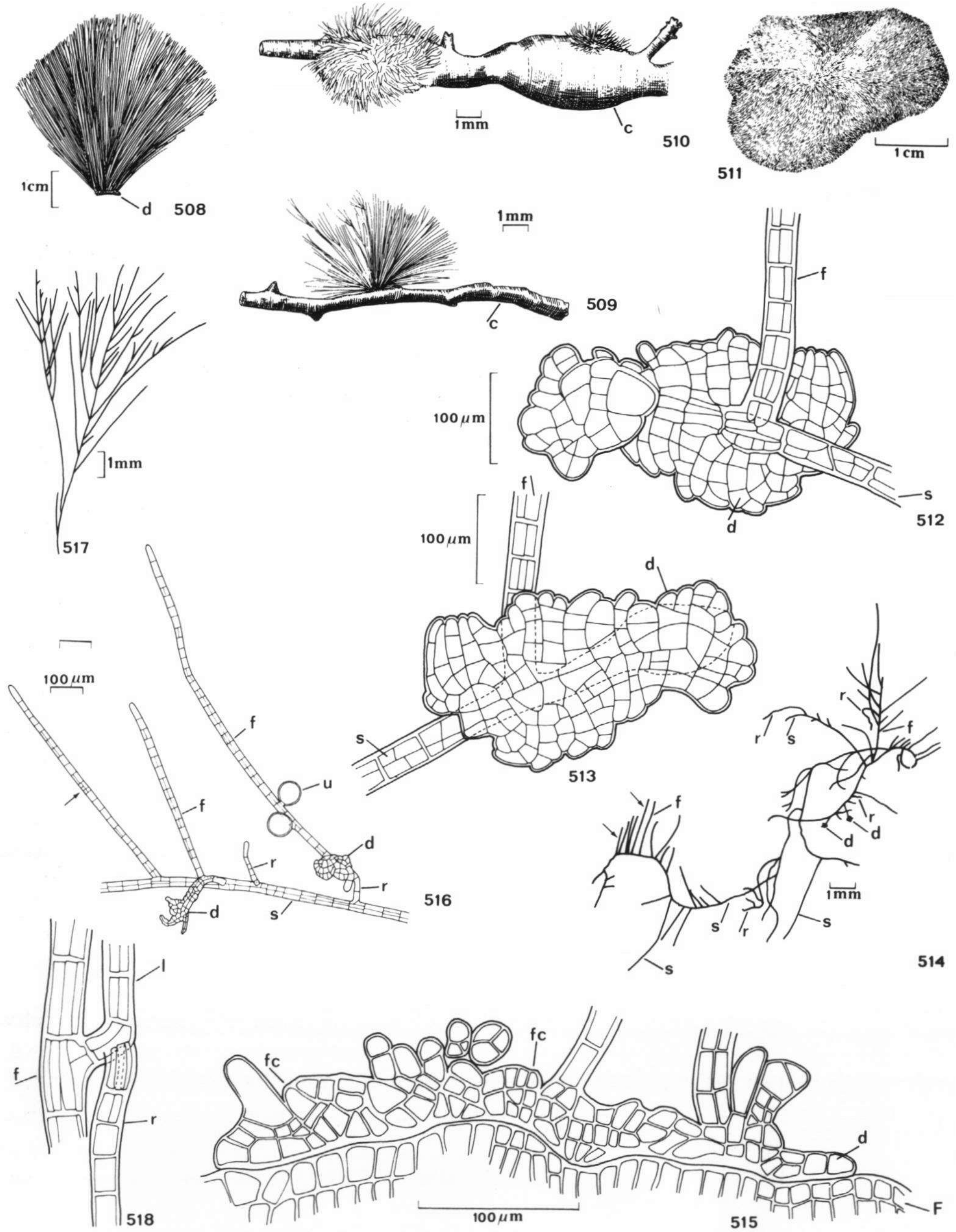


Fig. 508–518. Sphacelaria rigidula. 508–511, 514. Habits; 512, 513, 515, 516. Basal parts; 517, 518. Branching. C. *Cystoseira* spec.; d. basal disc; F. *Fucus vesiculosus*; f. erect filament; fc. vertical file of cells; r. rhizoid; s. stolon; u. unilocular zoidangium. 508, 517. Roscoff, *Prud'homme van Reine 8-1964* (formalin); 509. Island Karak, *Lenormand 314* (L, sheet 937.714-72, holotype of *S. furcigera*); 510. Red Sea, *Schimper* (L, sheet 937.117-229, holotype of *S. rigidula*); 511. Gorishoek, *Huwae* (L, soaked); 512, 513. Culture 68-13-1; 514, 516. Culture 66-10-1; 515. Gorishoek, *Prud'homme van Reine 66-6* (formalin); 518. Culture 66-55-1.

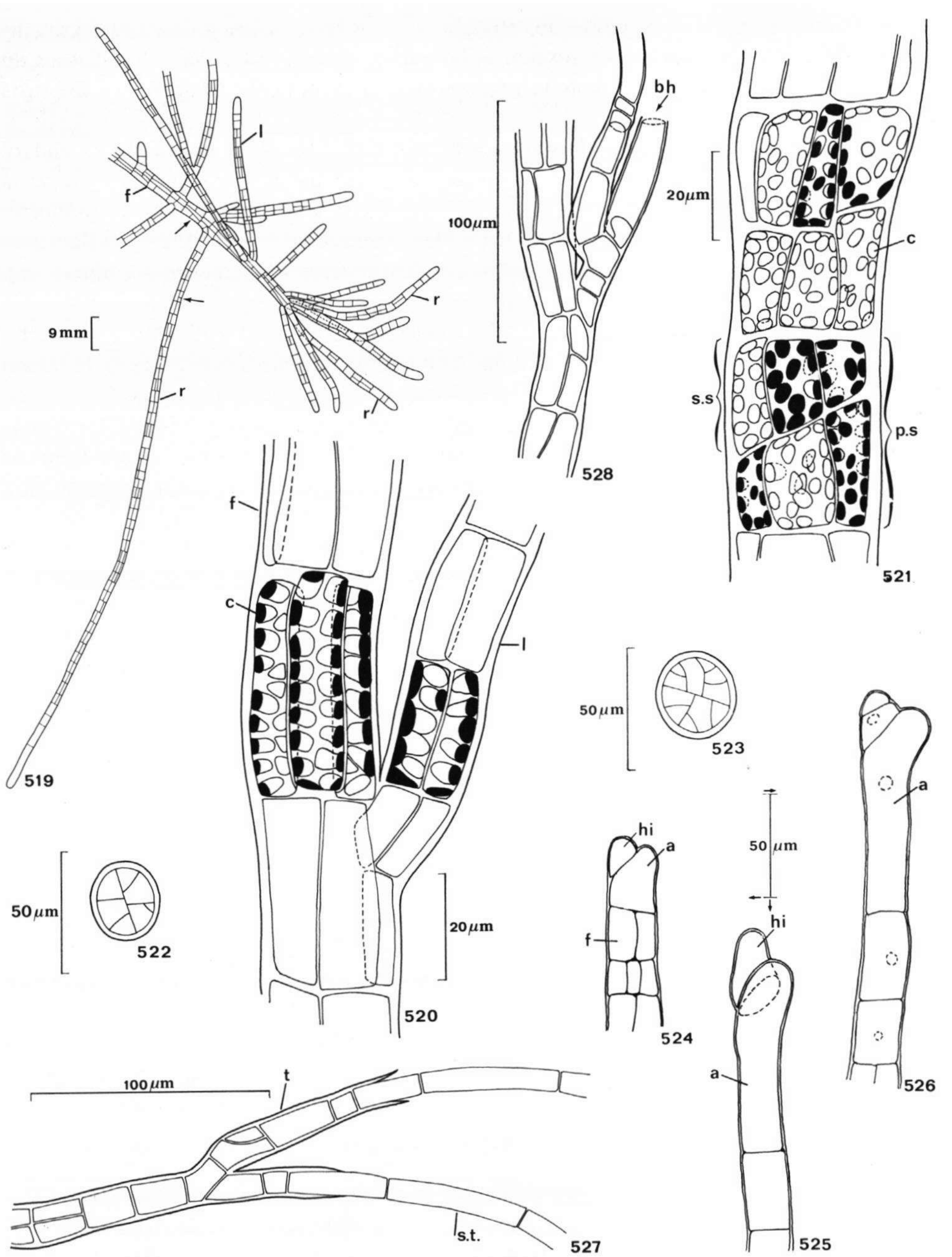


Fig. 519–528. Sphacelaria rigidula. 519–526. Parts of erect filaments (522, 523. Cross-sections). 527, 528. Hairs. a. apical cell; bh. branched hair; c. chloroplast; f. erect filament; hi. hair initial; l. lateral; ps. primary segment; r. rhizoid; ss. secondary segment; st. subterminal hair; t. terminal hair; 519. Culture 66-55-1; 520. Culture 68-32-5; 521. Fife Ness, *Prud'homme van Reine 71-19* (fresh); 522, 523. Roscoff, *Prud'homme van Reine 8-1964* (microslides); 524. Culture 66-41-4; 525, 526. Culture 66-25-3; 527, 528. Culture 66-25-1.

smaller. Often several laterals grow into straight or irregularly twisting downward growing rhizoids (fig. 519), or rhizoids are formed as laterals of the second order. The rhizoids do not form a cortication, but by their intricate growth they bind the filaments of the tufts together.

The dimensions of the usually elongate apical cells (fig. 516; 519) and of the secondary segments are very variable. Often the secondary segments are longer than they are wide (fig. 516; 520), but in old filaments or in laterals secondary segments are frequently shorter than they are wide (fig. 521; and f. 4–8 in De Haas-Niekerk, 1965). In the erect filaments the inferior secondary segments are occasionally longer than the superior secondary segments.

The secondary segments are subdivided by radial and semi-radial walls into a parenchymatic tissue without subdivision into medullar and peripheral cells (fig. 522; 523). In lateral view (0–) 1–4 (–6) longitudinal walls can be observed in secondary segments. In the cells secondary transverse walls occur occasionally and in variable number (fig. 516; 519, arrows).

Solitary hairs are absent, scarce, or abundant (fig. 524–528). Propagules are frequent on the distal parts of the erect filaments in specimens collected in late spring, summer, and autumn. Mature propagules consist of a narrow, straight, cylindrical, or slightly broadening stalk and (1–) 2–3 (–4) narrow, straight, divaricate, cylindrical arms (fig. 529–533). Both stalk and arms consist of a variable number of secondary segments, which are subdivided by 0–2 longitudinal walls. Usually all arms are of the same length. A small, lenticular, apical cell is formed between the arms on top of the stalk (fig. 529; 530). This lenticular cell never grows into a hair, but occasionally it may form an additional arm (fig. 534–536). The terminal cells of the arms of the propagules occasionally grow into (1–) 2–3 new arms and a small lenticular cell again, and this process may be repeated several times (fig. 530). The basal cell of a propagule persists on the filament as a unicellular stalk after the propagule has been shed. It often forms new propagules.

Unilocular zoidangia occur occasionally scattered on the filaments of specimens collected in winter. Usually their bent stalks are unicellular (fig. 538; 539), occasionally a new unilocular zoidangium may be formed laterally from these unicellular stalks (fig. 540). Unilocular zoidangia are globular, ovoid, or obovoid when mature, clavate when young. Unizoids are pear-shaped, with 1–9 small chloroplasts and an eye-spot.

Plurilocular zoidangia are very rare on specimens collected in Europe, but Van den Hoek & Flinterman (1968) found them on cultured specimens originating from Hoek van Holland. They found and figured microzoidangia and macrozoidangia of stout-cylindrical or spherical (rarely elongate-cylindrical) form on short 1–3-celled stalks, which are unbranched or branched and then monochasial or dichasial (see also my fig. 541–544). They also described female gametes with several brown chloroplasts and an eye-spot, and male gametes with one chloroplast and an eye-spot.

Dimensions: Plants 3–30 (–70) mm high and confluent low mats covering an area of a few cm^2. Diam. basal discs 100–300 μm. Stolons 30–100 μm in diam., rhizoids 7–20 (–25) μm in diam. Angle of ramification (0–) 15–45 (–90)°. Diam. of erect filaments (10.5–) 16–45 (–52) μm. Height of secondary segments 20–80 (–100) μm. Diam. of hairs 11–16.5 μm (with sheath) or 7–14 μm (without sheath). Chloroplasts 4–9 X (2–) 3–6 μm in surface view (fig. 520; 521). Stalks of propagules 150–200 (–290) X 20–23 (–25) μm, arms 100–250 (–400) X 15–20 (–25) μm. Unilocular zoidangia (40–) 45–75 (–90) X

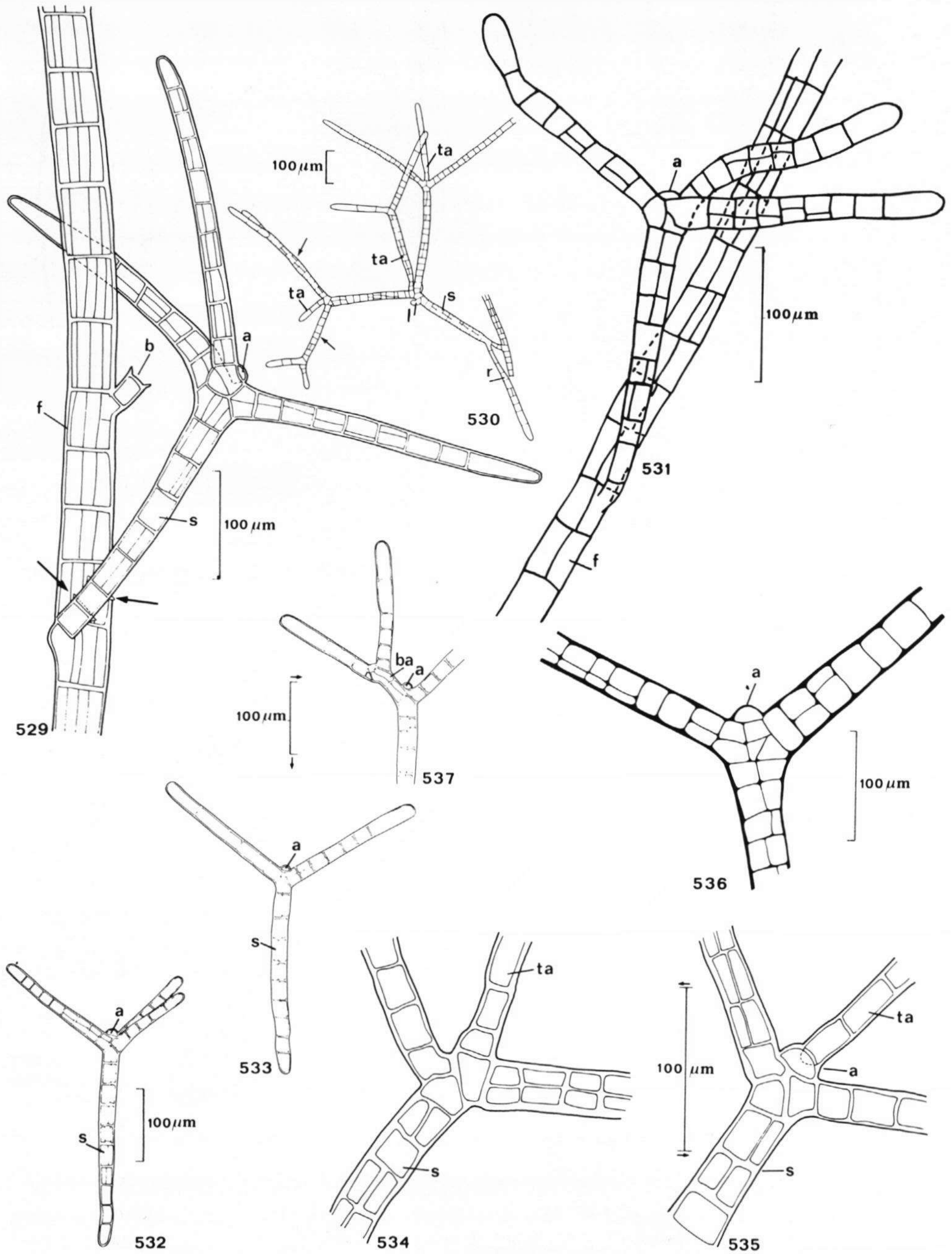


Fig. 529–537. Sphacelaria rigidula. Propagules. a. apical cell; b. basal cell of a shed propagule; ba. branched arm; f. erect filament; l. lateral; r. rhizoid; s. stalk; ta. terminal arm. 529, 530. Hoek van Holland, *Van den Hoek*, spring 1960 (culture); 531. Paignton, Holmes Exsicc. n. 123 (BM, soaked); 532, 533. Muggia, *Pignatti* (TSB, microslide); 534–537. Culture 66-57-3.

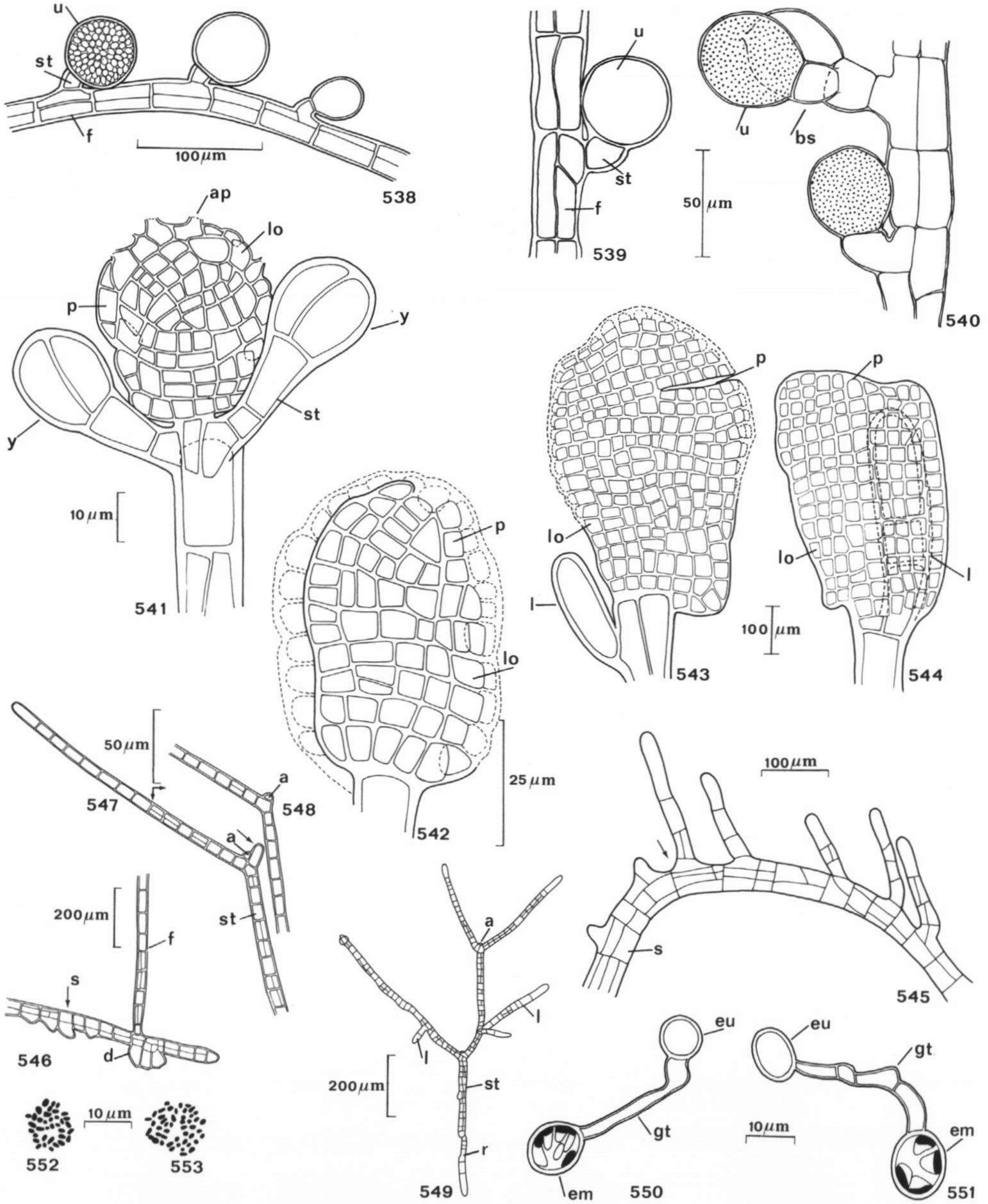


Fig. 538–553. Sphacelaria rigidula. 538–540. Unilocular zoidangia; 541–544. Plurilocular zoidangia (541, 542. Macro; 543, 544. Micro); 545, 546. Basal parts; 547–549. Propagules; 550, 551. Germinating unizoids; 552. Mitosis-metaphases (or early anaphases) or diploid nuclei of secondary segments in erect filaments. a. apical cell; ap. aperture; bs. branched stalk; d. basal disc; em. embryospore; eu. empty unizoid; f. erect filament; gt. germination tube; l. lateral; lo. loculus; p. plurilocular zoidangium; r. rhizoid; s. stolon; st. stalk; u. unilocular zoidangium; y. young. 538. Culture 71-30; 539. Culture 66-12-1; 540. Culture 66-55-2; 541–544, 552, 553. Hoek van Holland, *Van den Hoek*, spring 1960 (Cultures: 541 in formalin; 542–544 soaked; 552, 553 microslides, coloured with acetocarmine). 545. Culture 66-34-2; 546. Culture 66-15-2; 547, 548. Culture 66-41-2; 549. Culture 66-60-9; 550, 551. Culture 66-6-2.

(35–) 40–75 (–90) μm. Unizoids 7–13 X 5–9 μm. Plurilocular macrozoidangia (34–) 57–126 (–200) X (25–) 37–58 μm, diam. loculi 5–10 μm. Microzoidangia (43–) 50–72 (–91) X 33–47 (–68) μm, diam. loculi (2.5–) 3.5–5.5 (–7.5) μm. Female gametes 4–13 μm long and male gametes 3–7 μm long (Van den Hoek & Flinterman, *l.c.*, p. 207).

Distribution. Europe: Faeroes, Norway, western Sweden, Denmark, Heligoland, The Netherlands, Belgium, United Kingdom, Eire, France (Atlantic and Mediterranean coasts), northwestern Spain, Portugal, Italy, Yugoslavia, Greece. Also on the Mediterranean coasts of Syria and Israel, on the Atlantic coasts of Morocco, on Madeira, and on the Canary Islands.

The species is also mentioned from many localities in Africa, America (North, Middle, and South), Asia (Red Sea, Persian Gulf, Indian Ocean, South China Sea, Japan, Australasian Archipelago), Australia, New Zealand, and on many of the islands in the Pacific Ocean.

European localities (and some localities on the coasts of northern Africa and western Asia) have been listed and are given in fig. 554.

For an extract of the list of collections and references see below.

FAEROES. Two collections.

NORWAY. Sör Trondelan. Trondhjemsfjord: Selva, littoral, *Polderman*, 17/8/1973 (L).—Hordaland. Five collections/references.—Rogaland. Espevaer: (as *S. olivacea*), *Gran*, 7/1891 (O). —Vest Agder. Svinör (Sauvageau, 1902, p. 399 = R. 212).—Aust Agder. Hövåg: on stipes of *Laminaria hyperborea*, 10–15 m deep, *Rueness*, 31/7/1964 (L).

SWEDEN. Bohuslän. Three collections/references.

DENMARK. Skagerrak. Off Hirtshals: 11–13 m deep, on *Laminaria hyperborea, Rosenvinge 6627*, 11/8/1899 (C).—Kattegat. Four collections/references.—Samsø area. Aarhus Bugt: Abelshoved, 400 m from the coast, 4–5 m deep, on algae, *Mathiesen 2-3*, 9/8/1972 (L).

GERMANY. Heligoland. More than five collections.

THE NETHERLANDS. Noord-Holland. Three collections.—Zuid-Holland. Four collections.—Zeeland. Schouwen-Duiveland: two collections. St. Philipsland: two collections. Tholen: more than seven collections. Noord-Beveland: Zandkreek, Kortgene, *Ascophyllum*-belt, (as *S. fusca*), *Brakman*, 14/11/1941 (L). Zuid-Beveland: more than six collections. Walcheren: more than five collections/references. Zeeuws Vlaanderen: four collections.—Noord-Brabant. Three collections, amongst which Kraaienberg, salt-marsh, dominant in undergrowth in pioneer-vegetation of *Spartina, Prud'homme van Reine* in: Algae Zeelandiae n. 69 (L, and many other herbaria).

BELGIUM. Zeebrugge: Pier, *De Vos*, 8/3/1979 (L).

UNITED KINGDOM. Shetland. Three collections/references.—Orkneys. Five collections/references.—Scotland. Ross & Cromarty: two collections/references. Argyll: Colonsay (Norton *et al.*, 1969, p. 130, as *S. fusca*). Bute: two collections. Fife: six collections. Midlothian: Inchkeith, shady rocks, (as *S. fusca*), *Irvine*, 11/8/1966 (L). East Lothian: two references.—Isle of Man. Five collections/references.—Wales. Anglesey: more than four collections/references. Caernarvon: Nevin Bay, (as *S. fusca*), *Schiller* in Schiffner: Algae mar. exs. n. 1204 (BM, L, S, W, WU). Cardigan: Aberystwyth, (as *S. cirrhosa*), *biology student excursion 114* (U). Pembroke: three references.—England. Northumberland: Berwick-upon-Tweed (Norton, 1976, p. 23, as *S. fusca*). York: Filey Brigg (Goodband, 1968, p. 132). Cornwall: five collections/references. Devon: five collections/references, amongst which Paignton, (as *S. fusca*), Holmes in: Algae Brit. rar. exs. n. 123 (BM, in other herbaria this number is *S. cirrosa*). Dorset: two collections/references.—Channel Islands. Three collections/references.

EIRE. Donegal: three collections/references. Galway: two collections. Kerry: two collections. Dublin: Dún Laoghaire, in rock pools, in *Ascophyllum* belt, *Houthuesen 66-38*, 31/7/1966 (L). Wicklow: Greystones, littoral pools, *Prud'homme van Reine 66-34*, 27/7/1966 (L).

FRANCE. Atlantic coasts. Pas de Calais: seven collections/references. Calvados: eight collections/references, amongst which Port-en-Bessin, (as *S. fusca*), *Fortin* in Algues de France n. 209 (L). Ille-et-Vilaine: six collections. Côtes du Nord: three collections. Finistère: more than ten collections/references, amongst which without exact locality, (as *S. cirrosa*), Crouan in: Algues mar. Finist. n. 33 (CO, in most other herbaria this is *S. cirrosa*), (as *S. cirrosa* var. *fusca*), Algues mar. Finist. n. 35 (M), and St. Guénolé, *Pelletier* in: Algues de France n. 209 (L). Morbihan: three collections. Pyrénées Atlantiques:

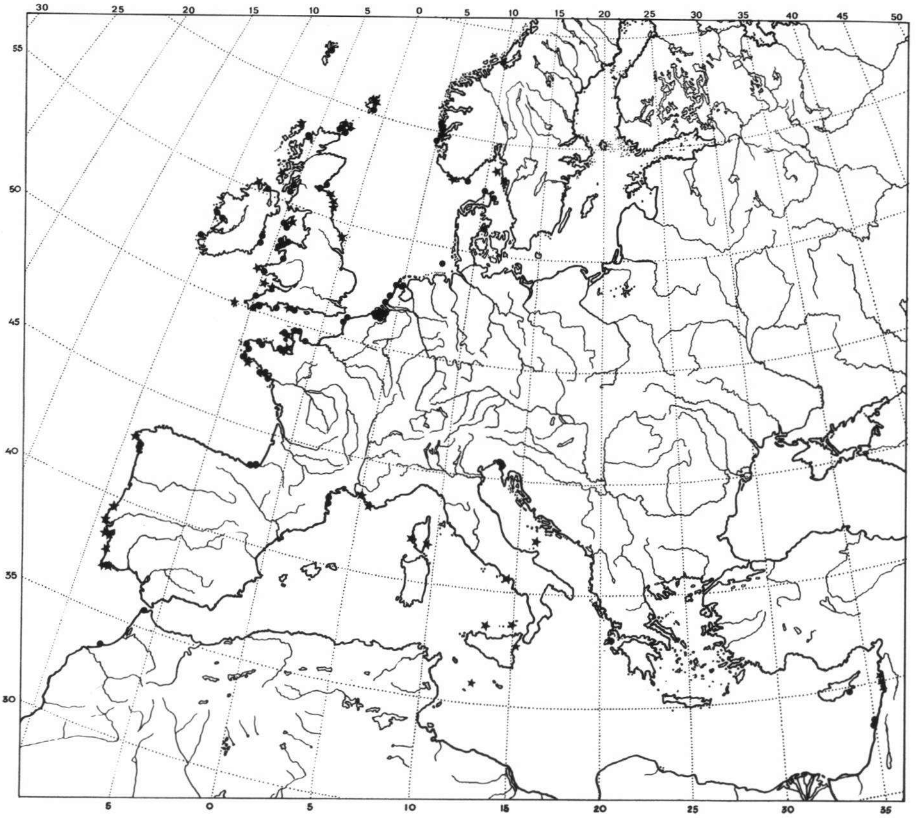


Fig. 554. Distribution of *S. rigidula* in Europe

● = Material seen by author.
★ = According to literature, most probably *S. rigidula.*

many collections.—Mediterranean coasts. Pyrénées Orientales: two collections. Bouches du Rhône: Riou Archipelago, Ilot du Grand Congloué (Magne, 1956, p. 182, as *S. fusca*). Var: Tour Fondue, Presqu'île de Giens (Boudouresque, 1971, p. 143). Corsica: two references.

SPAIN. Galicia. More than six collections.

PORTUGAL. Estremadura: four collections/references. Baixo Alentejo: Sines (Ginsburg-Ardré, 1963, p. 376, as *S. fusca*). Algarve: three references.

ITALY. Campania: Salerno & Calabria: Réggio di Calabria (Giaccone, 1969, p. 499, as *S. fusca*). Sicilia: four references. Venezia-Giulia: three collections. Puglia: Testa del Gargano (Giaccone, 1969, p. 499).

YUGOSLAVIA. Istra: Rovinj (Sauvageau, 1901, p. 368 = R. 145). Dalmatia: Ilot de Jabuka (Ercegović, 1957, p. 56).

GREECE. Ionian Archipelago: (as *S. nana*), *Mazziari* (W). Aegean: without exact locality (Giaccone, 1968, p. 223).

CYPRUS. Cape Pyla: Cohen 2181, 26/10/1969 (TELA).

SYRIA. Very common (Mayhoub, 1976, p. 135).

ISRAEL. Six collections.

MOROCCO. Tanger, (as *S. secundata*), Algae Schousboeanae n. 114, 12/1827 (PC, mixed with *S. cirrosa*). Atlantic coasts: three collections/references.

MADEIRA. Porto Santo: Punta Calleta, on *Cystoseira discors*, together with *S. cirrosa*, *CANCAP 792*, 16/10/1978 (L). Madeira: Caniçal, harbour mole, 0–3 m deep, *CANCAP 1038*, 20/10/1978 (L).

CANARY ISLANDS. Gran Canaria. Two collections/references.—Tenerife. Six collections. —Hierro. Punta Restinga: tidal pool, CANCAP 360, 3/9/1977 (L).

Notes on nomenclature. (1) See notes on nomenclature 1 of *S. fusca* (p. 222).

(2) Holmes & Batters (1891), Irvine (1956), Goodband (1971), and Russell & Fletcher (1975), considered British specimens of *S. fusca* and specimens of *S. rigidula* as belonging to one single species. Reinke (1891) incorporated the extra-European species *S. biradiata* Askenasy into his descriptions of *S. furcigera*. De Haas-Niekerk (1965) figured as *S. fusca* in her figures 14–16 and 21 and 22 details of a specimen of *S. cirrosa*.

Notes on morphology. In the secondary segments of *S. rigidula* only few longitudinal walls are formed. All walls are more or less radial, never periclinal. The sequence of the formation of the longitudinal walls, as can be observed in cross-sections, have been described by Askenasy (1888, p. 21) and by Zimmermann (1925, p. 18). De Haas-Niekerk (1965, f. 27a–c) figured cross-sections of filaments of *S. rigidula* (as *S. fusca*), but she did not discuss these figures in the text. Her figures agree with my figures 522; 523.

Primary laterals are formed by hemiblastic branching of young secondary superior segments. These segments may carry one (occasionally more) somewhat protruding cell, containing a large nucleus and much dense protoplasm. These cells grow into the primary laterals without much delay. Zimmermann (1925, p. 18) and Zimmerman & Heller (1956, p. 293) called the initials of laterals (and comparable cells from which propagules arise) 'perizyten' (= pericysts). The initials in *S. rigidula* are, however, inconspicuous and are not comparable to the marked pericysts as described for *S. radicans*. All mature cells of the filaments are peripheral and in consequence they all can function as branch-initials. Usually only cells of superior secondary segments form laterals, but occasionally laterals arise from inferior secondary segments too (fig. 545, arrow).

Laterals of the first order arise in an irregular helicoid pattern and in a rough acropetal sequence. Laterals of the second and third order may arise in a later stage of growth; they are formed without order. All laterals have indeterminate growth. In dense bushes growing epiphytically on other algae in summer most laterals grow almost parallel to the main filament (fig. 517). The main filaments and laterals grow until they have reached a common height, resulting in a flat or semi-globular outline of the bushes (fig. 508). In less dense tufts the angle of branching is usually quite variable (fig. 518; 519), and in these cases the branching-system as a whole does not show any sign of determinate growth.

Usually the erect parts of the plants are more prominent than the creeping parts, but occasionally the creeping parts are more conspicuous (fig. 514). Most erect filaments are straight and show only small gradual changes in diameter. Stolons and rhizoids, however, may be quite tortuous and the diameter of their secondary segments may vary considerably, sometimes resulting in an undulating outline of these filaments (fig. 521).

Basal discs of *S. rigidula* are usually small and monostromatic (fig. 512; 513; 516). They are often formed by rhizoids or stolons which happen to meet a suitable substrate (fig. 514; 516). Usually basal discs are formed terminally on stolons, rhizoids, or their laterals, but sometimes basal discs are formed by lateral proliferation of stolons (fig. 546). Occasionally polystromatic basal discs can be formed by large specimens growing on a smooth substrate (fig. 515). In a deep tidal pool near Morgat, France, I observed *S. rigidula* growing on *Padina* *pavonica*. These plants formed several minute tufts and long stolons which were not prostrate but formed an arch. A new minute tuft was formed on the spot where the several mm long arch of the stolon re-encountered the *Padina* thallus. From the new minute tuft usually one or more new arch-forming stolons arose and so this way of growth was similar to that of stoloniferous strawberry-plants. In suitable substrates (*Codium*, some Fucaceous algae*)* *S. rigidula* may form an extensive endophytic network of long rhizoids or even a sub-epidermal endophytic basal disc. This endophytic way of growth had been described as a specific character for *S. rigidula* (as *S. furcigera*) by Reinke (1890a, p. 208 & 1891, p. 14 & t. 4, f. 5–13) and many other authors (including Goodband, 1971, p. 979 who still used endophytism as the main character to separate *S. fusca* and *S. furcigera*). Sauvageau (1901, p. 370 = R. 147), however, mentioned already epiphytic and epilithic growth of *S. rigidula* (as *S. furcigera*) in Guéthary (France) and other European localities.

Hairs in *S. rigidula* are acroheteroblastic or terminal and always solitary (fig. 524–528). There is no relation between hairs and laterals in this species—hairs and laterals seem to be independent of each other. The hairs may be very long, but often only the sheaths can be traced in older filaments. Occasionally a hair may be branched (fig. 528).

Proliferations are often frequent. De Haas-Niekerk (*l.c.*, f. 29) figured small ones, Van den Hoek & Flinterman (1968, f. 12–14; 17–20; 34, 35), who called these proliferations nodules, observed that the nodules may develop into basal discs. See also my figure 516. There is no strict difference between small proliferations and the formation of narrow laterals from broad stolons (fig. 545).

Notes on ecology. *Sphacelaria rigidula* can be found on rocks and on other algae in many localities all over the world. In Europe it is particularly common in tidal pools in the littoral and in between the small filamentous algae forming the undergrowth of vegetations of Fucaceous algae. It is, however, also found on *Laminaria* stipes, other algae, shells, and spider-crabs in the sublittoral in Scandinavia, Scotland, southwestern France, northwestern Spain, and in Yugoslavia. In warmer seas it is frequently epiphytic (often partly endophytic) on *Cystoseira, Sargassum*, and other *Fucales*. When growing in tidal pools *S. rigidula* often grows in and on the *Corallina*-turfs. Zimmermann (1925, p. 17) and Goodband (1968, p. 131–132) gave lists of algae on which they found *S. rigidula* (as *S. fusca*) on Heligoland and on the coasts of the British Isles respectively.

Sphacelaria rigidula can occasionally be found together with *Rhodochorton floridulum*, *S. radicans*, and *Cladostephus spongiosus forma spongiosus* on sandy rocks, where these algae function as sand-binding organisms. I observed this sand-binding vegetation in Yerseke and Katse Veer in The Netherlands, on the Pointe de la Crèche, Wimereux, France and in the Bush, near the Bridge of Waith, Orkney Mainland. Den Hartog (1959, p. 152, as *S. fusca*) noted this vegetation at the Pointe aux Oies, Wimereux, France, and Goodband (1968, p. 132) noted it at Penmon, Anglesey, Wales and Filey Brigg, Yorkshire, England. In Gorishoek, Tholen, The Netherlands, *Huwae* collected small stones on which he found a sand-binding vegetation dominated by *S. rigidula* (fig. 511).

On salt-marshes sand-binding vegetations dominated by *S. rigidula*, can be found in pioneer vegetations of *Spartina townsendii.* In the most exposed and lowest parts of some sandy salt-marshes isolated groups of *Spartina* occur, with as undergrowth a 1–2 cm thick algal turf, dominated by *S. rigidula.* This algal turf may cover several square metres. The

Spartina—S. rigidula combination has only been found so far in The Netherlands in the province of Zeeland.

Sphacelaria rigidula may also form confluent mats, or a low algal turf of gregarious specimens, on vertical rocky substrates which have a constant supply of water flowing down. I observed these dark-brown algal mats on the northern side of the ruined Fort du Croï, Wimereux, France and at the outer side of the wall of an enlarged rock-pool, used as a swimming pool at Punta Ancha, Guia, Gran Canaria. On woody substrates *S. rigidula* may grow in a higher part of the littoral than when growing on rocks and stones. Occasionally it has been found growing together with *S. nana* on wooden poles in The Netherlands (Hoek van Holland, Zuid-Holland; Gorishoek, Tholen; Yerseke, Zuid-Beveland; and Vlissingen, Walcheren). Rhizoids of *S. rigidula* may enter the vessels of the wood, but the special mode of growth encountered in *S. nana* has not been evolved.

Sphacelaria rigidula is a genuine marine species. It does not enter very far into narrow sheltered bays or estuaries. In Hardangerfjord (Jorde & Klavestad, 1960, p. 97) and Sullom Voe, Shetland (Tittley *et al.*, 1977, p. 408) it has only been found in the outermost areas. In the Westerschelde (The Netherlands) it has been found in a locality where chlorinity may become as low as 10‰ Cl.

Form range and cultures. Morphological variation in *S. rigidula* is quite conspicuous. The habit of plants growing epiphytically on algae in tidal pools in summer is quite characteristic (fig. 508), but more loose tufts occur as well (fig. 509) or crowded short feebly branched filaments may form felty cushions (fig. 510). These cushions as well as dense or loose tufts may grow together into confluent mats (fig. 511), or algal turf. In the dense penicillate tufts the angle between the main axes and their laterals is usually very small (fig. 517) just as in the crowded short filaments of the felty cushions. In looser tufts, however, and especially in plants creeping parts of which are more prominent than the erect filaments, the angle of branching is quite variable (fig. 514; 519). In these creeping plants perpendicular branching occurs as well as laterals which are almost parallel to the main filaments.

Most specimens from the Red Sea and the Persian Gulf (including the holotype) are very short (2–3 mm) reddish-brown plants (fig. 510). The sample labelled '*Exs. Pl. Pers. austr. Th. Kotschy*, Ed. R. F. Hohenacker 1845, *Ad oram insulae Karek, sinus Persici*, D.jan. 1842, *S. rigida* Hering et Mart.—Mart.', however, consists of a piece of a Fucaceous alga on which there are several olivaceous 7–10 mm high erect penicillate plants of *S. rigidula*. These plants are very similar to the characteristic plants found in summer in southwestern Europe. The holotype of *S. furcigera* (fig. 509) is in all characters intermediate between the holotype of *S. rigidula* (fig. 510) and the Kotschy specimens.

Morphological variation of the creeping parts is also quite conspicuous. In some specimens one or only a few small monostromatic basal discs occur, while in other specimens luxuriant growth of stolons, rhizoids, and basal discs can be observed. The monostromatic basal discs occasionally become polystromatic by upright growth and formation of small files of cells (fig. 515) or by secondary attachment of irregular cell-clumps (nodules) formed by proliferation of degenerating plants (see Van den Hoek & Flinterman, *l.c.*, f. 20).

Cultures have been isolated from material collected from the coasts of The Netherlands (Katwijk, Hoek van Holland, Gorishoek, Mosselhoek, Katse Veer, Sas van Goes, Kattendijke, Vlissingen, and Baalhoek), Eire (Salthill, Dun Loaghaire and Greystones), and France (Cap

Griz Nez, Wimereux, St. Lunaire, St. Efflam, Roscoff, Le Caro, Pointe du Bindy, Morgat, Locmariaquer, Port-Vendres and Collioure). Most of these cultures and their subcultures have been maintained during more than twelve years.

Sphacelaria rigidula grew well in cultures at 4°C, 12°C, and 20°C. Vegetative growth at these temperatures had already been described by Van den Hoek & Flinterman (*l.c.*, p. 200–201). They also observed reduced vegetative growth under very low light-intensities (3–10 Lx) and dominance of prostrate parts in plants grown on partly immersed discs of filter-paper. I agree when they state: 'This suggests that the dominance of the prostrate system in high littoral populations is an expression of environmental modification.' In some of my cultures, however, dominance of the prostrate system occurred in all cases, even in completely immersed specimens. This was especially the case in my cultures of material collected from the shores of the Irish Sea (Dún Loaghaire and Greystone, fig. 545). In some of these Irish cultures, however, longer erect filaments and appressed laterals were formed, on which propagules were often found. Zimmerman (1923, p. 165) studied the growth of *S. rigidula* (as *S. fusca*) at different light-intensities. He observed an increase of rhizoids and a decrease of erect laterals at lower light-intensities. Van den Hoek & Flinterman (*l.c.*, p. 199) stated that a rich production of phaeophycean hairs is indicative of a depleted culture-medium. I observed also a richer production of hairs in older cultures, but on the other hand in some cultures (from Salthill in Eire and from Roscoff, Pointe du Bindy, and Locmariaquer in France) I found always many hairs while other cultures often showed no hairs at all.

Usually in cultures started from isolated fragments of sterile erect filaments the algae did not become attached to the substrate. When fragments of stolons were transferred into new culture-tubes, however, they often attached quite easily and formed plants in which the prostrate system dominated. Only when larger fragments of plants, provided with stolons, rhizoids, and erect filaments, were transferred the new cultures may contain well attached plants with many erect filaments after a few weeks. Often short stolons or rhizoids formed new small monostromatic basal discs. The morphological plasticity of *S. rigidula* is remarkable and as a consequence no taxonomic conclusions can be drawn from the observed variation.

Reproduction and life-history. Van den Hoek & Flinterman (1968) described the life-history of *S. rigidula* (as *S. furcigera*) accurately and extensively. I will summarize and discuss their results and add some more information. Research of Colijn & Van den Hoek (1971) demonstrated a distinct influence of both daylight and temperature on the life-history of *S. rigidula.*

The propagules were not mentioned or illustrated in Kützing's descriptions of *S. rigidula*, but they were present in the type material. Kützing did, however, mention and illustrate the bifurcate propagules in his description of *S. furcigera.* The development of the propagules has been described by Pringsheim (1874, p. 175, as *S. olivacea* var. *solitaria*), Askenasy (1888, p. 21, as *S. furcigera*), Sauvageau (1901, p. 374 = R. 151 as *S. furcigera*), Zimmermann (1925, p. 19 as *S. fusca*), and Zimmermann & Heller (1956, p. 293, as *S. fusca*). In the last-mentioned paper the authors described and illustrated this development in much detail. After formation of the small lenticular apical cell the subapical cell functions like a meristematic apical cell and forms a large inferior primary segment and a smaller superior primary segment. The inferior primary segment soon divides into two secondary segments, but the superior primary segment forms protrusions which grow into the arms of the propagule.

When a propagule is shed, its basal cell remains on the plant (fig. 529) and can form several successive propagules. Often new propagules bear a collar formed by the remnants of walls of their predecessors (fig. 529, arrows, see also Jaasund, 1969, f. 8D). The number of arms is variable (fig. 530–536) and occasionally the arms behave as stalks and form new arms again (fig. 530; 537). This variability of the propagules gave rise to much discussion. Sauvageau (1901, p. 375 & 376 = R. 151 & 152) stated that branching of the arms of the propagules (as described earlier by Reinke and by Kuckuck) is exceptional and accidental in *S. furcigera*, but common in the related extra-european species *S. divaricata* Montagne and *S. variabilis* Sauvageau. I found many of these branched propagules, however, in nature as well as in my cultures. Zimmermann (1925, p. 19) observed 2–4 arms on *S. rigidula* plants collected from the coasts of Heligoland. Three-armed propagules were more common than two-armed ones, and four-armed propagules occurred only occasionally. De Haas-Niekerk (1965) and Goodband (1971) analysed the number of arms of propagules from specimens collected in nature as well as from specimens in culture. Both authors concluded that the proportion of two- and three-armed propagules was extremely variable. Usually all arms of three-armed propagules arise from the sub-apical segment (fig. 531), but occasionally the small lenticular apical cell may grow into the third arm (fig. 534; 535). Goodband (*l.c.*, p. 973) also mentioned occasional examples of one-armed propagules. Sauvageau (1901, p. 375 = R. 152) described these single-armed propagules from specimens collected in the Faroes. I observed several of these propagules in my cultures (fig. 547; 548). The small lenticular apical cells were present, but the subapical cells only formed one arm each. Occasionally a second arm may develop in a later stage of growth (fig. 547, arrow).

Usually propagules are produced in abundance in the warmer months of the year and at temperatures of 12°C or more in culture. Often many shed propagules can be found in culture-tubes, but only occasionally germinating ones. Of the few germinating propagules I observed, most germinated by prolonging their stalks (fig. 532; 533) and others formed laterals (fig. 549), or extended their arms. Development of laterals may also occur in propagules which are still attached to the mother-plant (fig. 530, see also Van den Hoek & Flinterman, *l.c.*, f. 38; 43; 44). Van den Hoek & Flinterman and Colijn & Van den Hoek obtained propagules on all plants grown at 12, 17, and 20°C, when grown at short-day conditions. In my cultures plants with narrow filaments formed often only a few propagules, while plants with broader filaments were usually covered by many propagules at temperatures of 12°C or more.

Unilocular zoidangia have not often been noted on European coasts. Knight & Parke (1931, p. 66 & 111, as *S. cirrosa* var. *fusca*) observed these unilocular zoidangia on the coasts of the Isle of Man in winter and Blackler (1956, p. 66) found them in the last three months of the year around St. Andrews, Scotland. The unilocular zoidangia described by De Haas-Niekerk (1965, p. 148) for *S. fusca* do not belong to *S. rigidula*. I only once observed unilocular zoidangia on specimens collected from nature (Cap Griz Nez, France, 8-3-1968). The unilocular zoidangia obtained in culture (4°C) by Van den Hoek & Flinterman did not differ from those described from extra-European localities (Askenasy, 1888, p. 21 and Jaasund, 1969, p. 261). The results of Colijn & Van den Hoek (1971) give some indications that short-day conditions might have an influence on the formation of unilocular zoidangia, but the evidence is inconclusive. In my own cultures I obtained unilocular zoidangia at 4°C and short-day conditions (material originating from Gorishoek, Katse Veer, Kattendijke, Yerseke, and Baalhoek in The Netherlands, from Salthill in Eire, and from Wimereux, Roscoff, and Pointe du Bindy in France).

Van den Hoek & Flinterman observed characteristic stages of meiosis in the initials of unilocular zoidangia. Sex determination takes place at meiosis and about one half of the unizoids grow into male haploid plants, and the other half into female plants. Unizoids escape from the mature unizoidangia in the same way as described by me for *S. radicans* (p. 78). When dehiscence of unizoidangia was observed in a sodium-alginate solution the unizoids sometimes formed aggregates or the undivided contents of unilocular zoidangia were released. I observed these aggregates in *S. radicans* and I suppose that the sodium-alginate is the main cause for their existence. In the culture-experiments of Van den Hoek & Flinterman all aggregates died. They observed several chloroplasts in free-swimming unizoids. I observed only one chloroplast in unizoids in a culture from Gorishoek, The Netherlands, but 5–9 chloroplasts in unizoids in a culture from Pointe du Bindy, France. I once observed germination of unizoids in a culture (fig. 550; 551) very similar to the germination of parthenogenetically developing macrozoids as described by Van den Hoek & Flinterman.

The haploid plants form plurilocular gametangia. They have been described and drawn by Sauvageau, Van den Hoek & Flinterman, and by Jaasund. All these authors distinguished microgametangia and macrogametangia. The dimensions of the gametangia, as given by these authors, differ much from each other (see table XV). In my cultures I never obtained plurilocular gametangia of *S. rigidula*, but I made measurements on soaked herbarium samples (and one sample preserved in formalin and seawater) of original cultures used by Van den Hoek & Flinterman for research on the life-history of *S. rigidula*. See also fig. 541–544. The dimensions I measured in these soaked herbarium samples are in agreement with the dimensions measured in the figures published by Van den Hoek & Flinterman for the macrogametangia. Of the four types of macrozoidangia distinguished by these authors I found only their types ‘a’, the stout cylindrical type. About the microzoidangia the authors gave less information, and they published details of only one (f. 46). The dimensions of that particular microzoidangium are larger than those of the microzoidangia I observed in soaked herbarium samples.

In the herbarium of the British Museum (Natural History) I observed filaments of *S. rigidula* mixed with those of *Stypocaulon scoparium* forma *scoparioides*. The plurilocular reproductive organs attached to the filaments of the *Sphacelaria* were well-preserved and the walls of the loculi seem to be quite persistent. For that reason I consider them as macrozoidangia. The dimensions of the supposed macrozoidangia are intermediate between those published by Sauvageau and by Jaasund (table XV). Macrogametangia observed in specimens from Morocco are smaller (table XV). The small number of loculi observable in the Arran specimens is also in agreement with the figures of macrozoidangia by Sauvageau and by Jaasund. In all published figures of microgametangia the numbers of loculi are more comparable to one another. The comparison of dimensions of gametangia of populations from localities scattered all over the world does not result in usable characters in this species. For that reason I mentioned only the dimensions of the gametangia obtained in cultures from Hoek van Holland material in the description of the European *S. rigidula*.

TABLE XV. Plurilocular gametangia in S. rigidula

(all dimensions in µm)

origin	microzoidangia		macrozoidangia	
	1 x b	diam. loculi	1 x b	diam. loculi
1	45–65 x 24–28	c. 3	30–45(–60) x 28–40	c. 6
2			49–61 x 26.5–32	4–5
3	(91 x 49)	3.5–7.5	(34–)61–125(–200) x (25–)45–58	6–10
4	43–65 x (29–) 33–47 (–68)	2.5–5.5	57–68(–78) x 43–58	5–9
5	60–83 x 25–28	c. 3	40–48 x 25–28	5–6
6			31–34 x 22–26	5–6

1. Sauvageau, 1901, p. 378 = R. 154 + f. 35, as S. furcigera, originating from Dirk Hartog Island, Australia.
2. Specimens collected by Barton, mixed in between Stypocaulon scoparium forma scoparioides from Arran, August 1892 (BM, soaked). Classification as macrozoidangia based on persistence of walls of loculi.
3. Van den Hoek & Flinterman, 1968 (as S. fusca). Dimensions of gametangia measured from their figures. Of the microgametangia only one had been figured. Dimensions of loculi mentioned in the text (p. 207).
4. My own measurements made on soaked herbarium specimens of samples of cultures of Van den Hoek & Flinterman.
5. Jaasund, 1969, p. 262 + f. 8, as S. furcigera.
6. From specimens from Aïn Seba, Morocco, Gattefossé 119, 20/3/1929 (MPU, soaked).

The plurilocular gametangia were obtained in cultures at 4°C and 12°C by Van den Hoek & Flinterman. Colijn & Van den Hoek found them at 4°, 12°, and 17°C when cultured in long-day conditions, but never in short-day conditions. At 17°C the plurilocular gametangia were only initially formed in these experiments, soon they were succeeded by propagules. In the few cases where plurilocular zoidangia have been found in nature they occurred in the warmer months. Jaasund (1969, p. 262) found a few propagules on these plants. The observation of Sauvageau (1901, p. 372 = R. 148), stating that the filaments of plants with plurilocular zoidangia are narrower than filaments of plants with unilocular zoidangia (or with propagules) has been confirmed by Van den Hoek & Flinterman (*l.c.*, p. 203). They observed that the robust diploid plants grow more vigorously than the narrow haploid plants. In my cultures specimens with narrow filaments (supposed to be haploid) formed less easily propagules than specimens with broader filaments, which were supposed to be diploid. Probably most specimens of *S. rigidula* with propagules in nature are diploid plants. The small male gametes in the cultures of Van den Hoek & Flinterman each contained a rudimentary pale yellowish chloroplast and a distinct eyespot, while the larger female gametes each bore several brown chloroplasts, on one of which was the red eyespot. Copulation of male and female gametes has been observed, but many female gametes germinated parthenogenetically (see f. 91–111 of Van den Hoek & Flinterman). Three types of offspring have been found as a result of copulation-experiments of male and female gametes: haploid female gametophytes (from macrogametes which germinated parthenogenetically), diploid sporophytes, and occasionally also haploid sporophytes. These haploid sporophytes were apparently also formed from macrogametes which germinated parthenogenetically. Their filaments were as narrow as filaments of the gametophytes, but they formed unilocular zoidangia which were not able to produce viable zoids. These unilocular zoidangia were small (compare f. 31 of Van den Hoek & Flinterman with their f. 37a), and are probably comparable to the mini-zoidangia as described for *S. nana* (p. 110).

Van den Hoek & Flinterman also carried out caryological investigations on plants from cultures. They found a diploid number of 50–60 chromosomes and a haploid number of 25–30. My own counts of diploid nuclei of *S. rigidula* obtained from the original cultures of Van den Hoek & Flinterman resulted in an estimate number of 35–46 chromosomes (fig. 552, 553). They concluded that *S. rigidula* (as *S. furcigera*) is a feebly heteromorphic, anisogamous diplohaplont and summarized their results in a conveniently arranged diagram (*l.c.* p. 208, see also my fig. 23). It is imaginable that some of the plurilocular zoidangia described in literature are asexual plurilocular zoidangia not mentioned in the diagram.

Systematic position. There has been much discussion about the possibilities and the necessity to separate *S. furcigera* from *S. fusca* and other related species. For a review of the criteria used see table XVI. Sauvageau based his description of *S. fusca* mainly on the same material Harvey used in 1848. Zimmerman (1923, p. 113 and 1925, p. 17), however, described p. 224 and table XVII.
incorporated in his '*S. pennata* var. *fusca*' *S. rigidula* with propagules with three arms as well as *S. fusca* (Huds.) S. F. Gray sensu Harvey. Goodband (1971) followed this point of view. De Haas-Niekerk (1965, p. 150) synonymized *S. furcigera* Kütz. with *S. fusca* (Huds.) Ag., and Van den Hoek & Flinterman (1968, p. 213) accepted her conclusions but preferred to use the name *S. furcigera* Kütz. In my opinion it is still necessary to separate the common *S. rigidula* (which name has to be used for the taxon described by Zimmerman and De Haas-Niekerk as *S. fusca* and by Van den Hoek & Flinterman as *S. furcigera*) from the rare *S. fusca*. The main differences between these two taxa are the diameter of their erect filaments which are 16–45 μm in *S. rigidula* and 35–80 μm in *S. fusca*. For comparison of *S. fusca*, *S. rigidula*, and of *S. cirrosa* see p. 224 and table XVII.

The criteria which Sauvageau (1901) used to distinguish *S. divaricata* Montagne and his newly described *S. variabilis* from *S. rigidula* (as *S. furcigera*) are irrelevant. As described before (p. 215) branching of the arms of the propagules is frequent in *S. rigidula*, and it cannot be used as a taxonomic character. I will not yet synonymize both taxa with *S. rigidula* because I have not studied these extra-European taxa in detail. For the same reason I do not yet incorporate species like *S. ceylanica* Sauvageau, *S. subfusca* Setchell & Gardner, and many of the new species described by Takamatsu (1943) into *S. rigidula*, although I suppose that they are all closely related.

The propagules of *S. rigidula* have never an apical hair and their arms are straight, cylindrical, and never constricted at their bases. As Zimmerman & Heller (1956, p. 293, as *S. fusca*) described, the formation of the propagules is quite different from the formation of propagules of the *cirrosa*-type or of the *tribuloides*-type. For this reason I wish to separate *S. rigidula* from these other species of the subgenus *Propagulifera* and to place it in the section *Furcigerae*.

TABLE XVI. Comparison of S. rigidula (= S. furcigera) and related species in literature

	hairs	height of tufts in mm	endophytism	number of arms in propagules	diameter of filaments in µm	dimorphic plurilocular zoidangia
Sauvageau, 1901, 1902:						
S. furcigera	+	2–30	+	(1–) 2	16–45	+
S. divaricata	+	2–20	+	2–6 x 2	20–30	0
S. variabilis	-	5	+	1–2 x 2–3	30–50	0
S. intermedia	+	2–4	+	0	20–80	+?
S. ceylanica	-	3	+	0	12–20	-
S. fusca	+	20–30	-	(2–) 3	60–80 (–110?)	0
Zimmermann, 1925:						
S. furcigera	0	0	+	2	0	0
S. fusca	+	0	+?	2–4	35–46	-
Irvine, 1956:						
S. furcigera	+	c. 10	+	2	20–30	0
S. pennata var. fusca	0	0	-	3	0	0
De Haas-Niekerk, 1964:						
S. fusca (incl. S. furcigera)	+	5–30	-	2–3	20–45	0
Goodband, 1971:						
S. fusca	-	0	-	(1–) 2–3 (–4)	10–70	-
S. furcigera	+	<5	+	2	45–45	+

+ = present; - = absent; 0 = not mentioned

TABLE XVII. Comparison between S. rigidula, S. fusca, and S. cirrosa with narrow filaments

characters	S. rigidula	S. fusca	S. cirrosa (the former f. septentrionalis)
branching of erect filaments	irregularly helicoid	irregularly helicoid	irregularly helicoid or irregularly pinnate
growth of laterals	indeterminate	mainly indeterminate	mainly determinate
diameter of erect filaments in µm	(10.5–) 16–45 (–52)	(20–) 30–80 (–90)	(20–) 40–60 (–70)
colour	dark brown or reddish brown	dark brown or reddish brown	light brown or olivaceous
propagules:			
apical hairs	absent	absent	usually present
form of the arms	cylindrical	cylindrical or slightly tapering	usually slightly fusiform, occasionally cylindrical
direction of the arms	straight, occasionally slightly recurved	straight or slightly recurved	recurved, occasionally straight
basal constriction of the arms	absent	usually absent	usually present
arising of young arms	simultaneous	simultaneous	successive
diameter of stalks	20–23 (–25)	29–47 (–58)	(20–) 30–40 (–50)
rhizoids	present	not known	usually absent
stolons	present	not known	present

As described before in the section on *S. nana* (p. 113) it is almost impossible to separate narrow (haploid) sterile and scarcely branched filaments of *S. rigidula* from those of *S. nana*. In the same section it is explained that *S. nana* and *S. rigidula* are not closely related. For comparison of *Sphacelaria* species with narrow filaments see table X and XI.

14. Sphacelaria fusca (Hudson) S. F. Gray—Fig. 555–564

Conferva fusca Hudson (1762) 486, (1778) 602; Dillwyn (1808) t. 95 (*p.p.*), (1809) 81.—*Ceramium fuscum* Dillwyn *non* Roth: Steudel (1824) 111 (*pro syn.*).—*Sphacelaria fusca* S. F. Gray (1821) 333; Greville (1824a) t. 96; C. Agardh (1828) 34; Harvey (1833) 324, (1841) 38, (1848) t. 149; J. Agardh (1848) 32; Kützing (1849) 464, (1855) 27, t. 90, f. III; Johnstone & Croall (1860) 159; Crouan (1867) 164; Sauvageau (1902) 399 (= R. 211); Hamel (1938) 260; Goodband (1971) 957 (*p.p.*); Prud'homme van Reine (1974) 174; Russell & Fletcher (1975) 766 (*p.p.*); Prud'homme van Reine (1978) 303.—*Sphacelaria cirrhosa* var. *fusca* Crouan (1852) Exsicc. n. 35 (*p.p.*, see Sauvageau (1902) 394 (= R. 207).—*Sphacelaria cirrhosa* forma *fusca* Holmes & Batters (1891) 81 (*p.p.*).—*Sphacelaria pennata* var. *fusca* Irvine (1956) 32 (*p.p.*).—Type: *Mrs. Griffiths s.n.*, Sidmouth, June 1827 (TCD, neo). See notes on nomenclature 1 and 2.

Plants forming small irregular bushes (fig. 555) or hemispherical cushions. They are dark brown or reddish-brown; solitary or gregarious, and epiphytic or epilithic. Many branched erect filaments arise from one or several small monostromatic basal discs.

The erect part of a plant is composed of many main axes and a variable number of laterals of up to the second or third order (fig. 556; 557). The sharply divaricate laterals with determinate or indeterminate growth arise in an irregularly helicoid pattern.

Usually the diameter of the axes exceeds the diameter of mature laterals of the first order, but the longest and oldest laterals are often as thick as or up to twice as thick as the axis.

Rhizoids and stolons have not been observed.

The dimensions of the usually elongate apical cells and of the secondary segments are very variable (fig. 558). Often the secondary segments are longer than they are wide but frequently secondary segments can be found which are shorter than they are wide. The succession of short and long secondary segments is without perceptible order.

The secondary segments are subdivided by radial and semi-radial walls into a parenchymatic tissue without subdivision into medullar and peripheral cells (fig. 560). In lateral view (0–) 1–5 (–6) longitudinal walls can be observed in secondary segments. Occasionally a transverse wall can be observed.

Solitary hairs are often frequent, especially in the terminal parts of the axes and the laterals.

Propagules are frequent on the distal parts of the erect filaments. Mature propagules consist of a narrow, straight, slightly broadening stalk and 2–3 narrow, straight or slightly recurved, divaricate, cylindrical or slightly tapering arms (fig. 561; 562). The stalk and the arms consist of a variable number of secondary segments, which are subdivided by 0–2 longitudinal walls (when observed by lateral view). Usually all arms are of the same length. A small, lenticular, apical cell is formed between the arms on top of the stalk (fig. 561; 563; 564). This lenticular cell never grows into a hair. The basal cell of a propagule persists on the filament as a unicellular stalk after the propagule has been shed. It often forms new propagules.

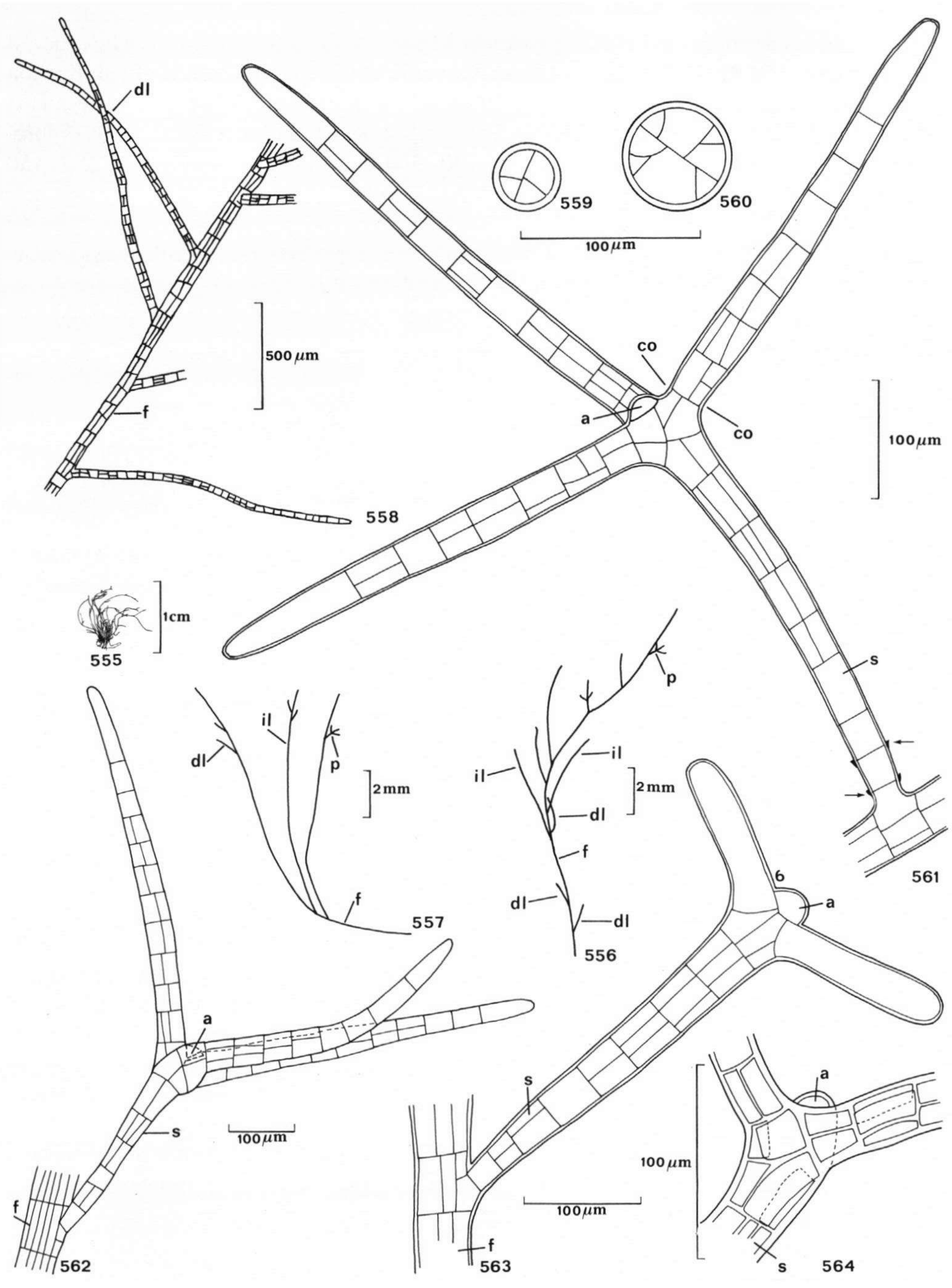


Fig. 555–564. ***Sphacelaria fusca.*** **555. Habit; 556–558. Branching; 559, 560. Cross-sections of erect filaments; 561–564. Propagules. a. apical cell; co. constriction; dl. determinate lateral; f. erect filament; il. indeterminate lateral; p. propagule; s. stalk. 555, 559, 560. Clew Bay, *Blackler* (L, in alcohol 96%); 556–558. Sidmouth, *Griffiths* (BM, soaked); 561, 563. St. Michaels Mount, *Marquand* (NMW, soaked); 562. St. Marc, *Crouan* (CN, soaked); 564. St. Malo, *Thuret* (PC, soaked).**

Unilocular and plurilocular zoidangia are not known.

Dimensions: Plants 5–30 mm high. Diam. basal discs 100–200 μm. Angle of ramification 15–60°. Diam. of erect filaments (20–) 30–80 (–90) μm. Height of secondary segments 18–120 μm. Hairs diam. 12–15 μm (with sheath) or 8–12 μm (without sheath). Chloroplasts 4–8 × 4–5 μm. Stalk of propagules 200–350 × 29–47 (–58) μm, arms 250–450 (–590) × 23–40 (–45) μm.

Distribution. Europe: Denmark, United Kingdom, Eire, France (Atlantic coasts, probably also on the Mediterranean coast) and probably Portugal.

Noted in many localities outside Europe, though much confusion exists regarding the discrimination of *S. rigidula* and *S. fusca.*

European localities have been listed below and are given in fig. 43.

DENMARK. Jutland: (as *S. cirrhosa*), *Haszlinsky* (Grunow 19597 in W).

UNITED KINGDOM. Orkneys. Kirkwall Bay: washed up, on *Phyllophora crispa, Prud'homme van Reine 1196*, 3/8/1973 (L).—Scotland. St. Andrews (Irvine, 1956, p. 33, as *S. pennata* var. *fusca*).—England. Cornwall: St. Michaels Mount, *Gourlie*, 5/1839 (GL); *Harvey*, 1847 (CN); *Tellam*, 12/4/1880 (BM) and *Marquand*, 26/6/1880 (NMW). *Ibidem*: Without exact locality, 'Cornwall', (as *Conferva fusca*), (FI). Devon: Exmouth, *Gulson 77*, 1851 (GL, TCD). *Ibidem*: Budleigh Salterton, (as *Conferva fusca*), *Griffiths* (K in BM). *Ibidem*: Sidmouth, *Griffiths*, 6/1827 (TCD mixed with *S. cirrosa*) and (as *S. cirrosa* var. *fusca*), *George*, 16/9/1892 (BM). *Ibidem*: Without exact locality, 'from *Mrs. Griffiths*' (?, BM).

EIRE. Clew Bay (as *S. furcigera*), *Blackler*, 19/8/1958 (L, STA, in both herbaria mixed with *S. cirrosa)*.

FRANCE. Atlantic coasts. Ille-et-Vilaine: St. Malo, Fort Royal, (as *S. cirrosa*), *Thuret*, 9/6/1872 (coll. Sauvageau in PC, mixed with *S. cirrosa*). *Ibidem*: St. Malo, on *Cladophora rupestris, Bornet*, 9/7/1872 (PC). Finistère: Anse de Berthéaume & Anse de Dellec, (as *S. cirrosa* var. *fusca*), Crouan: Algues mar. Finist. n. 35 (CO, M, in other herbaria often different species). *Ibidem*: Rade de Brest, *Crouan*, 1861 (CN, PC). *Ibidem*: St. Marc, on stones (CN, CO, LD).—Mediterranean coasts. Banyuls-sur-Mer (Coppejans, 1977, t. 75, according to dimensions in figures).

PORTUGAL. Estremadura: Cascais & Cruz Quebrada (Rodrigues, 1963, p. 31, as *S. pennata* var. *fusca*, according to dimensions in description).

Notes on nomenclature. (1) Hudson's descriptions (1762, 1778) of *Conferva fusca* were too incomplete to make an identification of this species possible. No type material seems to be extant (see also Dixon, 1959 and 1963b). Dillwyn (1808, t. 95) also described a *Conferva fusca* in the herbarium at Kew (now in the British Museum) and Lund (Ag. nr. *fusca* of Hudson. Dillwyn's figure suggests a *Sphacelaria* with three-armed propagules, young clavate propagules and unilocular zoidangia. The figure may, however, also depict a *Polysiphonia.* It is not possible to tell whether the figured presumptive *Sphacelaria* is *S. fusca* (in the sense this name is used in my publication*), S. rigidula* or *S. cirrosa.* Specimens of *Conferva fusca* in the herbarium at Kew (now in the British Museum) and Lund (Ag. nr. 45328) labelled as 'Mr. Dillwyn 1808' and as 'Spec. orig. Dillwyn' are not *Sphacelaria* at all, but in both cases they consist of a *Polysiphonia.* This resulted in the publication of the new combination *Hutchinsia fusca* by C. Agardh (1817, p. XXVI) based on '*Conferva fusca* (Hudson) Dillwyn'. Nevertheless Lyngbye (1819, p. 107) suggested that *Conferva fusca* Dillwyn ought to be incorporated into his new genus *Sphacelaria.* He did not publish it as a new combination, however. This was done by S. F. Gray (1821, p. 333), giving *Conferva fusca* Hudson as the basionym. Greville (1824a, t. 96), Harvey (1833, p. 324), C. Agardh (1828, p. 34) and J. Agardh (1848, p. 32) also used the name *Sphacelaria fusca*, without mentioning the publication of Gray and apparently without having seen a specimen. J. Agardh (*l.c.* p. 33) did already mention the disagreement between the figure (a genuine *Sphacelaria* according to J. Agardh) and the herbarium specimen. In a new publication of Harvey (1841, p. 38) the author mentioned new specimens from Sidmouth (*Mrs. Griffiths*, June 1827) and St. Michaels Mount (*Ralfs*). These are the only specimens Harvey has seen of *S. fusca*; he did not study other material. These specimens are still present in the herbarium of Trinity College, Dublin and the description of *S. fusca* can be based on this material of which a specimen from Sidmouth is here designated as the neotype of *S. fusca* (Huds.) S. F. Gray. Several other descriptions and several figures of *S. fusca* are also mainly based on this material: Harvey (1848, t. 149), Kützing (1855, p. 27), Sauvageau (1902, p. 399 = R. 211), Hamel (1938, p. 260). Many recent publications, however, use the combination *S. fusca* for *S. rigidula.* A list of these publications is given in the chapter about *S. rigidula.*

De Haas-Niekerk (1965) studied specimens of what she supposed to be *S. fusca* together with the type specimen of *S. furcigera.* She concluded that there is no reason to separate *S. furcigera* (= *S. rigidula*) from *S. fusca.* She designated a neotype for *S. fusca* (*Van den Hoek 3695*, Roscoff, Ile Verte, 30/6/1958, in L). In my opinion the specimens studied by De Haas-Niekerk all belong to *S. rigidula*, and consequently the neotypification of *S. fusca* was incorrect.

I prefer to use the well-known combination *S. fusca* (and in the same sense as Harvey, Sauvageau and Hamel) rather than to propose a new name for this taxon.

(2) see notes on nomenclature 2 of *S. rigidula* (p. 211).

Notes on morphology. In the secondary segments of *S. fusca* several longitudinal walls are formed. All walls are more or less radial, never periclinal. The formation sequence of the longitudinal walls, as can be observed in cross-sections, has not been figured before. It is very similar to the same process in *S. rigidula.* See also fig. 559; 560.

Primary laterals are formed by hemiblastic branching of young superior secondary segments. The initials of laterals and propagules are inconspicuous. The primary laterals arise in an irregular helicoid pattern and in a rough acropetal sequence (fig. 556; 557). Most laterals have a similar growth as the main axes. They all grow until they have reached the periphery of the mature plant. Near this periphery the erect filaments form usually many solitary hairs and their growth cease. Some laterals may cease growing in an earlier stage (fig. 556; 558). The diameter of these determinate laterals is usually much smaller than the diameter of indeterminate laterals.

Notes on ecology. The habitat in which *S. fusca* grows is not known accurately. It has been found as an epiphyte on various algae, of which *Cladophora rupestris* has often been mentioned in literature.

Sphacelaria rigidula, however, is far more common as an epiphyte on this *Cladophora.* Most published information about the habitat of *S. fusca* is not related to that species, but to *S. rigidula.*

When growing as an epiphyte the form of the plants of *S. fusca* is usually quite irregular and its outline is without a definite form (fig. 555). When growing on rocks, however, *S. fusca* may form hemispherical cushions with a diameter of 1–2 cm and very similar to the cushions which may be formed by *S. tribuloides.*

Most specimens of *S. fusca* have been found growing in the littoral zone, but the specimens from the drift material collected in Kirkwall Bay, Orkney, suggest its occurrence in deeper water too.

Form range and cultures. Morphological variation in this rare species cannot be described due to the lack of adequate, complete and mature plants. In several herbaria only fragments are present. I have not been successful in collecting living specimens to grow them in culture.

Reproduction and life-history. Vegetative propagation is the only stage of reproduction known of *S. fusca*. These propagules have already been figured by Harvey (1848, t. 149). Sauvageau (1902, p. 396 = R. 208) discussed Harvey's figures. According to Sauvageau the arms of the propagules are never acute, but in dried specimens the apical cells of the arms may be more shrunken, withered and wrinkled, resulting in an apparent acute tip. In reality the arms are cylindrical or slightly tapering according to Sauvageau. This slight tapering is shown in my figure 562, the cylindrical arms in fig. 561. Usually three-armed propagules occur (fig. 561; 562) but two-armed propagules can also be observed (fig. 563; 564). Usually the two arms are projections in the plane of the stalk (fig. 563) but occasionally the arms project in another plane (fig. 564). In all propagules a distinct small lenticular apical cell can be observed and these apical cells never grow into apical hairs. In some propagules a small constriction can be observed at the base of one of the arms (fig. 561), but usually no trace of a constriction can be found.

The ontogeny of the propagules could not be studied in detail for lack of young propagules in the herbarium specimens. The youngest propagule I have seen is figured in fig. 563. This figure suggests that the ontogeny of the propagules is of the '*fusca*-type' as defined by Zimmermann & Heller (1956, p. 292). In the '*fusca*-type' (and in my figure 563) all arms of the propagule arise simultaneously from the sub-apical secondary superior segment of the stalk, while in the '*cirrosa*-type' the arms arise successively from the undivided subapical primary segment. In older propagules the arms are usually of about the same length and in the same stage of development (fig. 561; 562). Germination of the propagules is similar to that process in *S. rigidula.*

Systematic position. *Sphacelaria fusca* is very similar to *S. rigidula.* The differences concern diameter of the erect filaments, dimensions and form of the propagules and perhaps also the prostrate parts of the plants. (See table XVI and XVII). The diameter of the proximal parts of the erect filaments of *S. fusca* is much larger than that of similar filaments in *S. rigidula.* In the distal parts, however, the differences in diameter of the erect filaments of both species are inconspicuous. The absence of rhizoids and stolons in *S. fusca* is probably a result of lack of sufficient material of this taxon.

A growth-form of *S. cirrosa* (*S. cirrosa* f. *septentrionalis* Sauvageau, 1902, p. 415 = R. 227 and *S. pennata* var. *pennata* f. *septentrionalis* Irvine, 1956, p. 31) can be confused with *S. fusca*, but it differs in its way of branching, its colour and the form of its propagules (see table XVII).

In *S. cirrosa* most propagules terminate in a hair, but occasionally propagules of that species can be found of which the small lenticular apical cell persisted and did not grow into a hair. In these cases the differences with regard to the propagules of *S. fusca* are very small. Nevertheless I suppose *S. fusca* to be more closely related to *S. rigidula* than to *S. cirrosa.* This supposition is partly based on the indefinite organization found both in *S. fusca* and in *S. rigidula* in contrast with the more definite organization of *S. cirrosa*. The consistent absence of apical hairs in the propagules of *S. fusca* and *S. rigidula* is another indication for the supposed relation and the similar ontogeny of the propagules of these two species may be a third character in common.

IVc. Section Propagulifera Prud'homme van Reine *nov. sect.*

Sphacelaria du groupe du *S. cirrosa* Sauvageau (1902) 331 = R. 173.—*Sphacelaria* sect. *Propagulifera* Prud'homme van Reine (1978) 312 (*nom. inval.*).—Type species: *S. cirrosa* (Roth) C.A. Agardh. Sauvageau (*l.c.*) described this group extensively, he included *S. fusca* in this group.

Filamenta lateralia determinata, plerumque distincte diversa filamentis principalibus, irregulariter spiraliter vel irregulariter pinnatim disposita. Propagula ramulis longis plerumque fusiformibus, pilo terminali praedita.

Laterals are determinate, usually distinctly different from the main filaments and arranged in an irregular helicoid or in an irregular distichous pattern. Propagules have long, usually fusiform arms and usually a terminal hair.

15. Sphacelaria cirrosa (Roth) C.A. Agardh—Fig. 565–646, plate 6

Conferva cirrosa Roth (1800b) 214; Wulfen (1803) 20; Turner (1804) 106 (incl. *bipinnata*); Roth (1806) 294.—*Ceramium cirrhosum* C. Agardh (1812) 21, (1817) 67; W. Hooker (1821) 86 (*p.p.*, as *C. cirrosum*).—*Sphacelaria cirr(h)osa* C. Agardh (1824) 164 (*p.p.*); Greville (1827) t. 317 (as *Sphacellaria cirrhosa*, incl. *bipinnata*); C. Agardh (1828) 27 (*p.p.*); Bonnemaison (1828) 110 (incl. *bipinnata*); Harvey (1833) 324; J. Agardh (1836) 210; Montagne (1840) 149 (incl. *hystrix*); Harvey (1841) 38 (incl. *bipinnata*); J. Agardh (1842) 29 (incl. *bipinnata*); Meneghini (1843) 332; Kützing (1843) 292, (1845) 239; J. Agardh (1848) 34; Harvey (1848) t. 178 (incl. *bipinnata*); Kützing (1849) 464, (1855) 26, t. 88, f. 2; Johnstone & Croall (1860) 157 (incl. *bipinnata*); Geyler (1866) 513, t. 36, f. 18–21 (is *bipinnata*); Janczewski (1872) 337 (= 1873, 253); Magnus (1872a) 72, (1873b) 131, t. 1, f. 1–12 (incl. *bipinnata*); Reinsch (1875) 25, t. 34, f. 2; Areschoug (1875) 21, t. 2, f. 6–7 (*bipinnata*); Hauck (1885) 344 (incl. *bipinnata*); Ardissone (1886) 207; Reinke (1890a) 90, (1891) 10 (incl. *bipinnata*); Vinassa (1891) 246; Bornet (1892) 240; Reinke (1892) 65, t. 42 & 43; Kuckuck (1894) 228, f. 2; De Toni (1895) 503; Sauvageau (1902) 415 (= R. 227), f. 44–46; Van Goor (1923) 79; Printz (1926) 164; Schingnitz-von Böselager (1936) 285, f. 1; Hamel (1938) 258; Kylin (1947) 29, f. 24E; Lund (1950) 32, f. 6; Sundene (1953) 158; Funk (1955) 43, t. 4, f. 8; Zimmermann & Heller (1956) 297, t. 2C, 4B, 5; A. Zinova (1953) 113, f. 92; Jorde & Klavestad (1960) 96; De Haas-Niekerk (1965) 156, f. 44–50; Jaasund (1965) 70; A. Zinova (1967) 148, f. 87; Goodband (1968) 26; Dimitrova (1969) 151; Goodband (1971) 957; Prud'homme van Reine (1974) 173; Russell & Fletcher (1975) 766; Prud'homme van Reine (1978) 303.—Lectotype: *Wulfen s.n.*, Triest, '*Innascitur fucorum ramentis, Conferva cirrosa*' (WU). See notes on nomenclature 1–4.

Conferva marina perbrevis villosa et cirrosa Dillen (1741) 23, t. 4, f. 21.—Lectotype: *More s.n.*, Herb. Sherard Europe 1988 (OXF). See notes on nomenclature 5.

Conferva pennata auct. non Hudson: Dillwyn (1806) t. 86 (*p.p.*; excl. syn.); Smith & Sowerby (1812) t. 2330 (*p.p.*); Hornemann (1813) t. 1486, f. 2; Withering & Withering (1818) 186 (incl. *bipinnata*).—*Sphacelaria pennata* Lyngbye (1819) 105, t. 31C (incl. *bipinnata*); Gray (1821) 332; Greville (1824b) 313; Gaillon (1828) 400; Kützing (1845) 239, (1849) 465, (1855) 27, t. 91, f. 2; Geyler (1866) 519, t. 36, f. 6–11; Rischawi (1874) 343, f. 1–19; Irvine (1956) 29 (incl. *bipinnata*); Rodrigues (1963) 29. —*Delisella pennata* Bory de St. Vincent (1824) 389.—*Cladostephus pennatus* Sprengel (1827) 346. —*Sphacelaria cirr(h)osa* var. *pennata* Hauck (1885) 345, f. 343; Woronichin (1908) 43; Schingnitz-von Böselager (1936) 288; Dimitrova (1969) 151, f. 4.—*Sphacelaria cirrhosa* forma *pennata* Reinke (1889) 40.—*Sphacelaria pennata* var. *pennata* Irvine (1956) 31, Rodrigues (1963) 29. See notes on nomenclature 2, 4, 6, and 7.

Conferva intertexta Roth (1797) 188, t. 3, f. 5, *nom. illegit.*, non Withering (1796) 132.—Lectotype: *Mertens s.n.*, Corsica, inter *Helminthochorton* (herb. Schreber in M).

Conferva halecina Dillwyn (1806) t. 86, f. C, *nom. illegit. pro syn.* (incl. *bipinnata*).—No type selected.

Sphacelaria pennata β gracilis Lyngbye (1819) 105.—*Sphacelaria plumosa β gracilis* C. Agardh (1828) 25. —*Sphacelaria cirrhosa b gracilis* Hornemann (1837) 694.—*Sphacelaria cirrosa* var. *pennata* forma *gracilis* Schingnitz-von Böselager (1936) 287.—Type: *Lyngbye s.n.* '*ad littus* Hofmansgave', Jan. 1816 (C). See note on nomenclature 7.

Sphacelaria cirr(h)osa var. *aegagropila* C. Agardh (1824) 165, (1828) 28; Harvey (1833) 324 (*bipinnata*),

(1841) 38 (*bipinnata*); Kützing (1845) 239, (1849) 464; De Toni (1895) 505 (*bipinnata*); Newton (1931) 190; Schingnitz-von Böselager (1936) 289.—*Sphacelaria cirrhosa* forma *aegagropila* Reinke (1889) 40; Kjellman (1890) 68 (incl. *bipinnata*).—Type: *Lyngbye s.n.*, (as *Conferva pennata*), Hals, '*qualis in Fl. Dan. depicta est*' (C).

Sphacelaria cirr(h)osa var. *patentissima* Greville (1827) t. 317 (as *Sphacellaria cirrhosa* var. ε *patentissima*); Harvey (1833) 324; Sauvageau (1903) 46 (=R.230).—*Sphacelaria cirr(h)osa* forma *patentissima* Reinke (1889) 40, (1892) 65; Prud'homme van Reine (1978) 303.—*Sphacelaria pennata* forma *patentissima* Irvine (1956) 32.—Type: probably lost, but Greville's figure is characteristic, although figured as being attached. See note on nomenclature 7.

Sphacelaria cervicornis auct. non C.A. Agardh: Kützing (1843) 292 (excl. syn.), (1845) 240 (excl. syn.), (1849) 465 (*p.p.*), (1855) 27, t. 92, f. 1A; Zanardini (1873) t. 90A; Ardissone & Strafforello (1877) 139 (*p.p.*)—*Sphacelaria cirrhosa* var. *cervicornis* Ardissone (1886) 91 (*p.p.*).

Sphacelaria confervicola Kützing (1843) 292, t. 18, f. 3, (1845) 239, (1849) 465.—Type: Lost. Proposed as Neotype: *Kützing 16*, Lesina (= Hvar) (L, sheet 937.71-759).

Sphacelaria firmula Kützing (1843) 292, (1849) 463, (1855) 26, t. 86, f. 3 (= partly *bipinnata*).—Type: *Endress s.n.*, Biarritz, on *Gigartina acicularis* (L, sheet 937.131-119).

Sphacelaria irregularis Kützing (1845) 239, (1849) 465, (1855) 27, t. 91, f. 3 (= *hystrix*).—*Sphacelaria cirrhosa* β *irregularis* Hauck (1885) 345.—*Sphacelaria cirr(h)osa* forma *irregularis* Reinke (1891) 11; Schingnitz-von Böselager (1936) 287.—Lectotype: *Kützing s.n.*, Spalato, auf *Zostera* (L, sheet 937.55-425). See note on nomenclature 7.

Sphacelaria irregularis β *radicans* Kützing (1845) 239.—Type: *Kützing s.n.*, Spalato (L, sheet 937.55-420).

Sphacelaria cirrhosa forma *nana* J. Agardh (1848) 35; Kjellman (1890) 68.—*Sphacelaria cirr(h)osa* var. *nana* Griffiths *ex* Crouan (1852) Exsicc. 34; Le Jolis (1863) 80; Crouan (1867) 164; Sauvageau (1903) 45 (= R. 228).—*Sphacelaria pennata* forma *nana* Irvine (1956) 32. —Lectotype: *Griffiths s.n.*, 'curious variety' (TCD). See note on nomenclature 6.

Sphacelaria rhizophora Kützing (1849) 463, (1855) 26, t. 89, f. 1; Sperk (1869) 25.—*Sphacelaria cirrosa* var. *rhizophora* Schiffner (1931) Exsicc. 920; Schingnitz-von Böselager (1936) 288.—Type: *Kützing 5*, Naples (L, sheet 937.71-715).

Stypocaulon bipinnatum Kützing (1855) 28, t. 95.—*Sphacelaria bipinnata* Sauvageau (1902) 393 (= R. 205), f. 41F, 42; Kylin (1907) 64; Chemin (1922) 244, f. 1, 2; Clint (1927) 5, f. 1–5; Papenfuss (1934) 437, f. 1–9; Hamel (1938) 257; Kylin (1947) 30, t. 1, f. 3; Lund (1950) 37, f. 7; Sundene (1953) 158; Irvine (1956) 35; Jorde & Klavestad (1960) 95; Jaasund (1965) 71, f. 20; Goodband (1968) 176, (1973) 175; Prud'homme van Reine (1974) 164; Russell & Fletcher (1975) 766; Pankow (1976) 464, f. 873; Rueness (1977) 182, t. 24, f. 4; Prud'homme van Reine (1978) 303.—Type: *Lenormand 197*, Morbihan (L, holo; isotypes in CN and PC). See notes on nomenclature 4 and 7.

Sphacelaria polycornua Sperk (1869) 25.—Type: probably lost.

Sphacelaria pilifera Reinsch (1875) 102, t. 35 (probably).—Type: lost.

Sphacelaria cirrhosa var. *subsecunda* Grunow in Piccone (1884) 53 (*hystrix* ?); De Toni (1895) 505.—Type: *Liebetruth s.n.*, Gran Canaria (W, sheet 19618 in herb. Grunow).

Sphacelaria cirrosa forma *typica* Wittrock (1884) 284 (*bipinnata*).—No type mentioned.

Sphacelaria hystrix Suhr *ex* Reinke (1890a) 208, (1891) 13, t. 3, f. 4–7; De Toni (1895) 506; Sauvageau (1898) 1672, (1902) 349 (= R. 191), f. 39–41; Schmidt (1931) 25; Hamel (1938) 256; Irvine (1956) 34; Nizzamudin & Lehnberg (1970) 119, f. 18, 20, 21; Prud'homme van Reine (1974) 173; Russell & Fletcher (1975) 766; Prud'homme van Reine (1978) 303.—Type: *Lenormand 97*, Canary Islands (herb. Suhr in KIEL). See note on nomenclature 6.

Sphacelaria amphicarpa Lebel *ex* Sauvageau (1900a) 343 (*nom. nud.*).

Sphacelaria Lebelii Sauvageau (1902) 380 (= R. 193) (*nom. nud. pro syn.*).

Sphacelaria cirrosa forma *mediterranea* Sauvageau (1902) 415 (= R. 228); Hamel (1938) 260.—Lectotype: *Durieu s.n.*, Alger, on *Dictyota dichotoma*, herb. Sauvageau in PC. See note on nomenclature 6.

Sphacelaria cirrosa forma *meridionalis* Sauvageau (1902) 415 (= R. 227), f. 45; Hamel (1938) 259.—*Sphacelaria pennata* forma *meridionalis* Irvine (1956) 32; Rodrigues (1963) 30, f. 1e.—Type: *Vickers s.n.*, Roscoff, on *Cystoseira discors*, 30/7/1900 (herb. Sauvageau in PC). See note on nomenclature 6.

Sphacelaria cirrosa forma *septentrionalis* Sauvageau (1902) 415 (= R. 227), f. 44; Schingnitz-von Böselager (1936) 290; Hamel (1938) 259.—*Sphacelaria pennata* forma *septentrionalis* Irvine (1956) 31; Rodrigues (1963) 30.—Type: *Foslie s.n.*, Vanvick, Trondjemfjord, 19/8/1892 (herb. Sauvageau in PC probably *bipinnata*). See note on nomenclature 6.

Plants forming small or extensive, dense or open, erect, penicillate, irregular or hemispherical bushes (fig. 565–567; 573), small rigid cushions, (fig. 568), free-floating rounded balls, (fig. 569), unattached entangled masses (fig. 570), or a continuous or semi-continuous cover on various substrates (fig. 574). They are reddish-brown, dark brown, yellowish-brown, or olivaceous; solitary, gregarious, or caespitose, and epilithic, epiphytic, partly endophytic, or unattached. Many branched erect filaments arise from the basal creeping parts (fig. 571; 576).

The basal parts consist of small monostromatic or polystromatic discs (fig. 571; 572; 575; 576), or obconical multicellular structures endophytic in large algae (fig. 578; 579), uncovered or covered by rhizoids which may form an entangled, sponge-like mass. Stolons absent or present (fig. 580), sometimes numerous.

The erect parts of the plants are composed of many branched erect main axes and usually many hemiblastic laterals of up to the second or third order (fig. 577; 581–584; 621; 622). The usually approximate, erecto-patent to perpendicular laterals with determinate or indeterminate growth arise in various patterns. The laterals are distichous and occasionally partly secund, or they arise from all sides of the axis. They may be opposite, alternate, or occur in small whorls of 3–4.

The main axes are usually distinctly broader than laterals of the first order (fig. 581; 582) and these laterals are usually broader than laterals of the second order (fig. 583). Mature laterals with determinate growth have acute tips. Proximal laterals grow into stolons, rhizoids, or attachment discs.

Downward growing branched or unbranched rhizoids are absent (fig. 571; 584) or they arise from the main erect filaments in very variable numbers (fig. 575; 585; 586). If present and numerous they often form a thick but quite open cortication of the proximal parts of main erect filaments (fig. 586).

The dimensions of the usually elongate apical cells of filaments with indeterminate growth are very variable, and so are the dimensions of the secondary segments. Often secondary segments of the main filaments are shorter than they are wide (fig. 571; 583), but in laterals of the second order they are usually longer than they are wide (fig. 587). Specimens in which all secondary segments are longer than they are wide (fig. 588) are of frequent occurrence, however. Usually the dimensions of the superior and inferior secondary segments of a filament are similar, but occasionally the inferior secondary segments are longer than the superior ones.

The secondary segments are subdivided by radial and semi-radial walls into a parachymatic tissue without subdivision into medullar and peripheral cells (fig. 589). In lateral view (1–) 3–8 (–10) longitudinal walls can be observed in secondary segments. In the cells secondary transverse walls are rarely found (present in fig. 571), except in cells from which laterals arise.

Solitary hairs are usually present and often abundant (fig. 582–584; 587; 588; 594; 595; 621; 622).

Propagules are frequent on the distal parts of erect filaments in specimens collected in spring, summer, and autumn in western Europe, and all the year round in the Mediterranean. Mature propagules consist of a narrow, straight, often distinctly broadening stalk and (1–) 2–4 (–6) short or long, straight or recurved, divaricate, cylindrical, or fusiform arms which are constricted at their base (fig. 582; 596; 597; 599–608; 610; 612; 613). Both stalk and arms consist of a variable number of secondary segments, which are subdivided by 0–2 (–3)

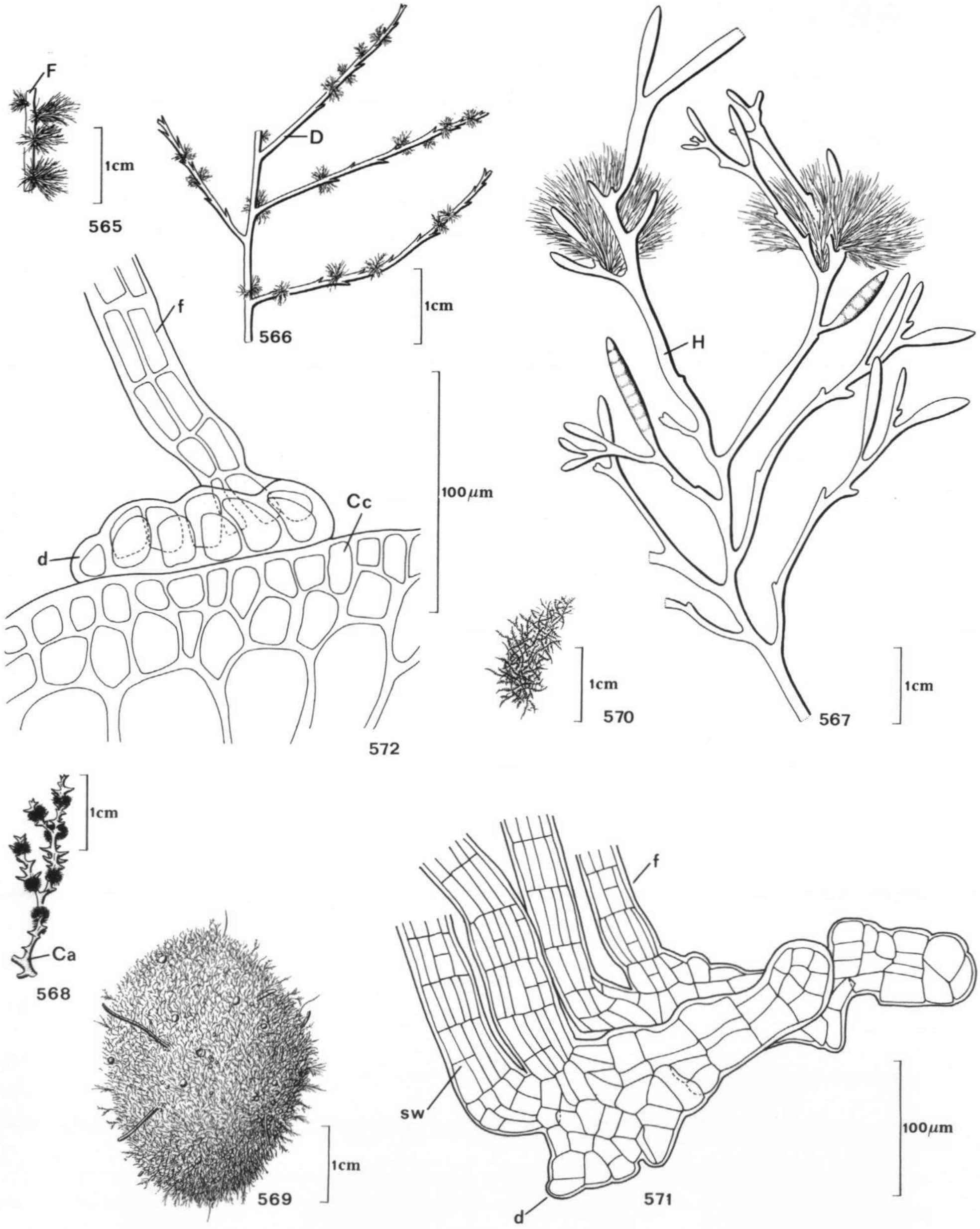


Fig. 565–572. Sphacelaria cirrosa. 565–570. Habits; 571, 572. Basal parts. Ca. *Cystoseira abies-marina*; Cc. *Cystoseira canariensis*; d. basal disc; D. *Desmarestia aculeata*; f. erect filament; F. *Furcellaria lumbricalis*; H. *Halidrys siliquosa*; sw. secondary transverse wall. 565. Fiskebäckskil, Areschoug, Alg. Scand. exs. ser. nov. n. 109 (L, sheet 937-71-758); 566. Cherbourg, *Bornet 207 bis* (L, sheet 937.71-657); 567. Derby Haven, Isle of Man, *Prud'homme van Reine 1284*; 568. Las Calettilas, Tenerife, *CANCAP 1362* (L); 569. Kieler Hafen, *Nolte* (L, sheet 973.71-495); 570. Roscoff, *Prud'homme van Reine 1964* (formalin); 571. Graesholm, *Rosenvinge 5655* (C, soaked); 572. Tenerife, *Van Steenis* (fresh). 565, 566, 571. Ecad *cirrosa*; 567. Ecad *bipinnata*; 568, 572. Ecad *hystrix*; 569. Ecad *aegagropila*; 570. Ecad *patentissima*.

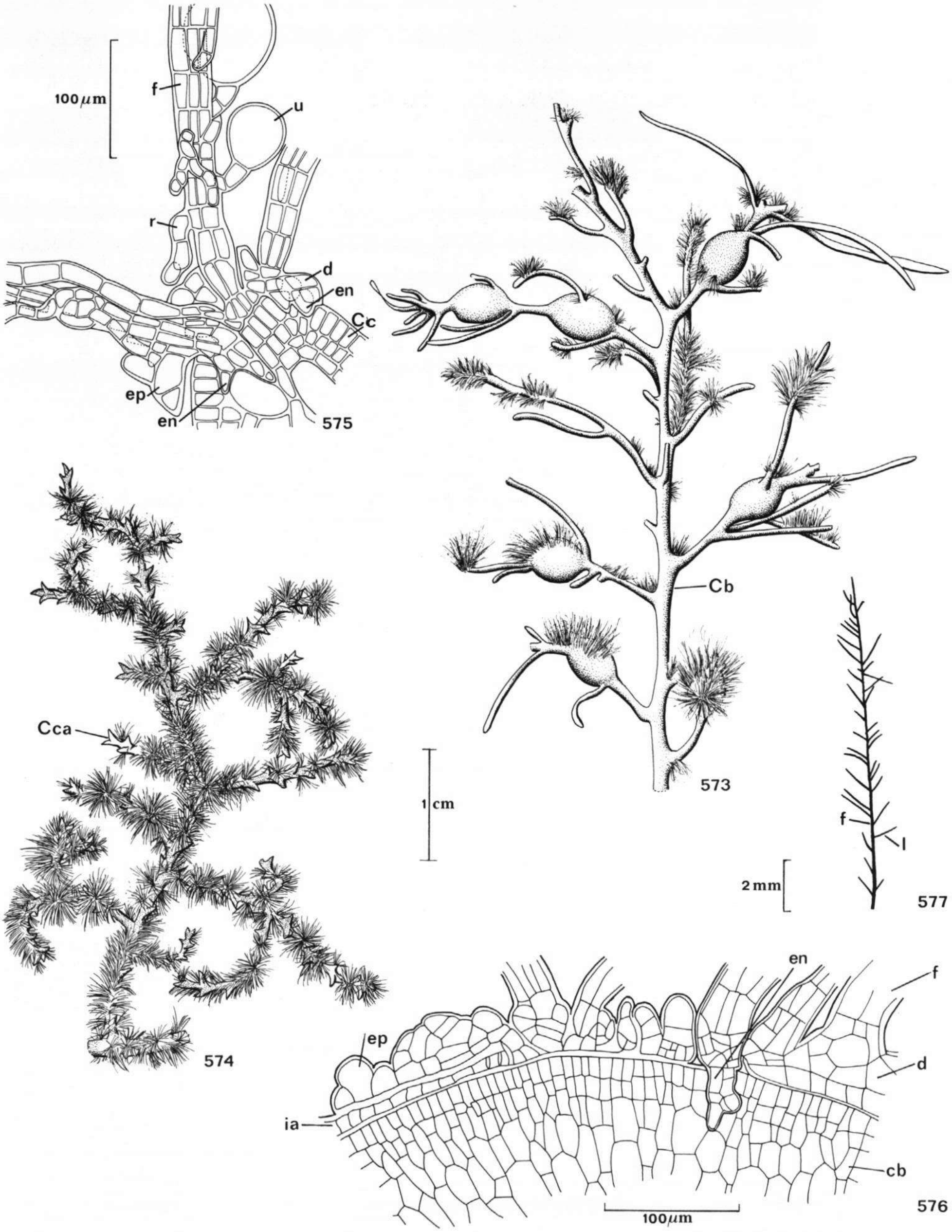


Fig. 573–577. Sphacelaria cirrosa. 573, 574. Habits; 575, 576. Basal parts; 577. Branching. Cb. *Cystoseira baccata*; Cc. *Cystoseira canariensis*; Cca. *Cystoseira caespitosa*; d. basal disc; en. endophytic; ep. epiphytic; f. erect filament; ia. incrusting alga; l. lateral; r. rhizoid; u. unilocular zoidangium. 573. Concarneau, *Prud'homme van Reine 386* (L, sheet 972.088-225); 574. Banyuls-sur-Mer, *Prud'homme van Reine 801* (L, sheet 972.046-624); 575. Tenerife, *Van Steenis* (fresh); 576. Roscoff, *Prud'homme van Reine 73-3-2* (soaked); 577. Sidmouth, *Griffiths* (TCD, soaked). 573, 576. Ecad *bipinnata*; 574, 575. Ecad *hystrix*; 577. Ecad *cirrosa*.

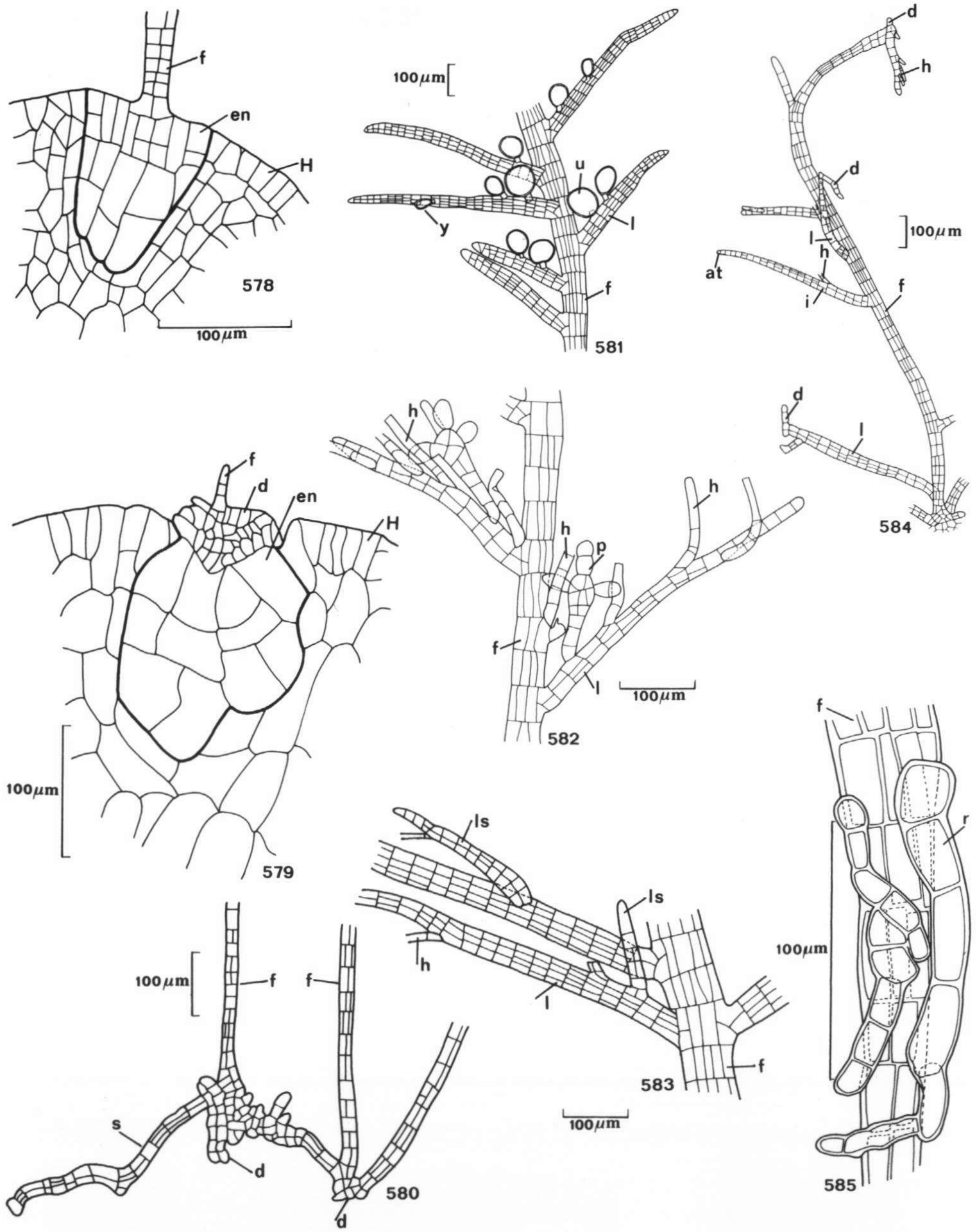


Fig. 578–585. Sphacelaria cirrosa. 578–580. Basal parts; 581–584. Branching; 585. Rhizoids. d. basal disc; en. cone-shaped endophytic part; f. erect filament; h. hair; H. *Halidrys siliquosa*; l. lateral; ls. lateral of the second order; p. propagule; r. rhizoid; s. stolon; u. unilocular zoidangium; y. young. 578, 579. St. Andrews, *Prud'homme van Reine 597* (formalin); 580. Börnestangen, *Prud'homme van Reine 67-25* (formalin); 581. Roscoff, *Prud'homme van Reine 66-69* (microslide); 582, 584, 585. Tenerife, *Van Steenis* (fresh); 583. Triest, *Pignatti* (TSB, microslide). 578, 579, 581. Ecad *bipinnata*; 580, 583. Ecad *cirrosa*; 582, 584, 585. Ecad *hystrix*.

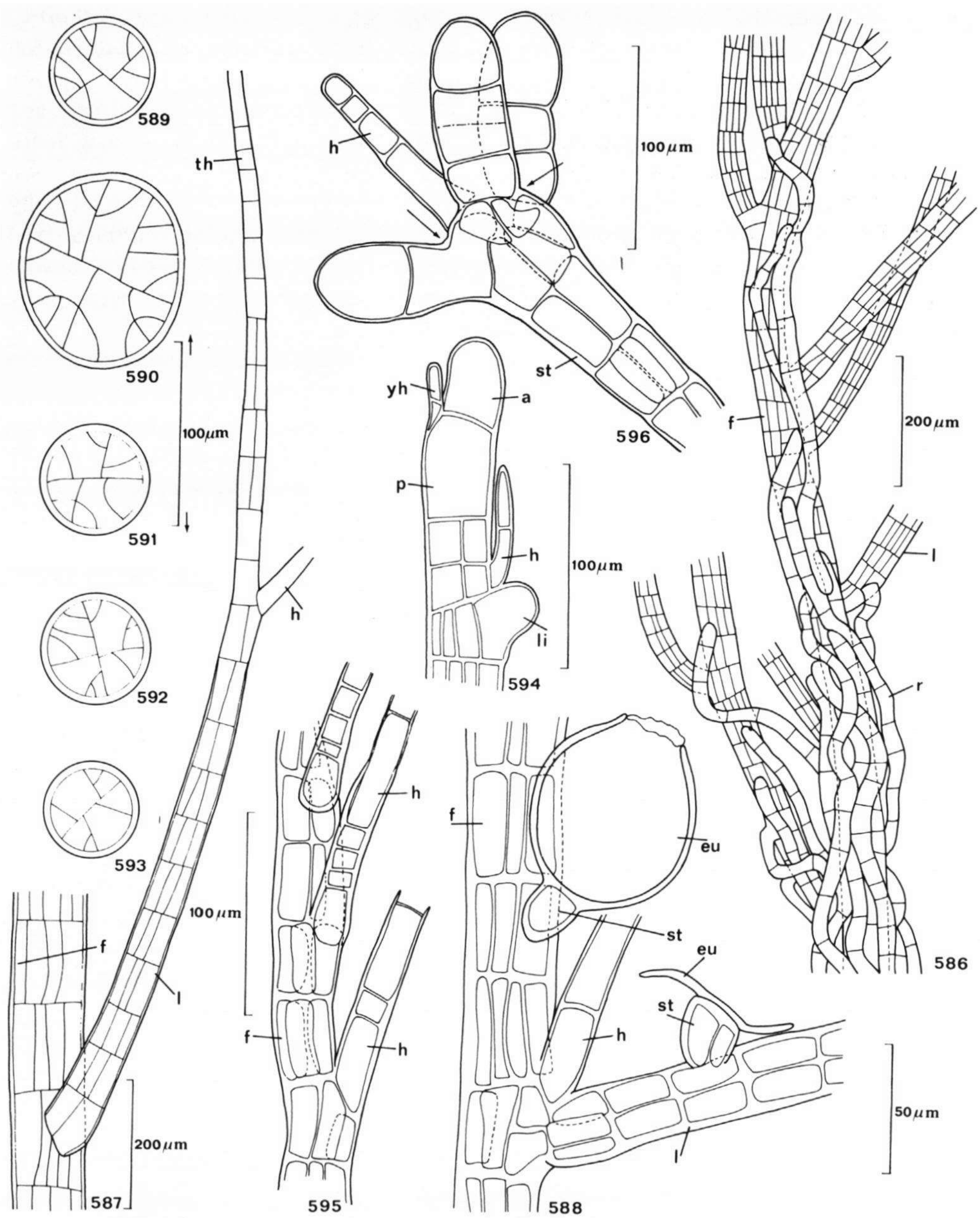


Fig. 586–596. Sphacelaria cirrosa. 586. Rhizoids; 587. Hairs; 588–595. Parts of erect filaments (589–593. Cross-sections); 596. Young propagule. a. apical cell; eu. empty unilocular zoidangium; f. erect filament; h. hair; l. lateral; li. lateral initial; p. primary segment; r. rhizoid; st. stalk; th. terminal hair; yh. young hair. 586, 587. Grandcamp-les-Bains, *Lenormand* (CN, soaked); 588. Tenerife. *Van Steenis* (fresh); 589. Locmariaquer, *Prud'homme van Reine 66-62* (microslide); 590. Le Caro, *Prud'homme van Reine 66-76* (microslide); 591. Roscoff, *Prud'homme van Reine 1964* (microslide); 592. Guéthary, *Sauvageau* (L, microslide); 593. Roscoff, *Heerebout 67-5* (L, microslide); 594. Island Pianosa, *Pignatti* (TSB, microslide); 595. Krk, *Pignatti 5* (TSB, microslide). 586, 587, 593. Ecad *bipinnata*; 588, 592. Ecad *hystrix*; 589, 590, 594–596. Ecad *cirrosa*; 591. Ecad *patentissima.*

longitudinal walls. Usually all arms of mature propagules are of the same length. A short or long apical hair is formed by a small apical cell located between the arms and on top of the stalk. Occasionally the small cell does not grow (fig. 606; 608). Less frequently still, it grows into a new propagule (fig. 611). The basal cell of a propagule persists on the filament as a unicellular stalk after the propagule has been shed. It often forms new propagules (fig. 609).

Unilocular zoidangia are common in some populations, but seem to be rare in other ones. They have been most frequently found in summer, autumn, and early winter, but occasionally also in late winter and spring. Unilocular zoidangia occur usually scattered on the adaxial side of laterals and they are (sub)globular when mature (fig. 575; 588; 614–616), obovoid or clavate when young (fig. 617). They have a unicellular stalk from which occasionally new apical unilocular zoidangia may arise, which can be formed inside the remaining wall of the dehisced old unilocular zoidangium (fig. 616). The unizoids are pear-shaped. They have (1–) 3–4 (–5) small chloroplasts and an eye-spot (fig. 618).

Plurilocular zoidangia occur as frequently as unilocular ones. They have been found in spring, summer, and autumn, occasionally also in winter. Plurilocular zoidangia occur usually on laterals (fig. 621; 622) and they are ellipsoid or cylindrical when mature (fig. 623–629), clavate or ellipsoid when young. They have a uni- or bi-cellular stalk from which only occasionally lateral new plurilocular zoidangia arise (fig. 619; 620). Plurilocular micro- and macrogametangia have been observed, as well as supposedly neutral plurilocular zoidangia. Propagules, unilocular zoidangia, and plurilocular zoidangia have been found in combinations together on one plant but also on separate plants.

Dimensions: Plants (0.1–) 1–30 (–40) mm high. Diam. basal discs 100–300 μm. Diam. endophytic structures in surface-view (10–) 40–160 μm, growing 40–150 (–180) μm deep into its host. Diam. stolons 40–85 μm. Diam. rhizoids (15–) 21–32 (–45) μm. Angle of ramification (30–) 47–55 (–90)°. Diam. of main erect filaments (10–) 20–85 (–100) μm; diam. of laterals of the first order (10–) 20–60 μm; diam. of laterals of the second order (10–) 20–38 μm. Height of secondary segments (20–) 25–75 (–90) μm. Diam. of hairs 12–17 μm (with sheath) or 8–14 μm without sheath. Chloroplasts (3–) 4–6 (–8) X (3–) 4–5 (–6) μm in surface-view (fig. 630–632). Stalk of propagules 200–400 (–600) X (10–) 17–31.5 μm (below) or (30–) 35–70 μm (widest part). Arms (50–) 150–200 (–600) μm long, diam. of constriction at their base 17.5–25 μm, in their middle 24.5–28 μm, and near their tips (17.5–) 21–24 μm. Unilocular zoidangia (54–) 60–100 (–120) μm in diam. Unizoids 10 X 5–6.3 μm. Small-partitioned plurilocular zoosporangia (45–) 65–100 (–150) X (26–) 35–60 (–70) μm, diam. loculi 3–4.5 (–5) μm. Large-partitioned plurilocular zoidangia (47–) 55–85 X (33–) 40–65 (–75) μm, diam. loculi 6–8 μm.

Ecads.

Ecad *aegagropila* (fig. 569; 633). Unattached, sterile plants forming compact free-floating rounded balls.

Ecad *bipinnata* (fig. 567; 573; 586; 634). Plants are epiphytic and partly endophytic in *Halidrys siliquosa* and *Cystoseira baccata.* Many appressed rhizoids form a cortex around the main filaments. Usually many zoidangia occur and only occasionally propagules.

Ecad *cirrosa* (fig. 565; 566; 582). Plants are epiphytic on other algae or epilithic. Appressed rhizoids are often absent. Usually many propagules occur and only occasionally zoidangia.

Ecad *hystrix* (fig. 568; 574). Plants are epiphytic and partly endophytic in *Cystoseira* div.

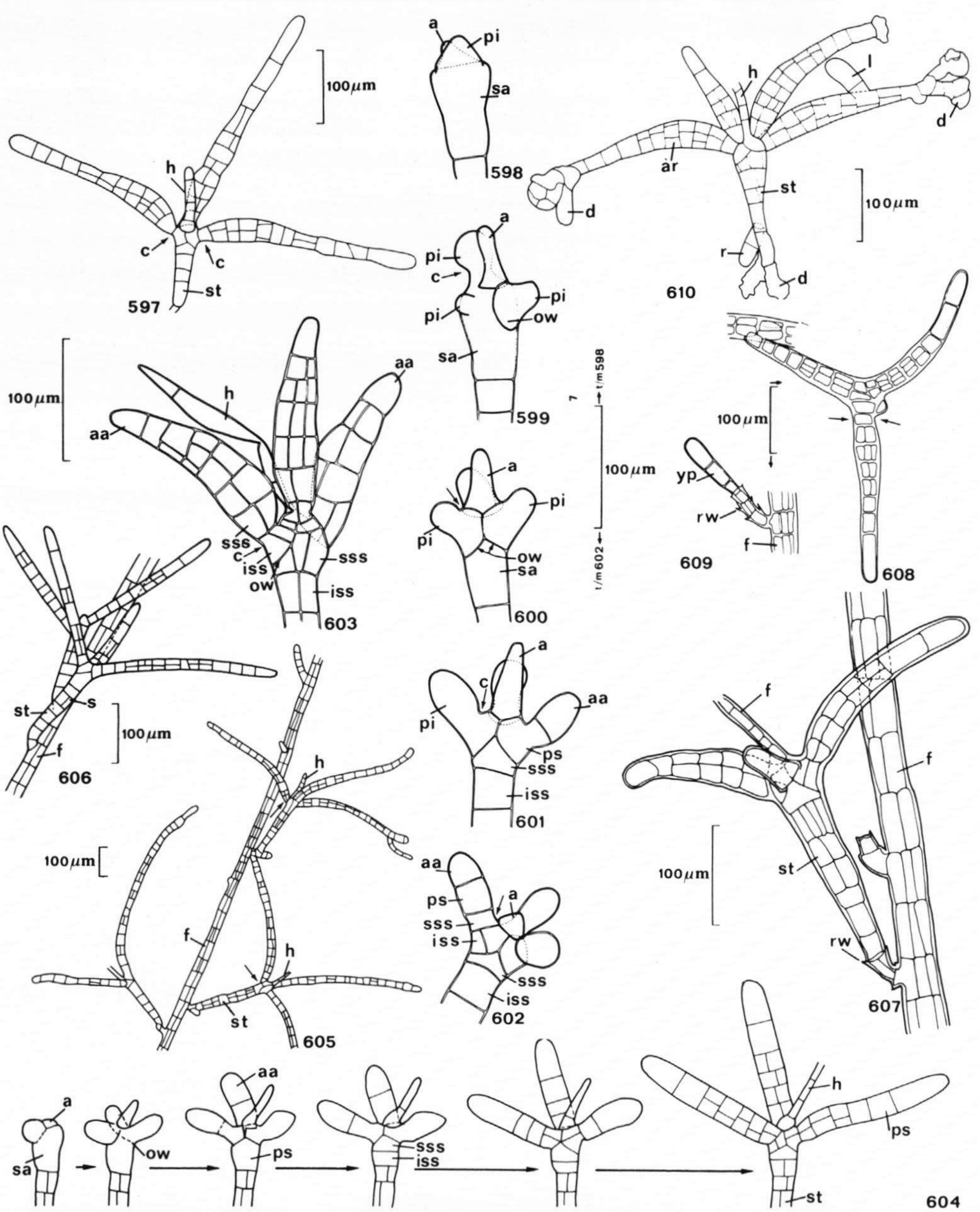


Fig. 597–610. Sphacelaria cirrosa, propagules. (598–604. Development, in 604 diagrammatic; 610. Germination). a. apical cell; aa. apical cell of an arm; ar. arm; c. constriction; d. attachment disc; h. hair; iss. inferior secondary segment; l. lateral; ow. oblique cell-wall; pi. protruding initial; ps. primary segment; r. rhizoid; rw. remnants of the wall of an earlier shed propagule; sa. sub-apical cell; sss. superior secondary segment; st. stalk yp. young propagule. 597, 610. Tenerife, *Van Steenis* (597. On *Cystoseira canariensis*; 610. On *C. discors*); 598–603. Locmariaquer, *Prud'homme van Reine 66-62* (microslides); 605. Culture 67-35; 606. Culture 67-74; 607. Kileströmen, *Boye* (O, soaked); 608, 609. Triest, *Pignatti* (TSB, microslide); 597, 610. Ecad *hystrix*; 598–606, 608, 609. Ecad *cirrosa*; 607. Ecad *bipinnata.*

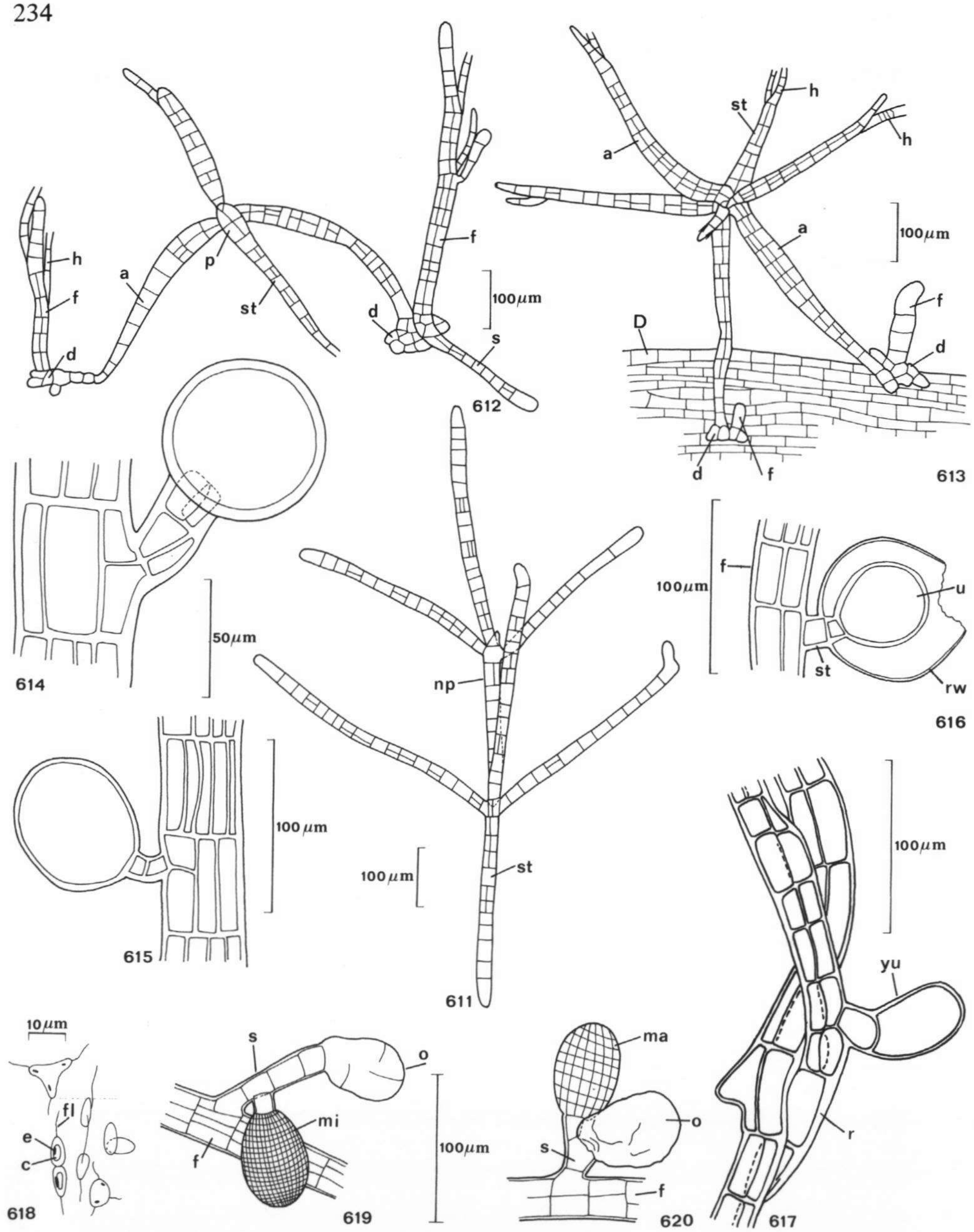


Fig. 611–620. Sphacelaria cirrosa. 611–613. Propagules (612, 613. Germinating); 614–617. Unilocular zoidangia; 618. Fusing unizoids; 619, 620. Plurilocular zoidangia. a. arm; c. chloroplast; d. attachment disc; D. *Dictyota* spec., e. eye-spot; f. erect filament; fl. flagella; h. hair; np. new propagule; ma. macrozoidangium; mi. microzoidangium; o. old zoidangium; p. propagule; r. rhizoid; rw. remnants of the wall of an empty zoidangium; s. stolon; st. stalk; u. unilocular zoidangium; yu. young unilocular zoidangium. 611. Culture 67-35; 612, 619, 620. Tenerife, *Van Steenis* (fresh); 613. Island Pianosa, *Pignatti* (TSB, microslide); 614. Triest, *Pignatti* (TSB, microslide); 615–617. St. Andrews, *Prud'homme van Reine 597* (formalin); 618. Roscoff, *Prud'homme van Rine 11-73* (fresh); 611, 613, 614. Ecad *cirrosa*; 612, 619, 620. Ecad *hystrix*; 615–618. Ecad *bipinnata.*

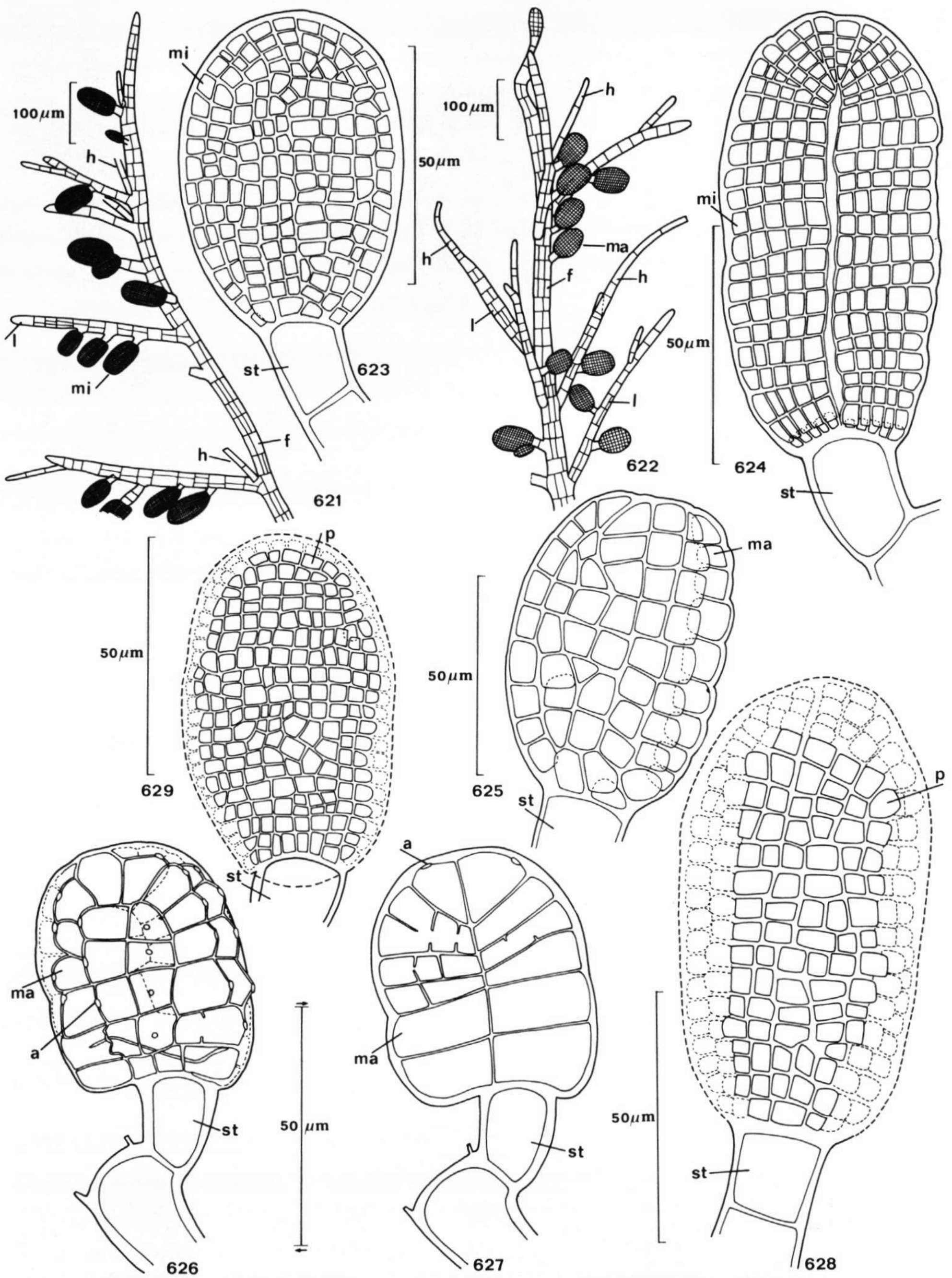


Fig. 621–629. Sphacelaria cirrosa, plurilocular zoidangia (624, 627. In optical section; 626, 627. Empty). a. aperture; f. erect filament; h. hair; l. lateral; ma. macrozoidangium; mi. microzoidangium; p. plurilocular zoidangium; st. stalk. 621–627. Tenerife, *Van Steenis* (fresh); 628. Rhosneigr, *Newroth* (BM, microslide 1114); 629. Roscoff, *Prud'homme van Reine 66-69* (microslide); 621–627. Ecad *hystrix*; 628. Ecad *cirrosa* (?); 629. Ecad *bipinnata*.

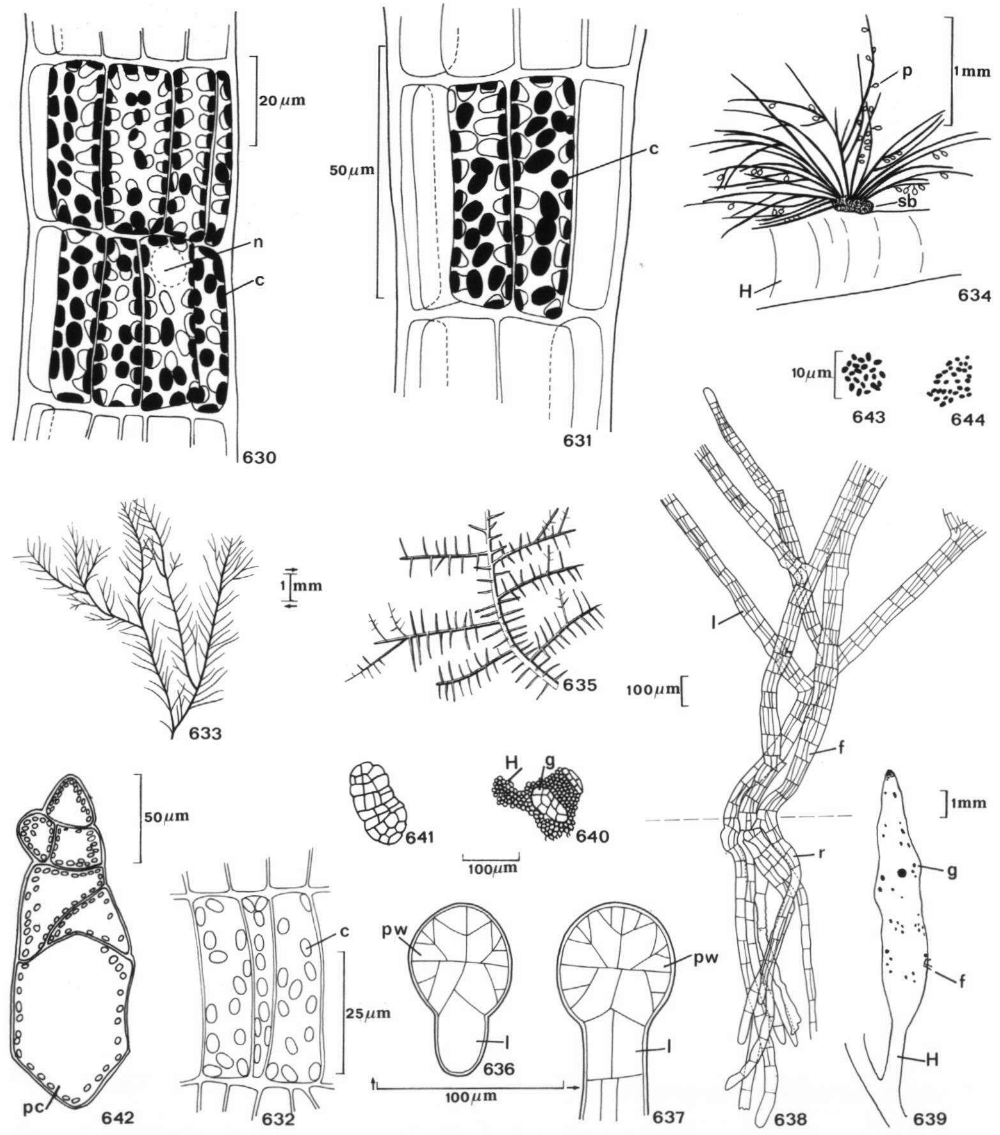


Fig. 630–644. Sphacelaria cirrosa. 630–632. Chloroplasts; 633, 635. Branching; 634. Habit; 636, 637. Cross-sections of erect filaments; 638–642. Endophytic parts (638. Rhizoids in *Codium* sp., 639–642. Germlings in *Halidrys siliquosa*; 640, 641. Seen from above; 642. Lateral view of a specimen which has been prepared free). 643, 644. Mitosis-metaphases or early anaphases of probably diploid nuclei of secondary segments of erect filaments. c. chloroplasts; f. erect filaments; g. germling; H. *Halidrys siliquosa*; l. lateral; n. nucleus; p. plurilocular zoidangia; pc. penetrating cell; pw. primary longitudinal wall; r. rhizoid; sp. sponge-like basal mass. 630. Fife Ness, *Prud'homme van Reine 667* (fresh); 631. Tenerife, *Van Steenis* (fresh); 632. Roscoff, *Prud'homme van Reine 66-69* (microslide, coloured with acetocarmine); 633. Kieler Hafen, *Nolte* (L, soaked); 634. Roscoff, *Prud'homme van Reine 67-25* (formalin); 635. St. Lunaire, *Prud'homme van Reine 290* (soaked); 636, 637. Roscoff, *Heerebout 67-5* (L, in alcohol); 638. Baie Ste Anne, *Crouan* (CO, soaked); 639–642. St. Andrews, *Prud'homme van Reine 71-8* (fresh); 643, 644. Culture 66-62-1; 630, 638 (?), 643, 644. Ecad *cirrosa*; 631. Ecad *hystrix*; 632, 634, 636, 637, 639–642. Ecad *bipinnata*; 633. Ecad *aegagropila*; 635. Ecad *patentissima*.

spp. Appressed rhizoids are absent or occur in small numbers. Often many propagules and/or many zoidangia occur.

Ecad *patentissima* (fig. 570; 635). Unattached, sterile plants with usually perpendicular branching; forming entangled masses between seagrasses.

Distribution. Europe: Faeroes, Norway, Sweden, Poland, Germany, Denmark, The Netherlands, Belgium, United Kingdom, Eire, France, Spain, Portugal, Italy, Yugoslavia, Greece, Turkey, Bulgaria, Romania, U.S.S.R. (coasts of the Black Sea).

Also on the Mediterranean coasts of Cyprus, Syria, Egypt, Tunisia, Algeria, and Morocco, and on the Atlantic coasts of Morocco, on the Madeira Archipelago, the Selvages, and the Canary Islands.

The species has also been recorded from Greenland, the Arctic coasts of the U.S.S.R., the Cape Verde Islands, Northern America (mainly from the Atlantic coasts), the Red Sea, Japan, Australia, and New Zealand. A selection of European localities (and some localities of the coasts of northern Africa and western Asia) has been listed and is given in fig. 645 and in 646. In fig. 645 localities of *S. cirrosa* proper are indicated; in fig. 646 localities of the ecads *bipinnata* and *hystrix*. The entities '*bipinnata*' and '*hystrix*' are mentioned behind the code of the collections in those cases where it was possible to discriminate.

For an extract of the list of collections and references see below.

GREENLAND. According to Rosenvinge (1893, p. 904) the citation of *S. cirrosa* as found on the coasts of Greenland by Lyngbye (1819, p. 105) and by Croall (1868, p. 458) is probably not correct.

ICELAND. Mentioned by Munda (1972b, p. 29 & 1978a, p. 363) for a locality in Iceland. From the supplementary information given by her it is obvious that the specimens are not ecad *bipinnata*, like she supposed. It is possible, however, that she found the typical *S. cirrosa*: northwestern Iceland, Dýrafjördur. I have not seen the specimens.

FAEROES. Two collections/references.

U.S.S.R. Arctic coasts. *S. cirrosa* has been mentioned as occurring in the northern parts of the U.S.S.R. by E. Zinova (1914, p. 233, 1929, p. 79) and A. Zinova (1953, p. 113). However, all specimens named *S. cirrosa* from this area I studied (all from the Leningrad herbarium) proved to be *S. arctica*.

NORWAY. Finmarken. Hasvik (Jaasund, 1965, p. 70).—Troms. Three collections/references; partly *bipinnata*.—Nordland. Two collections; partly *bipinnata*.—Nord Tröndelag. Trondhjemfjord: Vanvik, rockpools in the littoral region, *Foslie*, 19/8/1892 (BG, PC; probably *bipinnata*).—Hordaland. Many collections/references; partly *bipinnata*.—Rogaland. Four collections/references; partly *bipinnata*.—Vest Agder. More than six collections (partly *bipinnata*), amongst which Svinör (= Svinöy): *Foslie* in: Hauck & Richter, Phycoth. Univ. n. 367, 19/8/1885 (L and many other herbaria; usually *bipinnata* except one specimen in BR).—Aust-Agder. Six collections; partly *bipinnata*.—Vestfold. Three collections; partly *bipinnata*.—Akershus. Drøbak: several collections.—Ostfold. Two collections; all *bipinnata*.

SWEDEN. Bohuslän. Many collections (partly *bipinnata*), amongst which Gravarne (as Grafvarne): Areschoug in Prospectus of the Algae Scand. exs. n. 7, (O; in HBG; *bipinnata*). Fiskebäckskil: (as *S. cirrhosa* forma *propagulifera*), Areschoug in Algae Scand. exs. ser. nov. n. 109 (L and many other herbaria; in W partly *bipinnata*). Without exact locality: 'in mari Bahusiae', Areschoug in: Rabenhorst, Algen Europ. n. 1457 (L and many other herbaria; all *bipinnata*; in BR partly *bipinnata*). *Ibidem*: Areschoug in: Algae Scand. exs. ser. nov. n. 108 (L and many other herbaria; all *bipinnata*). *Ibidem*: (as var. *nana*), *Akermark* in: Areschoug Algae Scand. exs. ser. nov. n. 219 (L and many other herbaria). *Ibidem*: Akermark in: Typsamling n. 62 (BR, GB, HBG, O, W; all *bipinnata*).—Halland. Many collections (partly *bipinnata*), amongst which Släp: Areschoug in: Algae Scand. exs. n. 35 (BR, HBG, KIEL, L, PC; probably all *bipinnata*). Varberg: (as var. *pennata*), Hylmö in: Skand. Meeresalgen n. 40, 26/9/1913 (GB, HBG, LD, M, O, WU). *Ibidem*: (as *S. bipinnata*), *Hylmö* in: Schiffner Algae mar. exs. n. 919, 21/9/1929 (M, PAD, WU; all *bipinnata*).—Skåne (Kristianstads Län). Three collections; partly *bipinnata*.—Skåne (Malmöhus Län). Many collections; partly *bipinnata* or ecad *aegagropila*. Waern (1964, p. 310) mentioned *S. cirrosa* from Småland & Södermannland, but without exact localities.

POLAND. Three references.

Fig. 645. Distribution of *S. cirrosa* (except ecads *bipinnata* and *hystrix*), mainly in Europe.

● = Specimens seen by the author. ★ = Data from literature. (●) = Drift specimens.

GERMANY. Baltic coasts. Many collections/references (partly ecad *aegagropila*), amongst which the specimens distributed in Breutel: Flora Germ. exs. ser. II, n. 127 which are from Travemünde (HBG, L, M, MPU, PC, W). Bülk, *Reinke* in Hauck & Richter: Phycoth. Univ. n. 367 (in L and many other herbaria). Flensburger Meeresbusen: *Häcker* in Rabenhorst: Algen Sachs. n. 754 (in L and many other herbaria) and also (as *S. cirrhosa β Aegagropila*) in Rabenhorst: Algen Sachs. n. 800 (in L and many other herbaria).—Northsea coast. Four collections, amongst which Sylt: List, (as *S. cirrosa* var. *aegagropila*), washed up, *Kuckuck* in Krypt. exs. Mus. Palat. Vindob. n. 1748 (in L and many other herbaria).

DENMARK. Kattegat. More than six collections/references; partly *bipinnata*.—Samsø area. Many collections (partly *bipinnata* or ecad *patentissima*).—Lillebaelt. Nord of Faenø Kalv: 13 m deep. *Rosenvinge 1378*, 29/6/1891 (C; *bipinnata*).—Storebaelt. Two collections/references; partly *bipinnata* and partly ecad *patentissima*.—Øresund. Three collections/references; partly *bipinnata*.—

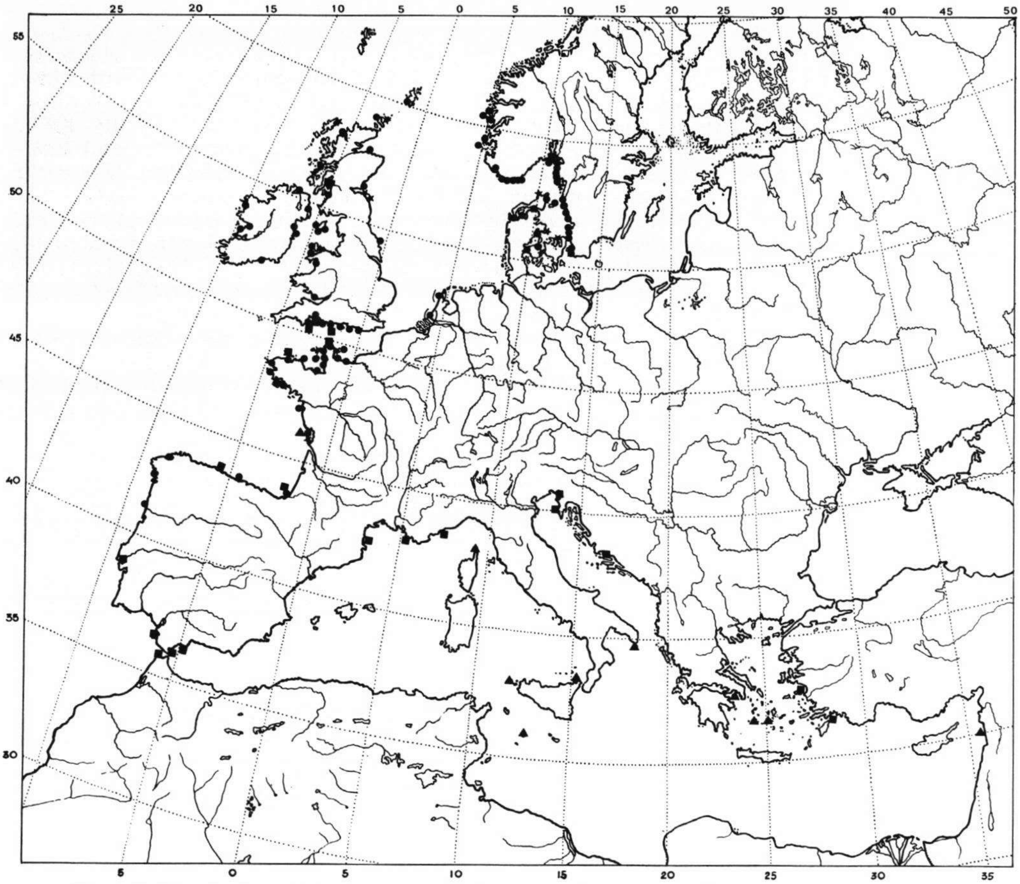


Fig. 646. Distribution of *S. cirrosa* ecad *bipinnata* and *S. cirrosa* ecad *hystrix*, mainly in Europe.

● = *S. cirrosa* ecad *bipinnata*: specimens seen by the author. ★ = *S. cirrosa* ecad *bipinnata*: data from literature. ▼ = *S. cirrosa* ecad *bipinnata*: uncertain material or locality. (●) = *S. cirrosa* ecad *bipinnata*: drift specimens. ■ = *S. cirrosa* ecad *hystrix*: specimens seen by the author. ▲ *S. cirrosa* ecad *hystrix*: data from literature.

Bornholm. Without exact locality: *Steetz*, 1/4/1831 (MEL).—Skagerrak. Hirtshals (Lund, 1950, p. 42; *bipinnata*).—Limfjorden. Seven collections; probably partly *bipinnata*.—North Sea. Jydske Rev (Lund, 1950, p. 37).

THE NETHERLANDS. Several collections; partly *bipinnata*.

BELGIUM. Oostende, on *Furcellaria*, (as *S. cirrhosa β nana*), *Westendorp*, 1872 (BR; probably washed up).

UNITED KINGDOM. Shetland. Several collections/references, partly *bipinnata*.—Orkneys. More than five collections/references; partly *bipinnata*.—Scotland. Ross & Cromarty: three collections; partly *bipinnata*. Invernessshire: Barra, (Sinclair, 1938, p. 434, as *S. cirrhosa* forma *pennata*). Argyllshire: four collections; partly *bipinnata*. Buteshire: two collections/references; partly *bipinnata* and partly ecad *patentissima*. Ayrshire: more than three collections; partly *bipinnata*. Kircudbrightshire: Little Ross, (as *S. pennata*), *James*, 8/1965 (BMf. Morayshire: two collections; partly *bipinnata*. Aberdeenshire: four collections. Fife: several collections; often *bipinnata*. East Lothian: two references; partly *bipinnata*. Without exact locality: (as *S. pennata*), Greville in: Algae Brit. n. 24 (BM, BR, L, MEL).—Isle of Man. Several collections; partly *bipinnata*.—Wales. Anglesey: More than five collections/references; partly *bipinnata*. Caernarvon: Nevin (= Nefyn), Penhryn, (as *S. racemosa*), *Schiller* in Schiffner: Algae mar. exs. n. 1203 (BM, S; both probably *bipinnata*). Merionethshire: two collections: partly *bipinnata*. Pembrokeshire:

two references. Glamorganshire: Barry Island, (as *Conferva scoparia*; young), *Lightfoot* (K in BM; *bipinnata*). —England. Cheshire: Hilbre Island, (as *S. scoparia*), 1/8/1863 (LIVU, on *Stypocaulon scoparium*). Northumberland: four collections/references; partly *bipinnata*. Yorkshire: two collections; partly *bipinnata*. Norfolk: Cley, (as *S. fusca*), *Batters 81*, 28/8/1886 (BM, KIEL, L, PC). Cornwall: two collections/references, amongst which Paignton, (as *S. fusca*), Holmes in: Algae Brit. rar. exs. n. 123 (BR, KIEL, LIVU, OXF, TCD; in BM probably partly *bipinnata*). Devon: many collections/references (partly *bipinnata* or *hystrix*), amongst which Torbay, in Wyatt: Algae Danm. n. 171 (in L and many other herbaria; in BM probably partly *bipinnata*). Dorset: Weymouth, four collections (partly *bipinnata* or *hystrix*), and Holmes, (as *S. cirrhosa* var. *patentissima*) in: Alg. Brit. rar. exs. n. 22 (KIEL, LD, OXF). Hampshire: several collections; probably partly *bipinnata*. Sussex: seven collections; partly *bipinnata* or ecad *patentissima*. —Channel Islands. More than four collections; partly *bipinnata*. —Northern Ireland. Donegal: two collections; partly *bipinnata*. Antrim: several collections, all *bipinnata*. —Without exact locality. Cocks: Algarum fasc. n. 76 (PC; *bipinnata*).

EIRE. Mayo: several collections; partly *bipinnata*. Galway: three collections; partly *bipinnata*. Clare: two collections; partly *bipinnata*. Kerry: Dingle Peninsula, Ferriter's Cove, *Andrews* (TCD). Cork: Bantry, (as *Conferva pennata*), *Mrs. Hutchins*, 7/1806 (BM; *bipinnata*). Dublin: three collections; partly *bipinnata*. Wicklow: Greystones, on *Desmarestia*, *Prud'homme van Reine 66-34*, 27/7/1966 (L). Cork: three collections. Waterford: Curragh, in deep narrow pools, *Guiry*, 19/8/1973 (L; *bipinnata*).

FRANCE. Atlantic coasts. Calvados: three collections; partly *bipinnata*. Manche: many collections/references (partly *bipinnata*, *hystrix*, or ecad *patentissima*), amongst which Cherbourg: Le Jolis in: Algues mar. Cherb. n. 39 (in L and several other herbaria; mainly *bipinnata*). Cherbourg, in Hohenacker: Arznei und Handelspfl. n. 217 (E, S; in L, OXF & TCD *bipinnata*) and in Hohenacker: Algae mar. sicc. n. 309 (GOET, HBG; in L, M, PC, and W *bipinnata*). Without exact locality: Chauvin in: Algues Norm. n. 36 (BM, CHE, PC, UPS). Ille-et-Vilaine: four collections/references; partly *bipinnata*. Côtes du Nord: Ile de Bréhat, on *Cystoseira baccata*, 8/1916 & 8/1919, *Lami* (DIN; *bipinnata*). Finistère: many collections (partly *bipinnata*, *hystrix*, or ecad *patentissima*), amongst which Roscoff, Ile Verte, *Miciol* in: Soc. dauphin. n. 4405 (FI, M, MPU, PC) and (as *S. cirrhosa* var. *fusca*), Baie de Berthéaume & Anse de Délec, Crouan in: Algues mar. Finist. n. 35 (M, PC; in other herbaria *S. rigidula* or *S. fusca*). Without exact locality: Crouan in: Algues mar. Finist. n. 33 (CO, M, PC; partly *bipinnata*). *Ibidem*: (as *S. cirrhosa* var. *nana*), Crouan in: Algues mar. Finist. n. 34 (CO, L, M, PC). Morbihan: several collections (partly *bipinnata*), amongst which Belle-Ile, in Lloyd: Algues Ouest France n. 113 (CO, partly *bipinnata*; in L and PC all *bipinnata*). Without exact locality: (as *S. cirrhosa* var. *aegagropila* or as *S. pennata*), Le Lièvre de la Mornière & Prouhet: Hydroph. mar. Morbihan (L; in PC *bipinnata*). Vendée: Ile de 'Yeu, on *Cystoseira baccata*, *Lami*, 8/1921 (DIN; *bipinnata*). Charente Maritime: four collections/references; partly *bipinnata* or *hystrix*. Basses Pyrénées: eight collections/references; partly *bipinnata* or *hystrix*. —Mediterranean coasts. Pyrénées Orientales: several collections; partly *hystrix*. Aude: La Nouvelle, on dead twigs of *Salicornia europaea*, *Maugeret* in Roumeguère: Algues France n. 465 (BR, L). Hérault: several collections. Bouches-du-Rhône: four collections, amongst which Marseille (as *Ceramium spinulosum*), in: Alg. Schousboeanae n. 111 (BM, MPU, PC). Ile Ratonneau, Pointe d'Escourbidon, *Berner* in Schiffner: Algae mar. exs. n. 921 (BM, LD, MPU, UPS, WU; *hystrix*). Calangue de Ratonneau, *Berner* in Schiffner: Algae mar. exs. n. 653 (BM, UPS, WU *hystrix*). Var: two collections. Alpes maritimes: more than four collections (partly *hystrix*), amongst which Antibes (as *S. cirrhosa* var. *irregularis* f. *laxa*), *Broeksmit* in Schiffner: Algae mar. exs. n. 397 (BM, UPS, WU). Corse: several collections/references; partly *hystrix*.

SPAIN. Atlantic coasts. Six collections; partly *bipinnata* or *hystrix*. —Mediterranean coasts. Six collections; partly *hystrix*.

PORTUGAL. Douro littoral: Leça de Palmiera, *Welwitsch* (LISU; partly *bipinnata*). Estremadura: three collections (partly *hystrix*), amongst which Lagôa d'Obidos, (partly as *S. spec.* or as *S. gomeziana*), Welwitsch: Phycoth. lusitana n. 66 and n. 74 (BM, E, L, LD, LISU, MEL, OXF, PC). *Ibidem*: Tago salso, Caxais, Cruz Quebrada, Welwitsch: Phycoth. lusitana n. 20; 8/1849 (BM, E, LD, OXF; *hystrix*, in LISU partly *hystrix*). Baixo Alentejo: Sines (Ardré, 1970, p. 390–391, partly as *S. hystrix*). Algarve: three references.

ITALY. Ligurian coasts. Four collections, amongst which Porto Maurizio: (as *S. cervicornis*), *Strafforello* in: Erb. critt. Ital. ser. 2, n. 1439 (FI, M, W). St. Nazaro: *Dufour* in: Erb. critt. Ital. ser. 1, n. 853 (BM, FI, PC, WU). —Sardegna. Alghero: *Marcucci*, 4–10/5/1881 (PAD). —Tyrrhenian coasts. More than three collections. —Sicilia. Four collections/references; partly *hystrix*. —Ionian coasts. Capo San Maria di Leuca (Giaccone, 1969, p. 499, as *S. hystrix*). —Adriatic coasts. Many collections (partly *hystrix*), amongst which Miramar, on *Cystoseira compressa*, *Schiller* in Schiffner: Algae mar. exs. n. 144 (BM, PAD, W).

YUGOSLAVIA. Many collections (partly *hystrix*), amongst which Izola: *Seefelder* in: Algae Adriat. exs. n. 86 (BR, HBG, M, PAD, ZA). Rovinj (as Rovigno): *Schiller* in: Krypt. exs. Mus. Palat. Vindob.

n. 1748b (in L and many other herbaria). Split (as Spalato): on *Cystoseira barbata*, (as *S. cirrhosa* var. *irregularis* f. *densior*), *Varda* in Schiffner: Algae mar. exs. n. 396 (BM, M, PAD, WU). Solta: Maslinica, on *Posidonia*, 1–3 m deep, (as *S. cirrhosa* var. *rhizophora*), Schiffner in: Algae mar. exs. n. 920 (M, UPS, WU). Vis (as Lissa): (as *S. cirrhosa* var. *irregularis* f. *deusta*), *Schiller* in Schiffner: Algae mar. exs. n. 651 (BM, LD, M, UPS, WU). Boka Katorska (as Bocche di Cattaro): (as *S. cirrhosa* var. *irregularis* f. *laxa*), *Schiller* in Schiffner: Algae mar. exs. n. 652 (BM, PAD, WU).

GREECE. Many collections/references; partly *hystrix*.

TURKEY. Four collections/references.

BULGARIA. Four references.

ROMANIA. Four collections/references, amongst which Constanta, washed up, (as *S. cirrhosa* var. *irregularis*), *Teodoresco* in: Krypt. exs. Mus. Palat. Vindob. n. 842 (in L and many other herbaria).

U.S.S.R. Black Sea. Six collections/references.

CYPRUS. Cape Pyla: *Cohen PHYT 2181*, 26/10/1969 (TELA, mixed with *S. rigidula*).

SYRIA. Five references; partly *hystrix*.

EGYPT. Alexandria, *Hedenborg* (UPS).

TUNISIA. Two collections, amongst which Sfax, (as *S. cirrhosa* var. *pennata* f. *laxa*), *Schussnig* in Schiffner: Algae mar. exs. n. 145 (BM).

ALGERIA. Three collections/references.

MOROCCO. Six collections/references (partly *hystrix*), amongst which Algae Schousboeanae 112 and 113 (BM, MPU, PC; *hystrix*), and Algae Schousboeanae 114 (PC, mixed with *S. rigidula*).

AZORES. Four collections/references; partly *hystrix*.

MADEIRA. Three collections (partly *hystrix*), amongst which without exact locality: in Mandon: Algae Maderenses n. 30 (CN, MEL, MPU, PC, W). Deserta Grande: in tidal pools and also 2–4 m deep, *CANCAP 869* and *980*, 18/10/1978 (L). Selvagem Grande: two collections; partly *hystrix*.

CANARY ISLANDS. Hierro: several collections. Tenerife: several collections (mainly *hystrix*). Gran Canaria: several collections (partly *hystrix*). Fuerteventura, Corralejo, *Lowe*, 9/4/1859 (BM; *hystrix*). Lanzarote, Arecife, 14–16/8/1882, *d'Albertis* (PAD).

Notes on nomenclature. (1) In his description of *Conferva cirrosa* Roth (1800b, p. 214) mentioned *Conferva marina perbrevis villosa et cirrosa* Dillen as a synonym. He had no access to Dillen's herbarium, however, but studied specimens from the Wulfen herbarium. The International Code of Botanical Nomenclature (Stafleu *et al.*, 1978), in the guide for the determination of types paragraph 4b, states that in a case like this a specimen should preferably be chosen as the lectotype. I follow De Haas-Niekerk (1965, p. 156) who selected the lectotype from the Wulfen collection.

(2) *Ceramium cirrosum sensu* W. Hooker (1821, p. 86) and *Conferva pennata sensu* Dillwyn (1806, t. 86) and *sensu* Smith & Sowerby (1812, t. 2330) comprise specimens of *S. cirrosa* (including its ecad *bipinnata*) as well as *S. plumigera*.

(3) The lectotype is without a number. The number cited by De Haas-Niekerk ('WU, sh 1261') is incorrect. On the sheet labeled by her 'TYPE, *Conferva cirrosa* Roth, T. Niekerk, V/1964' is stamped 'Acq. Journ. No 1263'. This stamped acquisition number can be found on all specimens obtained from the Wulfen collection and many other old herbaria. Dr. M. Fischer of the Botanical Institute of the University of Vienna informed me that all plants of Acq. Journ. No. 1263 are old herbaria which had been found in the loft of the old museum on 10/4/1892.

(4) As will be explained later (see sections on characters of entities and on systematic position) it was not possible to maintain the entities *S. bipinnata* and *S. hystrix* as separate species. I could not find a sound basis to separate them consistently from the rest of the *S. cirrosa* complex. I realize, however, that reliable characters may be detected in future. For that reason I will keep them apart under the informal names 'ecad *bipinnata*' and 'ecad *hystrix*'. In most of the sections I will use these ecad names in cases it is relevant and possible to discriminate, using the same characters as used by Sauvageau (see table XIX).

(5) There are also specimens of *Conferva marina perbrevis, villosa et cirrosa* in the herbarium of the *Historia Muscorum*. This herbarium had been made by or for Dillen in February 1744, so a few years after the publication of the *Historia Muscorum*. Turner (1804, p. 106), who studied this herbarium, remarked 'The specimens in the herbarium differ extremely from the magnified figures . . .'. In the Sherardian herbarium, however, on the sheet of *Conferva marina perbrevis, villosa et cirrosa* the specimen figured may be present (plate 6). The specimen on the left is a fragment of *Furcellaria lumbricalis* covered with many epiphytes, but mainly by *S. cirrosa*. The middle specimen is a fragment of *Fucus vesiculosus*, and the specimen on the right is *Chondrus crispus*. Both specimens are mainly covered by *S. cirrosa*. The figure 21 of Dillen shows a fragment of a dichotomously branched larger alga on which the epiphytic *S. cirrosa* is growing. The lower part of this larger alga is figured as being terete. For that reason I suppose the fragment used for the figure 21 by Dillen had been cut from the *Furcellaria* and not from the narrow *Chondrus*.

(6) The nomenclatural status of *Conferva pennata* Hudson (1762, p. 486) was discussed by Dixon & Parkes (1968, p. 80). They decided that it was impossible at the present time to locate the original material of any of the (three) elements cited by Hudson in the initial description of his *Conferva pennata*. I also tried to locate these elements, but without success. So the name *Conferva pennata* Hudson is a nomen dubium confusum.

(7) The significance of infraspecific taxa within *S. cirrosa* is discussed in the section on Characters of entities (p. 245) and in the section on Systematic position (p. 256).

Notes on morphology. In the secondary segments of *S. cirrosa* a varying number of longitudinal walls is formed. All walls are more or less radial, never periclinal (fig. 589–593). Figures of transverse sections of filaments by Geyler (1866, t. 36, f. 9–11), Reinke (1892, t. 42, f. 3A–B) and Sauvageau (1902, f. 41, M, as *S. hystrix*) agree well with my figures. Geyler (1866, t. 36, f. 18–20) also figured (as *S. cirrosa*) transverse sections of filaments of *S. cirrosa* ecad *bipinnata*. His fig. 19 is presumably a misinterpretation. In this figure Geyler showed two laterals arising from a secondary segment. The laterals are separated from the other cells of the segment by periclinal walls parallel to the primary longitudinal wall, and each lateral has obviously been formed by two peripheral cells. Actually, laterals arise always from a single peripheral cell and usually almost perpendicular to the primary longitudinal wall of the secondary segment of the axis. Usually the next longitudinal walls in the axis are radial (but not always medial) and perpendicular to primary wall. Often they are oblique or bent, forming a peripheral cell which is larger than usual. This large peripheral cell is an initial which can form a lateral (fig. 636; 637). In a later stage longitudinal walls of the lateral may divide the large peripheral cell into two or more smaller ones, but structures similar to Geyler's f. 19 were never observed by me.

Primary laterals arise in a very variable pattern and in a rough acropetal sequence. Many primary laterals of the first order are narrow and show determinate growth (fig. 577). When *S. cirrosa* is growing in dense algal turfs, however, most laterals are indeterminate. Determinate laterals taper distinctly into narrow acute apical cells (fig. 581; 584), or into apical hairs. Sometimes these hairs are subapical (fig. 587; 622). Occasionally very narrow laterals of the second and third order arise (fig. 583), especially in plants forming dense bushes or in unattached plants (fig. 633; 635). Almost all mature cells of the filaments are peripheral and they can all function as branch-initials. Usually only one or two (occasionally more) cells of a superior secondary segment form laterals, but occasionally laterals arise from inferior secondary segments too.

The angle of ramification is variable but usually the laterals are distinctly spreading with sharp angles (fig. 577; 633). In unattached entangled specimens ramification is usually perpendicular (fig. 635). If the tips of erect filaments meet a suitable substrate they can form secondary attachment discs (fig. 584) from which new erect filaments are to arise. Secondary attachment discs can also be formed by rhizoids or stolons. Basal discs as well as secondary attachment discs are usually monostromatic when young (fig. 572; 584), but on suitable hosts they are often massive obconical parenchymatous structures anchoring the plants in the host (fig. 578). The development of these multicellular endophytic structures has been described in detail by Goodband (1973), see also the section on Reproduction and life-history in the present paper (p. 255). Older discs are usually polystromatic (fig. 571) and on suitable hosts they are often partly endophytic (fig. 575). When growing on *Codium* species *S. cirrosa* usually forms many long rhizoids, similar to those of *S. rigidula, S. plumula* and *S. tribuloides* growing on that spongy green alga (fig. 638). The endophytic basis has been used as a specific character to separate the ecads *bipinnata* and *hystrix* from *S. cirrosa* ecad *cirrosa*. As will be explained later (in the section on Characters of entities, p. 245, and in the section on Systematic position, p. 256), endophytism cannot be used as a taxonomic criterion in *S. cirrosa*, however.

Hairs in *S. cirrosa* are acroheteroblastic or terminal and always solitary (fig. 582–584; 587; 588; 594; 595; 621; 622). In this species solitary hairs can often be found near the axils of laterals (fig. 582; 588; 594; 621) or just above the point where the basal cell of a propagule is attached to the axis (fig. 582). Sauvageau (1903, p. 84 = Ʀ. 255) observed these pseudo-axillary hairs mainly in *S. rigidula* and *S. tribuloides*; less often in *S. cirrosa* and in its ecad *hystrix*. He figured these pseudo-axillary hairs, however, only for '*S. hystrix*' (1902, f. 39) and in a diagram resembling a *Sphacelaria* of the *cirrosa*-group (1903, f. 48). Coppejans (1977) figured the relation of hairs, laterals and propagules in *S. cirrosa* (f. 72), *S. rigidula* (f. 73), his supposed *S. fusca* (f. 75, 1 and f. 76) and *S. tribuloides* (f. 78). From these published figures it is clear that no distinct relation between laterals and pseudo-axillary hairs exists.

Notes on ecology. *Sphacelaria cirrosa* is the most common member of the *Sphacelariaceae* in Europe. It can be found in tidal pools in the littoral, growing on and between Coralline algae. It grows also directly on the rocks and on many algae in the littoral and the sublittoral, to depths of 20–30 m. Funk (1955, p. 43) found it near Naples at a depth of 50 m. It is often found as an epiphyte on *Cystoseira* spp. and on *Halidrys siliquosa*. Specimens of *S. cirrosa* growing on (and also partly endophytic in) these larger *Phaeophyceae* have often been named '*S. hystrix*' and '*S. bipinnata*' respectively. As will be explained later (in the section on Systematic position, p. 256) these two entities are to be considered as growth-forms caused by ecological factors (ecads). Specimens of the ecad *bipinnata* have been found in north-western Europe, growing on *Halidrys siliquosa*, as well as in south-western atlantic Europe, growing on *Cystoseira baccata*. On many species of *Cystoseira* growing in south-western atlantic Europe, along the coasts of the Mediterranean and in the North African part of the Atlantic the ecad *hystrix* occurs. Occasionally the last-mentioned ecad can also be found on *Sargassum desfontainesii*.

Sauvageau (1912, p. 274) remarked that in Guéthary, France, *Cystoseira nodicaulis* is the winter host of '*S. hystrix*'. In February and March in 1911, when *Cystoseira tamariscifolia* started growth again after the winter rest, ecad *hystrix* on *Cystoseira nodicaulis* had many plurilocular gametangia. After some weeks young ecad *hystrix* plants could be found on the young thalli of *Cystoseira tamariscifolia* which were possibly germlings of zygotes from fused gametes of the *hystrix* plants growing on *C. nodicaulis.*

Sphacelaria cirrosa cannot stand desiccation very well. As a consequence it usually cannot be found outside the tidal pools in the upper parts of the littoral. On coasts where small algae form a thick algal turf, however, *S. cirrosa* can usually be found as a member of the turf-community, even in parts of the turf that may emerge for prolonged periods.

Sphacelaria cirrosa is not a common inhabitant of salt-marshes. In mediterranean France (Aude: la Nouvelle), however, it has been found growing on dead twigs of *Salicornia europaea.*

Unattached populations of *S. cirrosa* are found in *Zostera*-meadows and on sandy shores. Specimens found among *Zostera* plants have often been called forma *patentissima.* They occur in Norway (Kalvåg, near Hardangerfjord), Denmark (Limfjord, Odense-fjord), Scotland (Oban), England (south coast) and France (Cotentin and Brittany). The unattached, usually sterile, specimens with perpendicular laterals (fig. 635) can be found in entangled masses (fig. 570), often together with other algae.

On sandy coasts in north-western Europe *S. cirrosa* sometimes forms algal balls (aegagropilae, fig. 569). In the Sound the algal balls often consists of several *Sphacelariales*, amongst which, besides *S. cirrosa*, usually *S. arctica* and *S. radicans.* Irregular algal balls have also been found near List on the northern German isle Sylt by *Kuckuck* before 1910. According to Kornmann (1952) these balls disappeared in the thirties when a disease killed *Zostera marina* in this area.

Sphacelaria cirrosa is a genuine marine species. It does, however, enter into narrow sheltered bays or estuaries as long as salinity is high enough. In Hardangerfjord (Jorde & Klavestad, 1960, p. 96), *S. cirrosa* has been found quite far in the inner area, but in these localities salinity was always well above 10‰. In Oslofjord (Sundene, 1953, p. 158; Klavestad, 1978, p. 95) and in Sullom Voe, Shetland, (Tittley *et al.*, 1976, p. 408), where salinity never drops very low, *S. cirrosa* can also be found in the innermost areas.

The ecad *bipinnata* never enters far into land-locked narrow fjords. Jorde & Klavestad (*l.c.*, p. 95) mentioned that on *Halidrys* growing in the innermost area of Hardangerfjord they found *S. cirrosa* without any characters of the ecad *bipinnata.*

Von Wachenfeldt (1975, p. 216) found *S. cirrosa* rather sparsely distributed in the northern and central part of the Sound, but not in the southern part. According to him *S. cirrosa* is a polyhalobe pleioeuryhaline species. He (Von Wachenfeldt, *l.c.*, p. 215) found ecad *bipinnata* only in the northern part of the Sound, and called it a polyhalobe meioeuryhaline 'species'. Its host, *Halidrys siliquosa*, does not occur further south either. Most specimens of *S. cirrosa* from the Baltic seen by me (see fig. 645) are from localities where salinity is always well above 10‰.

Form range and cultures. Morphological variation is extensive in *S. cirrosa*, as appears from the species description.

Specimens collected from the Baltic are often dark in colour and very reminiscent of *S. arctica.*

Sauvageau (1902, p. 384 = R. 198, f. 42D) observed often in ecad *bipinnata* that the superior secondary segments were shorter than the inferior ones. In these cases he found several transverse walls in the long inferior secondary segments. I observed long inferior secondary segments (72–90 (–101) μm) and shorter superior ones (54–65 μm) in living filaments (36–45 μm in diameter) of *S. cirrosa* growing on rocks and Rhodophytes near Kristineberg, Sweden in May 1967.

Cultures have been isolated from Norway (Espegrend, Øystese and Drøbak), Sweden (Kristineberg and Fritlesås), and France (Grandcamp-les-Bains, St. Lunaire, Roscoff, Rade de Brest, Morgat, Locmariaquer, and Banyuls-sur-Mer). Four cultures derived from unattached specimens ('forma *patentissima*'); two from specimens growing on *Desmarestia aculeata* ('forma *nana*'), six from specimens growing on *Halidrys siliquosa* (*S. 'bipinnata'*), two from plants growing on *Cystoseira baccata* (*S. 'bipinnata'*; Concarneau & Roscoff), one from *C. nodicaulis* (*S. 'hystrix'*; Roscoff) and one from a plant growing on *C. caespitosa* (*S. 'hystrix'*; Banyuls). The other original specimens have been collected from a number of substrates, amongst which rocks, wood, Coralline algae, *Cystoseira* spp. and other algae (*S. 'cirrosa'*).

Most cultures could be maintained during several years. For some results see table XVIII.

Rhizoids were not formed in my cultures, not even in attached germlings from plurizoids found at 12°C in culture 67–92 ('*bipinnata*'). At 4°C most cultures remained sterile and died within some months after having been transferred to those low temperatures. Some cultures of Scandinavian origin, however, grew well at 4°C and did even form propagules. At 20°C my cultures of *S. cirrosa* did not usually grow very well. Many apical cells died in an early stage and often the cultures died before they had ever produced propagules. In the cultures of French Atlantic origin where propagules were formed the production of these structures was often so profuse that the erect filaments suddenly died.

In all cultures the erect filaments were quite flexible (not rigid) and the laterals showed no distinct determinate growth. Most or all secondary segments of these filaments were longer than wide and at 12°C and 20°C many hairs were formed. The colour of the filaments was light brown, yellowish brown or reddish brown, the fertile filaments of ecad *bipinnata* being almost colourless. Cultures started as *S. cirrosa*, *S. cirrosa* forma *patentissima*, *S. cirrosa* forma *nana* and *S. hystrix* were quite similar, those started as *S. bipinnata* differed mainly in colour and fructification.

Characters of entities within the *S. cirrosa* complex. When separating the different species and infra-specific taxa within the section *Propagulifera* Sauvageau (1902, p. 325–349, 379–416 & 1903, p. 45–53 = R. 167–237) used many characters of the prostrate system, the erect system, the substrate, the propagules and the zoidangia (table XIX). The characters of the vegetative system used by Sauvageau will be discussed below.

Endophytism. The small basal disc is often slightly or distinctly polystromatic in older specimens of *S. cirrosa*, also in basal discs which are not endophytic (fig. 571). Endophytic, epiphytic as well as epilithic specimens occur in *S. rigidula* and in *S. caespitula*. Presence or absence of endophytism (usually the term 'parasitism' was used) had formerly been used to separate *S. furcigera* from *S. fusca* and *S. olivacea* from *S. caespitula*. In both cases it has been demonstrated that endophytism occurs when the substrate is suitable for it, but that the same species can grow purely epiphytic or epilithic as well. There is no reason to

TABLE XVIII. Reproductive structures of ecads of S. cirrosa observed in culture

culture	locality and entity	propagules						zoidangia at 12° C	
		arms			temp. °C			pluriloc.	uniloc.
		2	3	4	4	12	20		
	ecad cirrosa								
66–46–4	Roscoff	-	+	-	-	+	+	-	-
66–54	Roscoff	-	+	-	-	+	-	-	-
66–60–8	Morgat	-	+	-	-	+	-	-	-
66–62–1	Locmariaquer	-	+	-	-	+	+	+	-
66–68–2	Roscoff	-	+	-	-	+	-	-	-
66–71	Roscoff	-	+	-	-	+	-	-	-
66–77	Le Caro	-	+	-	-	+	-	-	-
66–89	Roscoff	-	+	-	-	+	-	-	-
66–94	Roscoff	-	+	-	-	+	-	-	-
66–96	Roscoff	-	+	-	-	+	-	-	-
67–10–2	Kristineberg	+	+	+	-	+	-	-	-
67–25	Espegrend	-	+	-	-	+	-	-	-
67–35	Espegrend	+	+	+	-	+	-	-	-
67–58	Øystese	+	-	-	+	-	-	-	+
67–62–1	Øystese	+	-	-	-	+	-	-	-
67–74	Drøbak	+	+	-	-	+	-	-	-
67–96	Banyuls	-	-	-	-	-	-	-	-
67–103	Banyuls	-	+	-	-	+	-	-	+
68–24	St. Lunaire	-	-	-	-	-	-	-	-
68–54	Grandcamp	-	+	-	-	+	+	-	-
	ecad patentissima								
66–42–3	Roscoff	-	+	-	-	+	-	-	-
66–85–1	Roscoff	-	+	-	-	+	-	-	-
66–105–2	Roscoff	-	+	-	-	+	-	-	-
68–25	Roscoff	-	-	-	-	-	-	-	-
	ecad cirrosa (as 'var. nana')								
67–16	Kristineberg	-	+	-	-	+	-	-	-
67–28	Espegrend	-	+	-	-	+	-	-	-
	ecad hystrix								
66–70	Roscoff	-	+	-	-	+	-	-	-
67–114	Banyuls	-	-	-	-	-	-	-	-
	ecad bipinnata								
66–98	Roscoff (H)	-	-	-	-	-	-	-	-
67–5	Roscoff (C)	-	-	-	-	-	-	+	-
67–6	Roscoff (H)	-	-	-	-	-	-	+	-
67–37	Espegrend (H)	-	-	-	-	-	-	-	-
67–44	Espegrend (H)	-	-	-	-	-	-	-	-
67–92	Frillesås (H)	-	-	-	-	-	-	+	-
68–45	Concarneau (C+H)	-	-	-	-	-	-	-	-

(H) = growing on Halidrys siliquosa
(C) = growing on Cystoseira baccata

suppose that in the section *Propagulifera* endophytism is a special case and can be used as a characteristic of separate species.

The large marine phaeophyte *Halidrys siliquosa* is probably especially suitable to be entered by the cone-shaped multicellular base of ecad *bipinnata*. Chemin (1922, p. 245, f. 1 & 2) and Goodband (1973, p. 177, f. 5) both came to the conclusion that '*S. bipinnata*' has no physiological dependence on *Halidrys siliquosa*, and that the penetration into the host was mainly by physical pushing apart of the host cells. Sauvageau (*l.c.*, p. 329 = R. 171 & 383 = R. 196) described endophytic as well as epiphytic parts in '*S. bipinnata*' growing on *Halidrys*, but Goodband (*l.c.*, p. 177, f. 6–8) found secondary endophytism of mature basal discs. Lund (1950, p. 41) found '*S. bipinnata*' once secondarily attached to the crab *Stenorhynchus*. Specimens very similar to ecad *bipinnata* (according to the characters used by Sauvageau) have been found growing on *Cladostephus spongiosus* (France, Portbail, *Lenormand*, 6/1839, with propagules, CN, and Saint-Germain-sur-Ay, *Meslin*, 26/6/1938, with unilocular zoidangia, PC), *Cystoseira nodicaulis* (France, Carteret, *Lenormand*, 1839, herb. Thuret in PC, with propagules), *Dictyopteris membranacea* (Spain, Lanzada, *Donze*, 11/8/1964, sterile, L) and on rocks (Eire, Galway Bay, in *Fucus serratus* belt, *Koster 6482*, 15/8/1958, with unilocular and plurilocular zoidangia, L). In these cases no endophytism could be demonstrated. Occasionally *S. cirrosa* had been found on *Halidrys siliquosa* without being endophytic (Lund, 1950, p. 37; Irvine, 1956, p. 35; Jaasund, 1965, p. 70). According to Sundene (1953, p. 177) and Jorde & Klavestad (1960, p. 95) the *Sphacelaria* growing on *Halidrys* in the innermost parts of fjords is never endophytic and always without rhizoids (so ecad *cirrosa*), but in more exposed localities it is always partly endophytic and has a distinct cortex of appressed rhizoids (so ecad *bipinnata*).

On *Cystoseira baccata* the endophytic part of ecad *bipinnata* is less conspicuous than on *Halidrys* (compare fig. 576 with fig. 578). This *Cystoseira* is often covered by crustaceous coralline algae (*Fosliella* sp.) and often most parts of the discs of *Sphacelaria* are epiphytic on *Fosliella* (fig. 576).

In ecad *hystrix* growing on *Cystoseira* spp. endophytism is not conspicuous either. According to Sauvageau (*l.c.*, p. 329 = R. 171) it is not sufficient to make one or two sections of basal parts of the *Sphacelaria* to detect its endophytism. The basal discs have only a small endophytic portion and are epiphytic in a much larger portion. In some collections (Banyuls-sur-Mer, on *Cystoseira mediterranea, Prud'homme van Reine 801*, 3/9/1967 and Roscoff, on *Cystoseira nodicaulis, Prud'homme van Reine 66-70*, 11/10/1966; both in L) strictly epiphytic plants were found amongst partly endophytic ones. The majority of the partly endophytic plants grew on the younger and softer parts of the hosts, and most strictly epiphytic plants could be found between other epiphytes on old and hard parts. Occasionally germinating propagules were observed on these hosts. The new basal discs they formed were always monostromatic and strictly epiphytic.

Rhizoids. *Sphacelaria* specimens growing on *Halidrys siliquosa* and *Cystoseira baccata* (ecad *bipinnata*) usually form many rhizoids which cover the main filaments and form a spongy mass over or around the basal disc, giving off many new erect filaments. Occasionally the number of rhizoids is very small or rhizoids are lacking in young plants or in very fertile ones. In the cultures indexed in table XVIII no rhizoids have been observed, not even in the attached germlings found in culture 67-92. Usually the plants in the cultures did not attach to the wall of the culture-tube, but germinating propagules were frequent and often formed new plants. Goodband (1968, p. 192) studied ecad *bipinnata* from Church Island, Menai Straits, north Wales for one year. In the months December, January and February most specimens growing on *Halidrys* were totally or almost devoid of rhizoids.

In ecad *hystrix* usually only few rhizoids are present. Many specimens which are devoid of rhizoids can be found in almost all collections.

Some specimens of *S. cirrosa*, growing on seagrasses in the Mediterranean, have many

TABLE XIX. Characters used by Sauvageau (1902, 1903) to separate taxa within the section Propagulifera

	Sphacelaria cirrosa			
	forma meridionalis	forma septentrionalis	forma mediterranea	var. nana
basal disc	epilithic or epiphytic	epilithic or epiphytic	epilithic or epiphytic	epiphytic
rhizoids	monostromatic rare	monostromatic rare	monostromatic rare	monostromatic rare
substrate	variable	variable	variable	Desmarestia aculeata
erect filaments	quite rigid	flexuous	quite rigid	rigid
diam. axis in µm	60–90	40–60	60–90	40–90
l:b sec. segments	≤ 1	≥ 1	≤ 1	< 1 >
longitudinal walls	many	few	many	not mentioned
laterals	short, determinate	long, indeterminate	short, determinate	variable
hairs	frequent	not frequent	frequent	not mentioned
propagules	frequent	frequent	frequent	frequent
number of arms	(2–) 3	(2–) 3	3–5	(2–) 3
forms of arms	fusiform	cylindrical	fusiform, rarely cylindrical	fusiform or cylindrical
uniloc. zoidangia	rare	rare	rare	rare
dimensions in µm	75–100	75–100	75–100	75–100
pluriloc. zoidangia	very rare all one form	not known -	not known -	not known -
loculi in µm	small	-	-	-
uniloc. and pluriloc. zoidangia	on same specimen	-	-	-

rhizoids which are occasionally forming an almost complete cortex around the main filaments and also a spongy mass over the basal disc. These specimens, which are always strictly epiphytic, were described as *Sphacelaria rhizophora* by Kützing and as *S. cirrosa* var. *rhizophora* by Schiffner.

Erect filaments. In nature erect filaments of *Sphacelaria* spp. of Section *Propagulifera* growing in colder waters (northern Europe or deep water) are slender and flexuous, and their laterals are long, narrow, and show no distinct determinate growth. These slender and flexuous filaments are common in specimens formerly identified as '*S. cirrosa* forma *septentrionalis*', '*S. cirrosa* var. *nana*' (specimens from northern localities only), and '*S. bipinnata*' (also specimens from northern localities only). In France and southern Britain the specimens of *Halidrys siliquosa* growing near low-water level (or in tidal pools) are usually devoid of epi- and endophytic *Sphacelaria* spp., but in drift specimens (which probably come from some depth) ecad *bipinnata* can often be found. In littoral pools and in the upper part

TABLE XIX (continued)

	S. cirrosa var. patentissima	S. hystrix	S. bipinnata
basal disc	absent	epiphytic party endophytic	epiphytic, partly endophytic
rhizoids	- absent	polystromatic few	polystromatic numerous
substrate	unattached	Cystoseira div. spp.	Cystoseira baccata or Halidrys siliquosa
erect filaments	flexuous or rigid	small, narrow and rigid, or larger, broader and quite rigid	flexuous
diam. axis in µm	40–90	34–45 or 60–100	50–80
l:b sec. segments	< 1 >	⩽ 1	⩽ 1
longitudinal walls	not mentioned	many	few
laterals	short, perpendicular	short or long, determinate	long, determinate
hairs	absent	frequent	frequent
propagules	absent	frequent	rare
number of arms	-	3	3
form of arms	-	fusiform	cylindrical
uniloc. zoidangia	absent	rare	frequent
dimensions in µm	-	not mentioned	85–100
pluriloc. zoidangia	absent	frequent two forms	frequent all one form
loculi in µm	-	3–4 or 4–8	4–5
uniloc. and pluriloc. zoidangia	-	separate specimens	usually on separate specimens

of the sublittoral of these areas ecad *bipinnata* can often be found on *Cystoseira baccata*. The tufts of ecad *bipinnata* growing on *C. baccata* are usually smaller and more rigid than those growing on the deep-water *Halidrys*.

In warmer waters (southern Atlantic, Mediterranean) filaments of *Sphacelaria* spp. of the section *Propagulifera* are broader and more rigid and their laterals are usually short, acute, and distinctly determinate. These stout filaments occur in specimens formerly identified as '*S. cirrosa* forma *meridionalis*', '*S. cirrosa* forma *mediterranea*', '*S. cirrosa* var. *nana*' (from southern localities) and '*S. hystrix*'.

Specimens of *S. cirrosa* growing in stagnant waters in southern Europe have a different habit. Specimens from the Lagoa d'Obidos in Portugal (collected by *Welwitsch* and distributed as *S. Gomeziana*) have long (up to 50 mm) main filaments which are 65–90 µm in diameter. The laterals of these plants are long and narrow and the angle of ramification is often quite large (50–80°). Sauvageau (1903, p. 47 = R. 231), when discussing this material, described the laterals as perpendicular and included it in '*S. cirrosa* var. *patentissima*'. I found a few propagules with cylindrical arms in this material. Rodrigues (1963, p. 33, t. 2, f. a–c) observed these propagules as well. Dried specimens are reddish brown. Even if *S. cirrosa* var. *patentissima* should be maintained as a separate taxon, these Portuguese specimens cannot be incorporated.

Near Collioure, Pyrénées Orientales, France, many large and deep pools occur which have often only limited exchange of water with the Mediterranean. The dark brown *S. cirrosa* plants growing profusely on *Cystoseira barbata* in these large pools have 3–4 cm long main axes, which are 70–95 µm in diameter. Most laterals are short and acute, but several indeterminate laterals form laterals of the second order. These large plants form few propagules, which usually have 4–5 arms. The plants are strictly epiphytic and have no rhizoids.

In the cultures listed in table XVIII all mature filaments were slender and flexuous, even specimens collected near Banyuls-sur-Mer and cultured at 20°C. Young specimens grown at 20°C or at fairly high light-intensities (3000 Lx) at 12°C were usually more rigid than mature specimens.

Other characters. Specimens of *S. cirrosa* ecad *patentissima* in culture did not differ from originally attached specimens in my cultures. None of them formed any perpendicular laterals, but always distinctly spreading laterals. Formation of aegagropilae was induced by culturing fragments in artificial marine wave conditions (shaking culture). Usually quite regular algal balls, which were very similar to *S. cirrosa* ecad *aegagropila*, were formed in these conditions.

Hairs were frequent in all my cultures grown at 12°C or at 20°C; at 4°C they were usually absent or scarce.

Taxonomic implications. Sauvageau (*l.c.*, p. 46 = R. 230) stated already that there is no reason to distinguish the variety *nana* as a separate taxon. Nevertheless Irvine (1956, p. 32) incorporated it as a forma of his *S. pennata* var. *pennata*, just as he did with the forma *patentissima*. Goodband (1968, p. 45 & 48) discussed these infraspecific taxa and concluded that both are merely ecological growth-forms which are not worth counting as taxa. The same author (1971, p. 957–980) published the results of his detailed study on specimens of *S. cirrosa*, in which he used cultures and several statistical methods. He stated that both stiffness of the filaments and the length-width ratio of the secondary segments are related to the number of longitudinal walls in these segments. Formation of many longitudinal walls results in stout and rigid filaments, and the thickness of these walls augments the diameter of the secondary segments. Goodband (*l.c.*, p. 979) concluded that no infraspecific taxa should be maintained within the species *S. cirrosa*. About '*S. bipinnata*' he stated that it is well delimited and still generally accepted (*l.c.*, p. 958). He did not study '*S. hystrix*' which, according to him, cannot be considered a British species.

The results of my cultures of the infra-specific taxa in *S. cirrosa* are in agreement with the statements and conclusions of Goodband. For the ecads *bipinnata* and *hystrix* the reproductive structures have to be discussed to come to a decision about their status.

Reproduction and life-history. The life-history of *S. cirrosa* has not been studied in full detail yet. Sauvageau (1898, p. 1672–1675 and 1902, p. 332–343 = R. 174–185) described several stages of the life-history of ecad *hystrix* (as *S. hystrix*). Clint (1927) and Papenfuss (1934) both investigated ecad *bipinnata* (as *S. bipinnata*). Their results, although partly conflicting, have often been combined into the image of an isomorphic diplohaplontic life-history.

Propagules. J. Agardh (1836, p. 210, t. 15, f. 42 & 43) was the first author who figured and described the propagules of *S. cirrosa.* His figures show propagules with three and four arms and with an apical hair (the latter was considered a rhizoid by Agardh). The development of these propagules has been described in detail by Janczewski (1872), Magnus (1873b), Rischawi (1874, as *S. pennata*), Vinassa (1891), and by Zimmermann & Heller (1950). In the last-mentioned paper the authors classified the propagules of *Sphacelaria* spp. in three types, according to their ontogeny. They state that in propagules of the *cirrosa*-type the arms arise in succession from the large subapical cell. According to their figure 2C the small lenticular apical cell usually already forms its apical hair in an early stage of growth. In the *cirrosa*-type the sub-apical cell is a primary segment which directly forms the arms. When the first small and distinctly constricted protruding initial is formed, the nucleus of the sub-apical cell divides and an oblique wall is formed between the largest portion of the sub-apical cell and the young arm. The protruded initial as well as the sub-apical cell function as primary segments again. In the young arm by a new division of the nucleus and the formation of a transverse wall an apical cell and the first primary segment of the arm are formed. The latter will soon divide into two secondary segments. From the remaining part of the sub-apical cell of the stalk a new protrusion arises and after division of the nucleus a new oblique wall will be formed. When all arms are produced, the remaining part of the sub-apical cell of the stalk divides into two secondary segments. My figures 598–604 agree with the descriptions given by Zimmermann & Heller.

Sauvageau used the number of arms of the propagules and the form of these arms as characters to separate three forms in *S. cirrosa* (see my table XIX). In all specimens of *Sphacelaria* spp. of the section *Propagulifera* from northern Europe the 2–3 (–4) arms are long, cylindrical and slightly constricted (fig. 605–607; 611). Most specimens from the southern European and northern African Atlantic coasts have (2–) 3 (–4) arms which are usually shorter, fusiform and distinctly constricted (fig. 603). In the Mediterranean the arms are usually fusiform or occasionally cylindrical (fig. 608) and the number of arms is usually 3–5 (fig. 613). Goodband (1971, p. 976) stated that in British specimens he often found specimens bearing both propagules with cylindrical arms and propagules with fusiform arms. He noted also that the arms of propagules of one single specimen can be fusiform when young, but cylindrical when mature. He suggested that a continuous variation exists in the shape of the propagule arms and that no taxa should be maintained which were mainly based on this character.

In my cultures I usually found propagules with cylindrical arms. When grown at 20°C, however, young propagules with fusiform arms could also be observed. I endorse Goodband's suggestions and I will add that variation in the shape of the arms of propagules of ecad *bipinnata* (fig. 607) and in ecad *hystrix* (fig. 597; 610; 612) is comparable to that in *S. cirrosa* ecad *cirrosa.* Sauvageau (1902, p. 408 = R. 220) discussed the number of arms mentioned in literature. Goodband (1971, p. 975) studied the number of arms in British material, both in nature and in culture. He usually found three arms (91.2–96.3%), less often two arms (2.6–6.9%), rarely one or four arms (0.3–1.0%) and only once five arms. I observed often two-armed propagules in cultures of Scandinavian origin (fig. 605), particularly in cultures kept at 4°C (see table XVIII). In two of the eight Scandinavian cultures of ecad *cirrosa* I found exclusively two-armed propagules, in three other cultures two-armed as well as three-armed (and occasionally four-armed) ones and in the other three cultures only three-armed propagules. In specimens collected from nature I never found many two-armed propagules in *S. cirrosa*, except in the slide from which I drew fig. 608 (from Triest in the Adriatic). Four- and five-armed propagules are common in specimens from the Mediterranean (fig. 613). I did not observe these in my cultures of Banyuls material. Dimitrova (1969, p. 151, f. 4, as *S. cirrhosa* forma *pennata*) and Rischawi (1874, p. 343, f. 11–16) figured four- or five-armed propagules on specimens from the Black Sea. It is possible that the number of arms produced in propagules of *S. cirrosa* is significantly different in northern and southern (southeastern) populations. This is possibly an expression of genetic difference. I am not yet inclined to use the number of arms in the propagules as a character of taxonomic importance.

For occurrence of propagules during the seasons see table XX. In *S. cirrosa* ecad *cirrosa* propagules have been found in all areas, mainly during summer. In the Mediterranean they have been found all over the year. In ecad *bipinnata* propagules are less common. They have mainly been found in summer and autumn, occasionally also in spring. In ecad *hystrix* propagules have mainly been found in summer, but on the Canary Islands they have been observed in winter and spring.

Germination of propagules has often been described in literature. Usually the apical cells of the arms as well as the first (or lowest) secondary segment of the stalk can grow into a basal disc when it contacts a suitable substrate (fig. 610; 612; 613). Apical cells not in contact with the substrate usually form terminal hairs (fig. 613). Occasionally laterals, rhizoids or stolons arise directly from germinating propagules (fig. 610). New erect filaments as well as stolons arise from the basal discs (fig. 612; 613).

In his Remarques Sauvageau (1902, p. 343 = R. 185) described the germination of propagules of ecad *hystrix* as being very similar to that in *S. cirrosa* ecad *cirrosa*. According to Sauvageau the young basal discs are immediately partly endophytic in the thallus of the *Cystoseira* host. I also observed germination of propagules of ecad *hystrix* on *Cystoseira* (fig. 610; 612) but I did not succeed in observing its endophytism. In the material I investigated (amongst which specimens from Algeciras, collected by Sauvageau provided with his remark: 'pour étudier la pénétration en propagules germant') basal discs of young plants, formed by germinating propagules, were always epiphytic (fig. 572).

Zoidangia. Unilocular and plurilocular zoidangia have often been described for *S. cirrosa*. In older literature it is often difficult or impossible to decide whether or not the material described was *S. cirrosa* ecad *cirrosa*, ecad *bipinnata* or ecad *hystrix*. Dillwyn (1806, t. 86, as *Conferva pennata*) was the first who mentioned globular (unilocular) zoidangia and Meneghini (1843, p. 332) was the first to describe the plurilocular zoidangia (as antheridia).

Sauvageau (1898) detected presumptive micro- and macrogametangia in '*S. hystrix*' from Guéthary, France. He found them on separate plants as well as together on one plant. He described and figured these structures in detail in his Remarques (1902, p. 339–341 = R. 181–183, f. 39, 41 A–D). He observed the dehiscence of the plurilocular zoidangia, but he did not observe clumping or copulation. The presumptive gametes in his cultures failed to germinate and the author could only hypothesize about the further course of the life-history of '*S. hystrix*'. About the dimensions of the loculi Sauvageau's information is conflicting. In 1898 he gave other dimensions of the loculi than he did in 1902. For dimensions of loculi of plurilocular zoidangia see table XXI.

TABLE XX. Occurrence of reproductive structures in ecads of S. cirrosa in nature

	ecad cirrosa			ecad bipinnata			ecad hystrix		
	propag.	uniloc.	pluriloc.	propag.	uniloc.	pluriloc.	propag.	uniloc.	pluriloc.
S. Norway	5–9	-	-	5, 8, 10	5–10	7–10			
SW. Sweden	6–8	-	-	5, 7	6–10	6–10			
Denmark	7–10	9	-	-	9	8			
Germany, Baltic	4, 10	10	-						
Scotland	5–9	1–2, 6–12	-	-	1–2, 6–12	1–2, 7–12			
England and Wales	(1–)6–9 (–11)	1(–2), 8–12)	8–9	8	6–10 (–11)	6–10 (–12)	8	8, 9	8, 9
Eire	4, 7, 10	8–10	8						
France, Normandy	4–9 (–12)	2, 6–8		6–9	7, 8	6–8	?	-	5
Brittany	4–11	5–11	8	4, 8, 10	5–10	7–11	6, 10	10, 11	10
Bay of Biscay	4–9	9	9	10	10	?	4–10	-	2–6
NW. Spain and Portugal	(1–)8–9	-	-				9	-	?
French & Italian Medit. coasts	1–12	2, 3	-				9	-	5
Adriatic Sea	4–9	5, 10	10				3, 6, 8	3	3
Black Sea	5–12	-	-						
Canary Islands	1, 9, 10	1, 12	-				1–4	1, 4, 9, 11	1–4, 10–12

- = not found; ? = no month mentioned; blanco = taxon not present or fructification not studied; 1–2 = months of the year.

TABLE XXI. Dimensions of zoidangia in ecads of S. cirrosa (in µm)

source	ecad cirrosa	ecad bipinnata	ecad hyxtrix
unilocular:			
Sauvageau (1902, 1903)	75–100	85–120	
Kylin (1947)		75–100	
Lund (1950)	(78–)82–86(–103)	70–86(–98)	
Goodband (1968)	75–100	(60–)75–100(–130)	
Roscoff, several coll	85–92	75–95	75–100
Galway, Koster 6482	85–100		
Canary Isl., several coll.			56–90
England, Torquay, Batters			54–80
plurilocular:			
Sauvageau (1902, 1903)	70–80 x 60–65 (dimensions loculi not given)	72–120 x 40–60 loculi 4 or 5	micro: 55–90 x 45–52 macro: 55–85 x 45–65 (loculi micro 4; macro 8)
Kylin (1947)		75–100 x 40–60 (dimensions loculi not given)	
Lund (1950)		(70–)86–94(–107) x (45–)49–53 (dimensions loculi not given)	
Goodband (1968)	(60–)65–95(–150) x (22–)50–60(–66) (dimensions loculi not given)	(60–)70–90(–120) x (20–)40–60(–70)	
Roscoff, 11/11/1973		70–90 x 55–60 loculi 4–5(–6)	
Eire, Galway, Koster 6482	61–71 x 36–44 loculi 3–4		
Canary Isl., several coll.			micro: 45–60 x 31–45 macro: 47–75 x 33–61 (loculi micro 4–5(–6); macro 5.5–7.5)
England, Torquay & Swanage, Batters			micro: 68–72 x 40–42 macro: 68–77 x 40–42 (loculi micro 2.5–3.5; macro 6–7)
Wales, Rhosneigr, Newroth	80–90 x 45–55 loculi 3.5–4.5		
France, Banyuls, Sauvageau			micro: 66–105 x 49–60 macro: 61–75 x 54–75 (loculi micro 3–5; macro 7–8)

Occasionally in herbarium collections (Canary Islands: Fuerteventura, *Lowe*, 9/4/1859 (BM), and Tenerife, *CANCAP 1362*, 27/10/1978 (L)), I found exclusively plants of ecad *hystrix* in which all plurilocular zoidangia had loculi which were (4.5–) 5–7 µm broad. Several of these loculi were empty and so the zoidangia seemed to be mature. It is imaginable that these plurilocular structures are in fact asexual zoosporangia.

Sauvageau observed unilocular zoidangia on material from the Canary Islands (Tenerife, winter 1904–1905, Sauvageau, 1912, p. 183). He found these unilocular zoidangia on filaments also bearing propagules. Filaments bearing propagules were longer and stouter than filaments only bearing plurilocular zoidangia and they arose somewhat later in the year.

In ecad *bipinnata* Sauvageau (1902) found unilocular zoidangia and plurilocular zoidangia in the same tuft, but usually on separate filaments. Clint (1927), Papenfuss (1934), Kylin (1947), Lund (1950), and Goodband (1968) found them on separate plants as well as on the same plants, and Chemin (1922) only on separate plants. Occasionally they were even found on the same filament (Clint, 1927, f. 6 and 7; Lund, 1950, f. 7). Zoidangia occur laterally on the filaments but also on rhizoids (fig. 617).

According to Papenfuss (1934) plurilocular zoidangia growing on the same plants as unilocular zoidangia can be considered as (neutral or asexual) sporangia. He interpreted plurilocular zoidangia found on separate plants are isogametangia. According to him the neutral zoids were 7.5 X 4.2 μm, the isogametes 7 X 3.7 μm. Sauvageau (1902) and Goodband (1968) found all loculi in plurilocular zoidangia of ecad *bipinnata* similar and 4–5 μm broad; I found usually the same dimensions, both in specimens from culture and from nature.

In three out of eight cultures of ecad *bipinnata* (see table XVIII) I obtained plurilocular zoidangia. In my cultures of specimens originating from Roscoff I found these plurilocular zoidangia on fragments which were sterile at the start of the culture. In the culture from Frillesås I found them also on a small number of germlings of plurizoids. I have not observed their germination, but in hanging drops originally inoculated with fragments of filaments with plurilocular zoidangia I once obtained some germlings at 12°C. These germlings were covered with plurilocular zoidangia when they were still very small. I found no unilocular zoidangia on them, although the original filaments bore both unilocular and plurilocular zoidangia. Clint (1927) noticed similar germlings in nature covered exclusively by plurilocular zoidangia in autumn. My fertile germlings all died suddenly, without any indication of cause. In preserved specimens of these germlings I observed plurilocular zoidangia with loculi which were 3–4 μm broad as well as with loculi which were 6–7.5 μm broad. I cannot indicate, however, whether these large loculi are immature and yet undivided, or perhaps anisogamous.

Clint (1927) observed unizoids fusing in clumps, but Papenfuss (1934) could not confirm this. In fresh material collected near Roscoff ('*S. bipinnata*' growing on *Cystoseira baccata*, 11/11/1973) I once observed many unizoids which fused in pairs, threes, or fours (fig. 618). Instead of containing 3–4 chloroplasts, as described by Clint and Papenfuss, the unizoids I observed contained only one chloroplast and an eye-spot (fig. 618).

Goodband (1973) studied the development of endophytic filaments of ecad *bipinnata* on *Halidrys siliquosa*. In the youngest sporelings on *Halidrys* he found a large unicellular endophytic part as well as an erect filament (his f. 1). He stated that this suggests that germination of the spore might be bipolar. In specimens of *Halidrys siliquosa* collected at St. Andrews, Scotland, on 3/2/1971 I observed small germlings of ecad *bipinnata* (fig. 639) as well as old specimens with rhizoids and unilocular zoidangia (fig. 617). Most germlings consist of a cone-shaped multicellular basal part only. These basal parts could be observed as disc-like multicellular structures amidst the cells of the host (fig. 640; 641). In sections of the host the young germlings with their large penetrating apical cell could be easily observed (fig. 642). In a later stage the number of cells in the endophytic germlings increases, the young plants become cone-shaped and erect filaments arise (fig. 578; 579). Further development of the plants is described in Goodband's paper (*l.c.*). That author observed also secondary endophytism by discs produced by stolons (his figures 6–8).

For *S. cirrosa* ecad *cirrosa* almost no information of the life-history has been published. Unilocular zoidangia have often, but plurilocular zoidangia only rarely been found. I only observed these plurilocular zoidangia in two collections (Eire, Galway Bay, *Fucus serratus* belt, on rocks, *Koster 6482*, 15/8/1958, L and Wales, Rhosneigr, on *Furcellaria, Newroth*, 27/8/1968, microslide *11114* in BM), of which the former is morphologically very similar to ecad *bipinnata*.

Unilocular zoidangia have occasionally been observed in culture (see table XVIII). In two cultures, profusely producing propagules, occurred a few isolated unilocular zoidangia (with diameters of 67–95 μm). No life-history studies could be started from these unilocular zoidangia. Zoids of unilocular or plurilocular zoidangia of *S. cirrosa* ecad *cirrosa* have not been observed until now. For a review of the occurrence of reproductive structures during the seasons see table XX. For dimensions see table XXI.

The differences in dimensions of unilocular and plurilocular zoidangia of the ecads of *S. cirrosa* are small. In ecad *hystrix* the smallest zoidangia occur, in ecad *bipinnata* they are usually larger.

Chromosome counts have been made by Clint (1927, p. 13) who estimated 12–16 as the haploid number for ecad *bipinnata*. Later Knight (1929, p. 317) gave 16 as the haploid number for this ecad. In incidental chromosome counts in vegetative filaments of ecad *cirrosa* I estimated 22–34 chromosomes (fig. 643; 644).

Our knowledge of the life-history of the *Sphacelaria* spp. in the section *Propagulifera* is still too deficient to construct a life-history model. It is possible, however, that asexual plurizoidangia occur as well as anisogamous and perhaps also isogamous plurigametangia.

Systematic position. Several taxa, infraspecific in *S. cirrosa* as well as separate species are currently recognized in the section *Propagulifera*. The infraspecific taxa in *S. cirrosa* are discussed in the section on Characters of entities (p. 245). There I conclude that I have no reasons to maintain these infraspecific taxa. Study of variation in propagules supports this view.

In the section *Propagulifera* attached specimens of the many populations often only differ in two characters: occurrence of appressed rhizoids on the main filaments and presence of a partly endophytic basal holdfast on *Cystoseira* spp. or on *Halidrys siliquosa*. Endophytism on *Halidrys siliquosa* and *Cystoseira baccata* (often combined with the presence of a cortex of appressed rhizoids on the main filaments) is often considered characteristic for *S. bipinnata* in literature (Sauvageau, 1902, p. 393 = R. 205; Lund, 1950, p. 37; Goodband, 1968, p. 176; and many others). Endophytism on *Cystoseira* div. spp. (*C. baccata* excluded) is often considered characteristic for *S. hystrix* (Reinke, 1890a, p. 208; Sauvageau, 1902, p. 349 = R. 191; Irvine, 1956, p. 34; and several others). Endophytism cannot be considered to be of taxonomic importance, however, and the number of rhizoids cannot be used as basis to separate taxa on species level (see also the section on Characters of entities, p. 247). Thus I have to consider '*S. bipinnata*', '*S. hystrix*', and '*S. cirrosa*' one single species. It is not possible to state, on basis of the present state of knowledge of these algae whether populations with *bipinnata*-characters or with *hystrix*-characters are genetically different, or whether the differences are mainly expressions of reactions to ecological factors in the different habitats. To affirm or reject the proposed partial amalgamation of species into the *S. cirrosa*-complex many culture-experiments and transplant-experiments have to be carried out. The culture-experiments of several authors, including myself, make it clear that this will be a very difficult task. As long as these experiments have not been undertaken, I will conside 'S. *bipinnata*' and '*S. hystrix*' as growth-forms of *S. cirrosa*. For the present I will use the informal entity ecad *bipinnata* for algae of populations with *bipinnata*-characteristics; ecad *hystrix* for algae of populations with *hystrix*-characteristics; and ecad *cirrosa* for all other attached populations.

Variation in number and form of the arms of propagules is similar in these three ecads, but differences can be found in the zoidangia (see table XIX and XX). The relative frequency of unilocular and plurilocular zoidangia (as well as of propagules) and the dimensions of the loculi of the plurilocular zoidangia are probably characteristic features. The general picture is as follows: In spring the ecads *cirrosa* and *bipinnata* are usually sterile, but differ in substrate and number of rhizoids. In ecad *hystrix* usually small, partly endophytic filaments can be found, covered with plurilocular gametangia. In summer the tufts of ecad *cirrosa* are usually covered with propagules, just as those of ecad *hystrix*. In this warmer season the tufts of ecad *bipinnata* are, however, usually covered by unilocular and plurilocular zoidangia. In autumn the picture is usually similar and in winter most specimens are sterile.

The differences in frequency of occurrence of zoids and propagules are possibly characteristic. The morphology and dimensions of these structures are similar in all ecads, and there are only differences in the plurilocular zoidangia. Micro- and macrogametangia have only been observed in ecad *hystrix*, but the possibility of their occurrence in the other taxa cannot be excluded. In ecad *hystrix* they have usually been found in small tufts and on the other hand all small tufts (of which endophytism is often not demonstrable) of a *Sphacelaria* of the section *Propagulifera* with plurilocular zoidangia and growing on a *Cystoseira* (except *C. baccata*) have to be regarded as belonging to ecad *hystrix*. In ecad *bipinnata*, however, small germlings are often also covered by plurilocular zoidangia. Observations on preserved specimens of these germlings suggest that zoidangia with small loculi and zoidangia with larger loculi may occur on one and the same individual. I also reported presumptive asexual zoosporangia in ecad *hystrix*. The few plurilocular zoidangia observed for ecad *cirrosa* are identical with those of ecad *bipinnata*.

Growth-forms of unattached specimens can be considered as separate (but less important) ecads: *S. cirrosa* ecad *patentissima* and *S. cirrosa* ecad *aegagropila*. See also the key below. I do not think the specimens with multi-armed propagules belong to a separate ecad, but it perhaps reflects a genetic difference. I consider this difference to be taxonomically unimportant.

Sphacelaria cirrosa differs from all other species of *Sphacelaria* subgenus *Propagulifera* in Europe by its propagules with terminal hairs. Its variable and irregular branching with usually determinate laterals are also characteristic of *S. cirrosa*. The ontogeny of the propagules, as discussed before, is a third character prompting us to consider *S. cirrosa* as different from all other propagule-bearing *Sphacelaria* spp. in Europe. For these reasons *S. cirrosa* will be classified in the separate section *Propagulifera*. For comparison of the slender growth-form of *S. cirrosa* (formerly called *S. cirrosa f. septentrionalis*) with *S. rigidula* and *S. fusca* see table XVII.

KEY TO THE ECADS IN S. CIRROSA

1a. Attached specimens 2
 b. Not attached 4
2a. Not endophytic; propagules usually frequent . . . . ecad cirrosa
 b. Partly endophytic in *Halidrys siliquosa* or in *Cystoseira* spp. 3

3a. Many appressed rhizoids present on the main filaments; unilocular and/or plurilocular zoidangia usually frequent; on *Halidrys siliquosa* or *Cystoseira baccata* . . . . **ecad bipinnata**
b. Appressed rhizoids absent or scarce; plurilocular zoidangia usually frequent on small, dense bushes; propagules on larger plants; growing on *Cystoseira* div. spp. . . . . **ecad hystrix**
4a. Free-floating rounded balls; on sandy coasts . . . . **ecad aegagropila**
b. Entangled masses between seagrasses . . . . **ecad patentissima**

V. Incertae sedis

The following species cannot be incorporated in one of the subgenera described before. Probably it is related to *Sphacelaria* species occurring in the southern hemisphere.

16. Sphacelaria sympodiocarpa Sauvageau—Fig. 647–660

Sphacelaria sympodiocarpa Sauvageau (1900) 309, f. 10 (= R. 39); Prud'homme van Reine (1974), 175, (1978), 303.—Type: Sauvageau *s.n.*, Guéthary, 15/9/1898, dredged, on *Cystoseira baccata* (PC), lecto; L).

Plants forming small compact tufts or small velvety mats (fig. 647; 648). The colour of fresh specimens is not known. They are solitary or matted and epiphytic or epilithic. Many scarcely branched erect filaments arise from the entangled prostrate parts which are composed of rhizoids, stolons and occasional small monostromatic or polystromatic basal discs (fig. 649; 650).

The erect parts of a plant are composed of many main axes and scarce laterals of up to the second order. The appressed or sharply divaricate hemiblastic laterals with indeterminate growth arise irregularly (fig. 651). The dimensions of laterals and main axes are similar.

The secondary segments are usually longer than they are wide, but occasionally they are shorter than they are wide. There is no difference in dimensions between superior secondary segments and inferior ones.

The secondary segments are undivided or they are subdivided by 1–3 longitudinal walls (fig. 652; 653).

Transverse walls occur only in superior secondary segments from which laterals or zoidangia arise. Solitary hairs occur in the distal parts of the erect filaments (fig. 654; 655). The chloroplasts have not been described. Branched or unbranched rhizoids arise from the proximal cells of laterals (fig. 651) or from stolons (fig. 650).

Propagules are not known.

Unilocular zoidangia occur in scattered cymose stands (see fig. 10A in Sauvageau, *l.c.*).

Each unilocular zoidangium has a unicellular stalk from which one or two lateral zoidangia with unicellular stalks may arise (fig. 656–660). Mature zoidangia are broad ellipsoid; younger zoidangia are narrower. Plurilocular zoidangia are not known.

Dimensions: Plants 1–2.5 mm high. Diam. velvety mats 2–8 mm. Angle of ramification 0–25°. Diam. of erect filaments and stolons (9–) 13–18.5 μm. Height of secondary segments 13–30 μm. Diam. rhizoids 7.5–9 μm. Diam. hairs 9–11 μm (with sheath) or 5.5–7.5 μm (without sheath). Unilocular zoidangia 32–44 X 24–32 μm. Length of cymes 20–110 μm.

Distribution. Only one locality, Guéthary in southwestern France, collected on 15/8/1898 and 15/9/1898 by *Sauvageau*. Specimens of the collection of 15/9/1898 (preserved in alcohol) in coll. Sauvageau in PC and in L (see fig. 43).

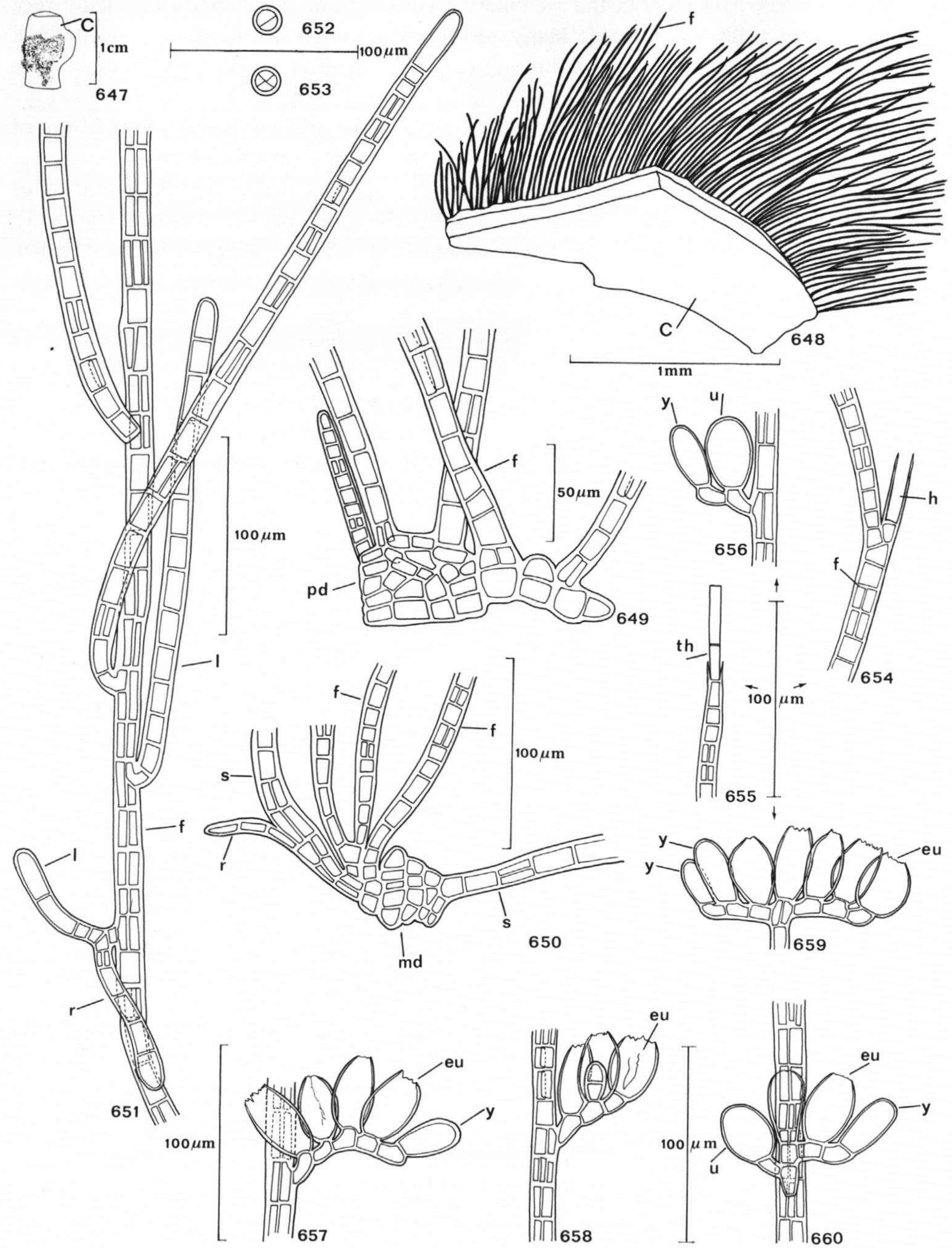


Fig. 647–660. Sphacelaria sympodiocarpa. 647, 648. Habit; 649, 650. Basal parts; 651. Branching; 652, 653. Cross-sections of erect filaments; 654, 655. Hairs; 656–660. Unilocular zoidangia. C. *Cystoseira baccata*; eu. empty unilocular zoidangium; f. erect filament; h. hair; l. lateral; md. monostromatic basal disc; pd. polystromatic basal disc; r. rhizoid; s. stolon; th. terminal hair; u. unilocular zoidangium; y. young. 647–660. Guéthary, *Sauvageau* (L, in alcohol 70%).

Notes on morphology. In the secondary segments of *S. sympodiocarpa* usually very few longitudinal walls are formed. Many secondary segments are devoid of longitudinal walls, in others only one wall can be found (fig. 652) or three cruciate longitudinal walls occur (fig. 653).

Owing to the preservation of the material in alcohol the original colour and the form of the chloroplasts, which have not been described by Sauvageau, remains unknown.

The solitary hairs have not been observed by Sauvageau. Usually only the remnants of the sheaths could be found (fig. 654), occasionally also a few cells of the hairs (fig. 655). The hairs are distinctly terminal but the subterminal cell forms a new erect filament, which is erecto-patent (fig. 654). Occasionally the subterminal cell does not sprout and the hair remains in terminal position (fig. 655).

The branched rhizoids described and figured by Sauvageau (his f. 10G & 10H) have not been observed by me, but unbranched rhizoids are common (fig. 650; 651). The basal discs are usually monostromatic, but they may become polystromatic (fig. 649).

The unilocular zoidangia are usually arranged in a drepanium (fig. 656; 657) or a cincinnus (fig. 658), but occasionally these monochasia may grow into more complex cymose structures (fig. 659; 660).

Notes on ecology. Sauvageau (*l.c.*) collected a small young tuft of *S. sympodiocarpa* on a shell of a large seasnail (*Triton* species) found in a lobster-basket. He found many specimens on a large *Cystoseira baccata*, obtained by dredging. On this *Cystoseira S. plumula* occurred as well. *Sphacelaria sympodiocarpa* is probably confined to the sublittoral.

Systematic position. On the basis of the information obtained from study of type-material which is the only material still present, *S. sympodiocarpa* cannot be incorporated in one of the three European subgenera of the genus *Sphacelaria*. Cymose stands of zoidangia have also been found in *S. rigidula* and *S. nana* but the cymes in these species are much smaller. Sauvageau (1900, p. 304–322 = R. 34–51) described several other species of *Sphacelaria* with cymose stands of unilocular zoidangia. All these species are only known from single collections from the southern hemisphere and the differences between some of them and the European *S. sympodiocarpa* are not yet clear. The plurilocular zoidangia, found in only one species (*S. chorizocarpa*) relate the sympodiocarpa-like *Sphacelaria* spp. to another group of species, arranged round *S. bracteata* (see Sauvageau, 1901, p. 250–259 = R. 25–34). The species of the *bracteata*-group have only been found in Australia. Perhaps *S. sympodiocarpa* is the only European representative of a southern-hemispheric subgenus of the genus *Sphacelaria*. A full description of this supposed subgenus is outside the scope of my revision of European *Sphacelariaceae*.

DOUBTFUL, ERRONEOUS, AND EXCLUDED NAMES

The type material of several names was untraceable or difficult to interpret. The descriptions are generally too vague to permit a conclusion as to their identity. On the other hand many names of species, formerly considered as belonging to the genus *Sphacelaria*, have been transferred to other genera. Besides the relevant specific and infraspecific names of the genus *Sphacelaria* the specific and infraspecific names of other genera, mentioned in literature as belonging to the genus *Sphacelaria*, are listed here. The sequence is alphabetical, according to the first epithets. Names already mentioned as synonyms in the sections on nomenclature of the different species, are omitted in this list.

Sphacelaria axillaris von Suhr (1831) 679. Type in KIEL. It belongs to *Halopteris filicina* (Grat.) Kütz.—*Sphacelaria bertiana* DeNotaris (1842) 302. Isosyntype in S. It is the fructification of *Cladostephus spongiosus* forma *verticillatus* (Lightf.) Prud'homme van Reine.—*Sphacelaria cervicornis* C. Agardh (1827) p. 640, as *S. curvicornis*, a typographical error; *S. cirrosa* var. *cervicornis* Ardissone (1886) 91. Type in LD (Ag. 45507), rhizoids of *Stypocaulon scoparium* (L.) Kütz.—*Sphacelaria compacta* Bory ex Montagne (1846) 40, t 5, f. 2. Type in PC, herb. générale. It belongs to *Stypocaulon scoparium* (L.) Kütz.—*Sphacelaria cristata* Bonnemaison (1828) 113. Type in Quimper (Bibliothèque municipale). It belongs to *Stypocaulon scoparium* (L.) Kütz.—*Sphacelaria disticha* Vahl *ex* Lyngbye (1819) 104, t. 31 A. Type in C. It belongs to *Halopteris filicina* (Grat.) Kütz.—*Ceramium filicinum* Grateloup (1806) f. 1; *Sphacelaria filicina* C.A. Agardh (1824) 166, incl. var. *aestivalis* J. Agardh (1842) 30 and var. *hyemalis* J.G. Agardh (1842) 30. Lectotype of the species in LD (Ag. 45769). It is *Halopteris filicina* (Grat.) Kütz.—*Sphacelaria filicina* var. *β patens* Harvey (1841) 37. Lectotype in TCD. It belongs to *Halopteris filicina* forma *recurva* (Mont.) Prud'homme van Reine.—*Sphacelaria filicina* var. *recurva* Montagne (1837) 353. Type in PC, herb. Montagne. It is the basionym of *Halopteris filicina* forma *recurva* (Mont.) Prud'homme van Reine *comb. nov.*—*Conferva fulva* Hudson (1762) 484. Probably a *Polysiphonia species.*—*Ceramium fuscum* Roth (1800a) 477. Probably a *Vaucheria species.*—*Hutchinsia fusca* C. Agardh (1817) XXVI, *comb. nov.* based on material of a *Polysiphonia species* erroneously sent by Dillwyn as *Conferva fusca* Hudson.—*Ceramium haensleri* C. Agardh (1817) XXVII, *nom. nud.*; *Sphacelaria haensleri* Bonnemaison (1828) 111. Type in Quimper (Bibliothèque municipale). It belongs to *Stypocaulon scoparium* (L.) Kütz.—*Sphacelaria hypnoides* Greville (1828) t. 348. Type in BM. It belongs to *Halopteris filicina* (Grat.) Kütz.—*Conferva intertexta* Withering (1796) 132. Probably a sponge.—*Sphacelaria intricata* Ardissone (1864) 404. Not a member of the *Sphacelariales.*—*Conferva marina pennata* Dillen in Ray (1724) 59. For discussion see Dixon & Parkes (1968) 81.—*Conferva marina pennata* Dillen (1741) 24, t. 4, f. 23. Material in OXF is the type of *Stypocaulon scoparium* (L.) Kütz.—*Conferva mertensii* Turner in Smith & Sowerby (1802) t. 999, *Ceramium mertensii* C. Agardh (1817) XXVII, *Sphacelaria mertensii* S.F. Gray (1821) 333. Is *Tilopteris mertensii* (Turn. in Sm.) Kütz.—*Sphacelaria cirrhosa γ minuta* C. Agardh (1824) p. 165. Probably not a member of the *Sphacelariales.*—*Sphacelaria minuta* C. Agardh (1824) 164. Type in LD (Ag. 45325). For discussion see Notes on nomenclature 2 of *S. tribuloides* (p. 185).—*Sphacelaria papilioniformis* Coppejans (1977) t. 80, *nom. nud.* Perhaps a *Sphacelaria* infected by a fungus.—*Ceramium pennatum* Roth (1800b) 171; *Conferva pennata* Sprengel (1809) 187; *Hutchinsia pennata* C.A. Agardh (1817) XXVI. Is *Pterosiphonia pennata* (C. Ag.) Falkenb. For discussion see Dixon & Parkes (1968) 80–82.—*Conferva pennata* Hudson (1762) 486. *Nomen dubium confusum.* For discussion see Dixon & Parkes (1968) 80–81. *Ceramium scoparium* var. *β pennata* Lamarck & De Candolle (1805) 41; *Sphacelaria pennata* Lyngbye (1819) 105, t. 31.—*Sphacelaria pumila* C. Agardh (1827) 640. Type in LD (Ag. no. 45309–45312): rhizoids of *Dictyopteris membranacea.*—*Sphacelaria radicans* var. *velutina* Traill (1886) 402. *Nomen nudum*, description of locality suggests *S. nana* Naeg. ex Kütz.—*Fucus rudis* Esper (1798) 61, t. 27. The figure and the description are obscure and are not incompatible with at least three species in *Sphacelariales* as well as with members of the *Hydrozoa.*—*Fucus rudis* Wulfen (1803) 57. Probably *Stypocaulon scoparium* (L.) Kütz.—*Conferva rufescens* Roth (1806) 294. Probably rhizoids of *Stypocaulon scoparium* (L.) Kütz.—*Sphacelaria rutilans* Kützing (1843) 291. Type in L, sheet 937.61-651. It belongs to *Giraudia sphacelarioides* Derb. et Sol. in Castagne.—*Sphacelaria rutilans* var. *β nuda* Kützing (1849) 463. Type in L, sheet 937.71-637. It belongs also to *Giraudia sphacelarioides.*—*Conferva scoparia* Von Linné (1753) 1165; *Ceramium scoparium* De Candolle in Lamarck & De Candolle (1805) 41; *Sphacelaria scoparia* Lyngbye (1819) 104, t. 31 B, incl. var. *aestivalis* J. Agardh (1842) 29; var. *corymbifera* Grunow (1867)

47: forma *disticha* Meneghini (1843) 345, excl. *syn. Sphacelaria disticha* Lyngbye; var. *glomerata* Grunow (1867) 47; var. *hyemalis* J. Agardh (1842) 29; var. β *pennata* C. Agardh (1828) 21; var. *virgata* Erb. critt. Ital (1858) n. 29. Type of the species in OXF (as *Conferva marina pennata* Dillen 1741). It is *Stypocaulon scoparium* (L.) Kütz.—*Sphacelaria scoparioides* Lyngbye (1819) 107, t. 32 C incl. var. *composita* C. Agardh (1824) 165. Type of the species in C. It is the basionym of *Stypocaulon scoparium* forma *scoparioides* (Lyngbye) Prud'homme van Reine *comb. nov.*—*Sphacelaria scoparioides* var. β *intricata* Kützing (1845) 240. Type in L (sheet 937.131-132). Mixture of algae, mainly *Sphacelaria cirrosa* (Roth) C. Ag.—*Sphacelaria sertularia* Bonnemaison (1828) 109. Type in Quimper (Bibliothèque municipale). It belongs to *Halopteris filicina* forma *recurva* (Mont.) Prud'homme van Reine.—*Sphacelaria simpliciuscula* C. Agardh (1824) 166. Neotype in LD (Ag. no. 45718). It belongs to *Halopteris filicina* (Grat.) Kütz.—*Sphacelaria spartioides* Meneghini (1840a) 3. Type in FI. It belongs to *Stypocaulon scoparium* (L.) Kütz.—*Sphacelaria spinulosa* Lyngbye. Type in C. It is the basionym of *Stypocaulon spinulosum* (Lyngbye) Prud'homme van Reine *comb. nov.*—*Sphacelaria tenuis* C.A. Agardh ex Bonnemaison. Type in Quimper (Bibliothèque municipale), probably same collection as type of *S. simpliciuscula.* It belongs to *Halopteris filicina* (Grat.) Kütz.—*Sphacelaria ulex* Bonnemaison (1828) 109. Type in Quimper (Bibliothèque municipale). It belongs to *Stypocaulon scoparium* forma *scoparioides* (Lyngb.) Prud'homme van Reine.—*Sphacelaria velutina* Greville (1828b) t. 350. It is *Herponema velutinum* (Grev.) J. Ag.—*Sphacelaria virens* Zanardini ex Von Frauenfeld (1855) 17. Specimens in a number of herbaria belong either to *S. cirrosa* (Roth) C. Ag. or to *S. tribuloides* Menegh., occasionally a mixture of both species can be found.—*Delisella vittata* Bory de Saint Vincent (1824) 389, a new name for a specimen of *Hutchinsia stricta* C. Ag. figured in Lyngbye (1819) t. 36, f. 5. It is *Polysiphonia urceolata* (Lightf. ex Dillw.) Grev.

GLOSSARY

Glossary of accepted descriptive phycological terms used in this book. Terms currently and consistently used by Hine (1977); Fritsch (1945, mainly p. 260–300); Rosowski & Parker (1971, p. 862–874); and Stearn (1966, p. 314–357 & 378–548) are usually not incorporated in this glossary. Several non-descriptive terms, for example terms used in the Hennigian phyletic-cladistic system, are also incorporated.

Acroblastic branching: Initials for this type of branching originate from (parts of) small lenticular segments of the apical cells of erect filaments (see p. 13 and fig. 9).

Acrohomoblastic branching: Only one type of structure is formed from the lenticular initial cell (fig. 9).

Acroheteroblastic branching: Two different types of structures are formed from the lenticular initial cell (fig. 9).

Adventitious branches: See laterals.

Aegagropilae = Aegagropilous forms: Unattached algae forming intermeshed, free-rolling balls (fig. 569).

Algal balls: see aegagropilae.

Angle of branching: The angle between the direction of a main filament and the direction of a lateral.

Anisogametangia: See gametangium.

Apomorphous: Derived state of expression of a character (Hennigian).

Apomorphy: A character in the apomorphous state of expression (Hennigian).

Appressed rhizoids: Rhizoids lying close to an erect filament and growing downwards.

Argumentation scheme: A scheme in which the arguments for the phylogenetic diagram are summarized (Hennigian) (fig. 24).

Autapomorphy: Apomorphy only occurring in one single taxon (Hennigian).

Axis: Central erect filament, from which the laterals arise. Main axis = primary central erect filament.

Basal part: See prostrate system (also for basal crust, basal disc and basal holdfast).

Bush: A densely branched, quite low plant with several intermixed axes and laterals.

Caespitose: Several plants growing so close together that they form dense patches or turfs.

Carpet: A low, felty, mat covering a distinct area.

Cladistic system: A system of classification established by the use of comparative morphology as basis to distinguish unique derived features inherited by the members from the immediate ancestor of the group (Hennigian).

Convergence: The development of apparently similar apomorphies from different plesiomorphous character state (Hennigian).

Daughter species: The (usually two) species derived from one other (the mother species) and differing from each other in expression of at least one single character (Hennigian).

Determinate lateral: See laterals.

Dichoblastic branching: Dichotomous branching resulting from division of the apical cell of an erect filament (fig. 9).

Direct hypacroblastic branching: See hypacroblastic branching.

Ecad: In specialized habitats the expression of environmental selection of specialized gene-complexes can in some species give rise to specialized growth-forms or ecads (see Heywood, 1959, p. 92). Ecads have no taxonomic status.

Endogenous hairs: Hairs formed by division of a meristematic basal cell of a divided hair-initial. When the cells of the hair elongate the original cell-wall ruptures and the remnants of this cell-wall remain as the sheath of the hair.

Entity: Grouping of specimens as an aid for the discussion and description of the variability within the species. Not a taxonomic subdivision and no sharply dilimited unit (see Vink, 1970, p. 315).

Ephebogenesis: Germination and further development and growth of unfused ♂ gametes.

Filament: An elongate thread, composed of segments attached end to end. Main (erect indeterminate) filaments: A term used to describe the axes as well as the larger indeterminate laterals (fig. 21).

Gametangium: Structure (plurilocular zoidangium) containing gametes. Anisogametangia: Signifies presence of plurilocular microzoidangia as well as plurilocular macrozoidangia. Copulation by anisogamy. Isogametangia: Used when all gametangia are morphologically similar. Copulation by isogamy or the gametes are physiologically differentiated (different behaviour) but morphologically alike.

Germination tube: A tube formed by the germinating zoid and through which the protoplast passes to form the embryospore.

Helicoid: Arranged in spiral.

Hemiblastic branching: See Fritsch (1945) p. 271, and p. 13 and fig. 9 of this book.

Horns: The short arms of propagules of members of *Sphacelaria* section *Tribuloides* (fig. 437).

Hypacroblastic branching: Initials for this type of branching originate from (parts of) secondary segments of erect filaments (see p. 13 and fig. 9). Direct hypacroblastic branching: laterals arise from immature peripheral cells (primary laterals). Tardy hypacroblastic branching: laterals arise from mature peripheral cells (adventitious branches or secondary laterals).

Indeterminate lateral: See laterals.

Isogametangia: See gametangium.

Laterals: Often used in the sense of branches or ramifications. Determinate laterals are laterals with definite growth; indeterminate laterals have indefinite growth. Primary laterals sprout from immature peripheral cells; secondary laterals from mature peripheral cells (= adventitious branches). Laterals of the first order arise from the axes; their laterals are laterals of the second order. Laterals of the second generation are new shoots arising from truncated perennial erect filaments. See also fig. 21.

Loculi: Compartments of a plurilocular zoidangium.

Main axis: See axis.

Main filaments: See filament.

Marked pericyst: See pericyst.

Medullar cells: Large central cells in erect filaments of the periclinal type. They differ from the peripheral cells in size and position.

Macrozoid: See zoid.

Macrozoidangium: See zoidangium.

Microzoid: See zoid.

Microzoidangium: See zoidangium.

Mini-zoidangium: See zoidangium.

Monophyletic: Derived from a common ancestor and comprising all descendants of that ancestor (Hennigian).

Mother species: A species from which daughter species (usually two) derive (Hennigian).

Neutral sporangia: Plurilocular zoidangia of which the zoids are not gametes.

Nodule: Irregular clump of vegetative cells, usually formed by proliferation and swelling of intercalary cells.

Parallelism: Independent development of similar apomorphies from the same plesiomorphous state (Hennigian).

Paraphyletic group: A group of taxa possessing a symplesiomorphy and excluding one or more descendants of the common ancestor (Hennigian).

Parthenogametes: Gametes which can germinate without fusion. In a strict sense only ♀ gametes (see also ephebogenesis).

Periclinal pattern: In this pattern are the longitudinal walls in the secondary segments of erect filaments all perpendicular to each other, resulting in a medulla of large cells and an outer core of small peripheral cells.

Periclinal type: Erect filaments in which in cross-section a periclinal pattern of division by longitudinal walls can be observed (fig. 40).

Pericyst: Mature peripheral cell which function as dormant initial. Marked pericysts differ from other peripheral cells in size, colour and contents (fig. 82).

Phenetic system: A system of classification based on overall similarity.

Phyletic system: A system of classification based on phylogeny.

Phylogenetic diagram: A diagram of phylogenetic reconstruction based on cladistic methods (Hennigian) (fig. 25).

Plesiomorphous: Primitive state of expression of a character (Hennigian).

Plesiomorphy: A character which is in the plesiomorphous state of expression (Hennigian).

Plurilocular zoidangium: See zoidangium.

Plurizoid: See zoid.

Polyphyletic group: A group based on false synapomorphies, inferred from parallelism (Hennigian).

Polystromatic: With more than one layer of cells.

Primary lateral: See laterals.

Primary longitudinal wall: The first longitudinal wall formed in a young secondary segment.

Proliferations: Protrusion of peripheral cells by vegetative cell division. In some cases caused by Chytridiaceous fungi.

Prostrate system = Prostrate part of basal part. The basal holdfast can consist of filaments (stolons; tuberculous filaments); basal discs (monostromatic or polystromatic) or several superposed discs forming a basal crust (which can be covered by rhizoids). See p. 15.

Pseudodichotomous branching: Branching resulting from unequal division of the apical cell of a filament, resulting in two new filaments which have almost the same size.

Radial pattern: In this pattern the longitudinal walls in the secondary segments of erect filaments make acute angles with each other, resulting in a number of cells of different sizes but without separation into medullar and peripheral cells.

Radial type: Erect filaments in which in transverse section a radial pattern of division by the longitudinal walls can be observed (fig. 39).

Rhizoid: All narrow filaments with negative geotaxic growth.

Schizogenous cavity: A cavity in plurilocular zoidangia originated by splitting of middle lamelles of primary longitudinal walls (fig. 187).

Secondary lateral: See laterals.

Secondary transverse cell-walls: Transverse cell-walls formed in the cells of secondary segments.

Secondary transverse division: Transverse division in cells of secondary segments.

Segment: See Fritsch (1945) p. 265, and p. 6 of the present publication.

Sister groups: Two groups of taxa derived from the closest ancestor common to both monophyletic groups (Hennigian).

Sphacelariaceae s.s.: Family *Sphacelariaceae* Decaisne *emend.* Oltmans (see p. 32).

Symplesiomorphy: Joint possession of a plesiomorphy (Hennigian).

Synapomorphy: Joint possession of an apomorphy (Hennigian).

Tardy hypacroblastic branching: See hypacroblastic branching.

Transformation series: A series of character states giving the sequence of possibly irreversible steps in the evolution of a given organ (table IV; Hennigian).

Tribuliform: Almost triangular, but with a small bulge in the middle of the longest side (fig. 437).

Tuberculous basal parts: Filaments swollen like a tubercle.

Tuft: A small cluster of elongated flexible erect filaments, close together at the base.

Unilocular zoidangium: See zoidangium.

Unizoid: See zoid.

Zoid: Motile reproductive unicell with flagella. Unizoid: Zoid of a unilocular zoidangium. Plurizoid: Zoid of a plurilocular zoidangium. Macrozoid: Zoid of a (plurilocular) macrozoidangium (possibly ♀ gamete). Microzoid: Zoid of a (plurilocular) microzoidangium (possibly ♂ gamete).

Zoidangium: A structure in which zoids are formed. Unilocular zoidangium: with one compartment containing several to many unizoids. Mini-zoidangia: Unilocular zoidangia of a small size and which never were observed to have reached maturity or to produce viable zoids (f. 200). Plurilocular zoidangium: with many loculi, each loculus contains one plurizoid. Macrozoidangium: Plurilocular zoidangium with loculi of relatively large dimensions (possibly ♀ gametangia). Microzoidangium: Plurilocular zoidangium with loculi of relatively small dimensions (possibly ♂ gametangia).

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EXSICCATAE

List of Exsiccatae-series mentioned in this book.
For details see Sayre (1969).

AKERMARK, S. 1870. Typ-samling af Skandinaviens Alger.

ALGAE ADRIATICAE EXSICCATAE. 1910–1914. Herausgegeben von der K.K. zoologischen Station in Triest.

ALGAE SCHOUSBOEANAE. 1883.

ALGAE ZEELANDIAE. 1976-X. Rijksherbarium, Leiden and Delta Institute for Hydrobiological Research, Yerseke.

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—— 1861–1879. Algae scandinavicae exsiccatae, seriei novae.

BREUTEL, C. F. 1842–1843. Flora germanica exsiccata, ser. 2.

CHAUVIN, J. 1826–1838. Algues de la France.

COCKS, J. 1855–1860. Algarum fasculi, or a collection of British seaweeds.

CROUAN, P. L. & H. M. 1852. Algues marines du Finistère. Vol. 1, Fucoidées.

DEBEAUX, J. O. 1864–1870. Algues de la Corse.

DESMAZIÈRES, J. B. H. J. 1825–1851. Plantes cryptogames du Nord de la France (partly called: Plantes cryptogames de France).

—— 1836–1851. Plantes cryptogames de France, ed. 2.

ERBARIO CRITTOGAMICO ITALIANO. 1858–1867. Ser. 1.

—— 1868–1885. Ser. 2.

GOBI, C. 1880. Algae rossicae exsiccatae.

GREVILLE, R. K. 1824–1825. Algae britannicae.

HAUCK, F. & P. RICHTER. 1885–1896. Phycotheca universalis.

HOHENACKER, R. F. 1852–1862. Algae marinae siccatae, edited by L. Rabenhorst & G. von Martens.

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HOLMES, E. M. 1883–1910. Algae britannicae rariores exsiccatae.

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KRYPTOGAMAE EXSICCATAE editae a museo Palatino Vindobonensi. 1894-X.

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LE LIÈVRE DE LA MORNIÈRE & F. PROUHET. 1841. Hydrophytes marines du Morbihan.

LENORMAND, R. 1844. Collection d'Hydrophytes.

LLOYD, J. 1847–1860. Algues de l'Ouest de la France.

MANDON, G. 1883. Algae Maderenses.

RABENHORST, L. 1848–1860. Die Algen Sachsens.
—— 1861–1879. Die Algen Europa's.
ROUMEGUÈRE, C. 1883–1893. Algues de France.
SCHIFFNER, V. F. 1926–1931. Algae marinae exsiccatae.
SCHIMPER, W. 1837. Unio itiner 1835.
SOCIETÉ DAUPHINOISE. 1880–1884. Exsiccatae.
THREDE, H. C. 1832. Die Algen der Nordsee....
WELWITSCH, F. 1842–1850. Phycotheca Lusitana.
WYATT, M. 1833–1840. Algae danmoniensis.

LIST OF CULTURES

List of cultures of *Sphacelaria* spp. mentioned in this book. Sequence of data: number, name of the taxon, locality of collection, date of collection, additional information.

66-1-1: *S. plumigera*, The Netherlands, Vlissingen, Nolledijk, on peat in the lower littoral, 31/5/1966, cancelled 12-12-1972.
66-3-1: *S. radicans*, The Netherlands, Kattendijke, east of the new sluice, on stones in *Ascophyllum* belt, 2/6/1966.
66-3-4: *S. nana*, data as in 66-3-1.
66-3-5: see 66-3-4.
66-3-6: see 66-3-4.
66-3-7: *S. rigidula*, data as in 66-3-1.
66-3-8: *S. nana*, germlings grown from unizoids in culture 66-3-6 on 11/3/1972.
66-4-1: *S. radicans*, The Netherlands, Goesse Sas, outside the sluice, on stones in *Ascophyllum* belt, 2/6/1966.
66-6-1: *S. nana*, The Netherlands, Tholen, Gorishoek, on stones in *Fucus serratus* belt, 3/6/1966.
66-6-2: *S. rigidula*, data as in 66-6-1.
66-10-1: *S. rigidula*, The Netherlands, Zuid-Beveland, Oude Katse Veer, west-side of the Veerdijk, on stones in border of *Ascophyllum* belt and *Fucus serratus* belt, 2/7/1966.
66-12-1: *S. rigidula*, The Netherlands, Kattendijke, near the old sluice, on stones in *Ascophyllum* belt, 4/7/1966, cancelled 4/2/1974.
66-15-1: *S. rigidula*, The Netherlands, Kattendijke, near the new sluice, on stones in *Ascophyllum* belt, 5/7/1966, cancelled 26/2/1973.
66-25-1: *S. rigidula*, Eire, Galway, Salthill, between Black Rock and Seaweed Point, in seagrass meadow, 22/7/1966.
66-26-3: *S. rigidula*, data as in 66-25-1, cancelled 17/4/1972.
66-34-2: *S. rigidula*, Eire, Co. Wicklow, Greystones, in tidal pools, 27/7/1966.
66-41-2: *S. rigidula*, France, Finistère, Roscoff, Pointe de Bloscon, tidal pools in *Ascophyllum* belt, 26/9/1966, cancelled 8/4/1972.
66-41-4: *S. rigidula*, data see 66-41-2, not yet cancelled.
66-42-3: *S. cirrosa* ecad *patentissima*, France, Finistère, Roscoff, Chenal de l'île Verte, in seagrass meadow, 27/9/1966, cancelled 14/11/1968.
66-46-1: *S. radicans*, France, Finistère, Roscoff, Penpoull, sandy tidal pools in *Ascophyllum* belt, 29/9/1966.
66-46-3: *S. radicans*, data as in 66-46-1.
66-46-4: *S. cirrosa* ecad *cirrosa*, data as in 66-46-1, cancelled 18/6/1969.
66-54: *S. cirrosa* ecad *cirrosa*, France, Finistère, Baie de Morlaix, Ile Callot, north-eastern side, small caves in *Laminaria digitata* belt, 30/9/1966, cancelled 21/5/1969.
66-55-1: *S. rigidula*, France, Finistère, Rade de Brest, Pointe du Bindy, high littoral, rockpools, 1/10/1966.
66-55-2: *S. rigidula*, data as in 66-55-1.
66-57-3: *S. rigidula*, France, Finistère, Rade de Brest, Pointe du Bindy, on rocks in *Ascophyllum* belt, 1/10/1966.
66-60-8: *S. cirrosa* ecad *cirrosa*, France, Finistère, Morgat, deep rockpools in the lower littoral, 2/10/1966, cancelled 5/6/1969.
66-60-9: *S. rigidula*, data as in 66-60-8, cancelled 9/12/1971.

66-62-1: *S. cirrosa* ecad *cirrosa*, France, Morbihan, Locmariaquer, near the Dolmen des pierres plattes, in tidal pools, 4/10/1966, cancelled 27/3/1972.

66-68-2: *S. cirrosa* ecad *cirrosa*, France, Finistère, Roscoff, Chenal de l'île Verte, on large boulders in *Fucus serratus* belt, 11/10/1966, cancelled 13/12/1969.

66-70: *S. cirrosa* ecad *hystrix*, France, Finistère, Roscoff, Chenal de l'île Verte, on sublittoral *Cystoseira nodicaulis*, 11/10/1966, cancelled 5/6/1969.

66-71: *S. cirrosa* ecad *cirrosa*, France, Finistère, Roscoff, Chenal de l'île Verte, on *Cystoseira tamariscifolia*, 11/10/1966, cancelled 5/6/1969.

66-85-1: *S. cirrosa* ecad *patentissima*, France, Finistère, Roscoff, Chenal de l'île Verte, in seagrass meadows, 11/10/1966, cancelled 6/8/1966.

66-89: *S. cirrosa* ecad *cirrosa*, France, Finistère, Roscoff, Ile Verte, northern coast, rockpools in *Ascophyllum* belt, on *Cystoseira foeniculacea*, 16/10/1966, cancelled 24/3/1971.

66-94: *S. cirrosa* ecad *cirrosa*, France, Finistère, Ile de Batz, northwestern coast, rockpools in *Fucus spiralis* belt, 21/10/1966, cancelled 23/3/1970.

66-96: *S. cirrosa* ecad *cirrosa*, France, Finistère, Roscoff, Guerhéon, 4–14 m deep, dredged from maerl, 17/10/1966, cancelled 20/1/1969.

66-98: *S. cirrosa* ecad *bipinnata*, France, Finistère, Roscoff, Le Vil, washed up, on *Halidrys siliquosa*, 25/10/1966, cancelled 13/10/1967.

66-105-2: *S. cirrosa* ecad *patentissima*, France, Finistère, Roscoff, Chenal de l'île Verte, in seagrass meadows, 29/10/1966, cancelled 16/1/1969.

67-1-3: *S. plumigera*, The Netherlands, Vlissingen, Nolledijk, on boulders in the lower littoral, 14/1/1967, collected by G. Heerebout, cancelled 10/3/1975.

67-5: *S. cirrosa* ecad *bipinnata*, France, Finistère, Roscoff, Per Roc'h, on *Halidrys siliquosa*, 25/4/1967, collected by G. Heerebout, cancelled 23/9/1971.

67-6: *S. cirrosa* ecad *bipinnata*, France, Finistère, Roscoff, Per Roc'h, on *Cystoseira baccata*, 25/4/1967, cancelled 15/1/1970.

67-9: *S. radicans*, from unknown locality, first observed 2/12/1970.

67-10.2: *S. cirrosa* ecad *cirrosa*, Sweden, Bohuslän, Kristineberg, Kylin's bathing place, on *Rhodophyceae* (*Chondrus* and *Phyllophora*), 2 m deep, 23/5/1967, cancelled 22/6/1972.

67-16: *S. cirrosa* ecad *cirrosa*, Sweden, Bohuslän, Kristineberg, Stångholmegrundet, 15–16 m deep, on *Desmarestia aculeata*, 24/5/1967, cancelled 30/6/1972.

67-18: *S. caespitula*, Sweden, Bohuslän, Kristineberg, Stångholmegrundet, 15–16 m deep, on boulders, 24/5/1967.

67-21-1: *S. plumosa*, data as in 67-18.

67-24-2: *S. plumosa*, Norway, Hordaland, Espegrend, Skjerholmen, 20 m deep, on stipes of *Laminaria hyperborea*, 29/5/1967, cancelled 10/3/1975.

67-25: *S. cirrosa* ecad *cirrosa*, Norway, Hordaland, Espegrend, Börnestangen, 9–16 m deep, on stipes of *Laminaria hyperborea*, 30/5/1967, cancelled 23/10/1972.

67-28: *S. cirrosa* ecad *cirrosa*, Norway, Hordaland, Espegrend, Börnestangen, 9–16 m deep, on *Desmarestia aculeata*, 30/5/1967, cancelled 8/5/1972.

67-31-1: *S. nana*, Norway, Hordaland, Skogsvåg, Barholmen, in crevices in sheltered shallow rocks in *Pelvetia* belt and *Fucus spiralis* belt, 29/5/1967.

67-34-3: *S. nana*, Norway, Hordaland, Espegrend, Mariholmen, on rocks in *Fucus spiralis* belt, 28/5/1967.

67-35: *S. cirrosa* ecad *cirrosa*, Norway, Hordaland, Skogsvåg, Barholmen, 16–22 m deep, on stipes of *Laminaria hyperborea*, 29/5/1967.

67-37: *S. cirrosa* ecad *bipinnata*, Norway, Hordaland, Espegrend, Kviturdvikpollen, opposite Synningane, on sublittoral *Halidrys siliquosa*, 31/5/1967, cancelled 20/1/1969.

67-44: *S. cirrosa* ecad *bipinnata*, Norway, Hordaland, Espegrend, Grunnansundsholmen, 1 m deep, on *Halidrys siliquosa*, 31/5/1967, cancelled 2/8/1968.

67-47-1: *S. caespitula*, Norway, Hordaland, Espegrend, Löholmen, 11–19 m deep, on stipes of *Laminaria hyperborea*, 30/5/1967.

67-49-1: *S. plumosa*, Norway, Hordaland, Fanafjord, Svartholmen, 7–16 m deep, on stones, shells and stipes of *Laminaria hyperborea*, 30/5/1967, cancelled 10/4/1973.

67-49-2: see 67-49-1, not yet cancelled.

67-52-1: *S. radicans*, Norway, Hordaland, Hardangerfjord, Øystese, direction Thorpe, on steep rocks, just below the *Ascophyllum* belt, 3/6/1967.

67-53-1: *S. plumosa*, Norway, Hordaland, Hardangerfjord, Øystese, direction Norheimsund, 2–4 m deep, on stones, 3/6/1967, cancelled 11/4/1973.

67-56: *S. arctica*, Norway, Hordaland, Hardangerfjord, Øystese, direction Norheimsund, 0.5–1 m deep, on *S. plumosa* and *Fucus vesiculosus*, 4/6/1967.

67-57: *S. nana*, Norway, Hordaland, Hardangerfjord, Øystese, on wood in the upper littoral, 3/6/1967.

67-57-4: *S. nana*, germlings probably grown from plurizoids of culture 67-57, 9/6/1978.

67-58: *S. cirrosa* ecad *cirrosa*; Unknown locality, probably from Øystese, first observed 2/11/1971.

67-59-1: *S. radicans*, Norway, Hordaland, Hardangerfjord, Øystese, direction Norheimsund, on a branch of an old drowned tree, from 1 m depth, 4/6/1967.

67-62-1: *S. cirrosa* ecad *cirrosa*, Norway, Hordaland, Hardangerfjord, Øystese, on stones, 0.5 m deep, 4/6/1967, cancelled 29/2/1972.

67-62-3: *S. radicans*, data as in 67-62-1, not yet cancelled.

67-62-5: *S. radicans*, data as in 67-62-3.

67-62-6: *S. radicans*, germlings grown from unizoids in culture 67-62-5, 26/8/1976.

67-64: *S. nana*, Norway, Akershus, Drøbak, south of Askholmene, 4–5 m deep, on stones, shells, and small algae, 7/6/1967.

67-64-1: *S. nana*, data as in 67-64.

67-64-2A: *S. nana*, germlings grown from unizoids of culture 67-64, 20/2/1975.

67-64-4: *S. nana*, data as in 67-64-2A.

67-64-5: *S. nana*, germlings, probably grown from plurizoids of culture 67-64-4; 17/12/1975.

67-65-1: *S. arctica*, Norway, Akershus, Drøbak, south of Askholmene, 4–5 m deep, on stones, shells, and small algae, 7/6/1967.

67-69: *S. radicans*, Norway, Akershus, Drøbak, Storskjaer, 4–5 m deep, on stones and shells, 8/6/1967, cancelled 23/11/1971.

67-71-1: *S. nana*, Norway, Akershus, Drøbak, south of harbour jetty, 1–1.5 m deep, on shell of *Mytilus*, 10/6/1967.

67-74: *S. cirrosa* ecad *cirrosa*, Norway, Akershus, Drøbak, Gylteholmen, pollen, 1 m deep, on rocks, 9/6/1967, cancelled 29/2/1972.

67-75-2: *S. radicans*, Norway, Akershus, Drøbak, Gylteholmen, pollen, 1 m deep, on rocks, 9/6/1967.

67-77-1: *S. nana*, Norway, Akershus, Emmerstadbukta, shadowed crevices in the rocks near the waterline, mixed with *Rhodochorton purpureum*, 12/6/1967, cancelled 31/8/1979.

67-82-2: *S. arctica*, Norway, Ostfold, Tjøme, Verdens Ende, shallow inlet between the rocks, 0.5 m deep, in seagrass meadow, 13/6/1967.

67-82-4: *S. radicans*, data as in 67-82-2.

67-89: *S. arctica*, Sweden, Södermanlands Län, Trosa, between the small isles Persö and Persöbådan, 14–17 m deep, on small stones and on rocks, 20/6/1967.

67-89-3: *S. arctica*, data as in 67-89.

67-90: *S. arctica*, Sweden, Gotland, Visby, washed up, 23/6/1967, cancelled 30/5/1972.

67-92: *S. cirrosa* ecad *bipinnata*, Sweden, Halland, Frillesås, Askloster, washed up, on *Halidrys siliquosa*, 25/6/1967, cancelled 27/1/1971.

67-96: *S. cirrosa* ecad *cirrosa*, France, Pyrénées Orientales, Banyuls-sur-Mer, Plage du Troc, in shallow inlet, 1/9/1967, cancelled 13/2/1969.

67-103: *S. cirrosa* ecad *cirrosa*, France, Pyrénées Orientales, Banyuls-sur-Mer, Cap Oullestreil, shallow sunny rockpools, on *Cystoseira mediterranea*, 3/9/1967.

67-112: *S. tribuloides*, France, Pyrénées Orientales, Banyuls-sur-Mer, Anse des Grandes Elmes, shallow shadowed inlets, 0.75–1 m deep. 8/9/1967.

67-114: *S. cirrosa* ecad *hystrix*, France, Pyrénées Orientales, Banyuls-sur-Mer, Anse des Petites Elmes, sheltered, shallow inlet, 0.25–0.4 m deep, on *Cystoseira caespitosa*, 8/9/1967, cancelled 27/3/1972.

67-122: *S. tribuloides*, France, Pyrénées Orientales, Port Vendres, Cap Béar, 20 m deep, on *Codium bursa*, 12/9/1967, cancelled 23/6/1971.

67-129-2: *S. radicans* (?). From unknown locality, first observed 14/3/1973.

68-3-1: *S. plumigera*, The Netherlands, Vlissingen, Nolledijk, on boulders, lower littoral, 2/2/1968, cancelled 4/8/1977.

68-5-1: *S. plumigera*, data as in 68-3-1, not yet cancelled.

68-13-1: *S. rigidula*, France, Pas-de-Calais, Wimereux, Fort du Croï, on a steep wall, upper littoral, 8/3/1968.

68-24: *S. cirrosa* ecad *cirrosa*, France, Ille-et-Vilaine, St. Lunaire, Pointe du Décollé, rockpools in *Pelvetia* belt, 16/3/1968, cancelled 15/11/1968.

68-25: *S. cirrosa* ecad *patentissima*, France, Ille-et-Vilaine, St. Lunaire, grève de Grand Lambert, seagrass meadow, 16/3/1968, cancelled 17/6/1969.

68-25-2: *S. plumula*, data as in 68-25, not yet cancelled.

68-32-5: *S. rigidula*, France, Ille-et-Vilaine, St. Lunaire, in front of the Grotte de Sirènes, in belt of *Laminaria digitata*, on rocks, 16/3/1968.

68-45: *S. cirrosa* ecad *bipinnata*, France, Finistère, Concarneau, Mole de la Croix, washed up, on *Halidrys siliquosa* and *Cystoseira baccata*, 20/3/1968, cancelled 5/5/1969.

68-48-1A: *S. radicans*, germlings grown on 21/4/1975 from unizoids of culture 68-48-1, collected from France, Finistère, Baie de Morlaix, Chateau de Taureau, 4–12 m deep, on maerl.

68-48-6: *S. caespitula*, data as for 69-48-1A.

68-49: *S. nana*, France, Finistère, Roscoff, pier of the old harbour, on rocks between *Fucus vesiculosus* and *Ascophyllum nodosum*, 24/3/68.

68-49-3: *S. nana*, data as in 68-49.

68-53-1: *S. nana*, France, Manche, le Béquet, harbour-walls, upper littoral, 29/3/1968.

68-54: *S. cirrosa* ecad *cirrosa*, France, Calvados, Grandcamp-les-Bains, rochers de Grandcamp, in tidal pools, on rocks, 30/3/1968, cancelled 27/3/1972.

71-11: *S. racemosa*, Scotland, Fife, St. Andrews, Hind Rock, in tidal pools at the steep northern side of the rock, 10/2/1971.

71-17-3: *S. mirabilis*, Scotland, Fife, St. Andrews, Step Rock, in shallow tidal pools at the foot of the rock, 11/2/1971.

71-17-3A: *S. mirabilis*, germlings grown from unizoids of 71-17-3, 6/5/1971.

71-17-3E: *S. mirabilis*, germlings grown from unizoids of 71-17-3, 10/7/1974.

71-17-3H: *S. mirabilis*, data as in 71-17-3E.

71-17-3H-2A: *S. mirabilis*, germlings probably grown from plurizoids of 71-17-3H, 15/4/1975.

71-17-3H-2B *S. mirabilis*, data as in 71-17-3H-2A.

71-17-5: *S. mirabilis*, germlings grown from unizoids of 71-17-3, 19/9/1971, cancelled 19/6/1973.

71-21: *S. racemosa*, Scotland, Fife, St. Andrews, Doo Craig, in sandy tidal pools in *Fucus spiralis* belt, 16/2/1971.

71-22-1: *S. plumigera*, The Netherlands, Vlissingen, Nolledijk, on boulders in the lower littoral, 27/2/1971, cancelled 3/7/1973.

71-22-2: as in 71-22-1.

71-30: *S. nana*, The Netherlands, Zeeuws Vlaanderen, Baalhoek, in open growth of *Fucus vesiculosus* and *Ascophyllum nodosum*, 2/3/1971, cancelled 29/4/1975.

72-13: *S. nana*, The Netherlands, Kattendijke, east of the new sluice, on stones in *Fucus spiralis* belt, 21/2/1972, cancelled 27/11/1972.

LIST OF TABLES

INDEX OF TAXONOMIC NAMES

For all taxa, except *Phaeophyceae*, indication is given about the taxonomic position. For the taxa of *Sphacelariales* accepted and described in this book the main pages are printed in **bold-face type** in this index.

EXPLANATION OF PLATES

Abbreviations used in plates 1a, b and 2d

CE, chloroplast envelope, CER, endoplasmatic reticulum associated with the chloroplast; Ch, chloroplast; Chr, chromatin; CW, cell wall; ER, endoplasmatic reticulum; FV, supposed fucoidan vesicle; G, genophore; IFL, inner fibrillary layer of the cell wall; LW, longitudinal cell wall; M, mitochondrion; Mb, microbody; N, nucleus; NL, nucleolus; OFL, outer fibrillary layer; OG, osmiophilic globule; OL, outer layer of the cell wall; PB, paramural body; Ph, physode; Pl, plasmalemma; PLa, photosynthetic lamella; Ps, paramural space; T, thylakoid; TW, transverse cell wall; UV, unstructured electron-dense vesicle; V, vacuole; VL, vesiculated layer of the cell wall.

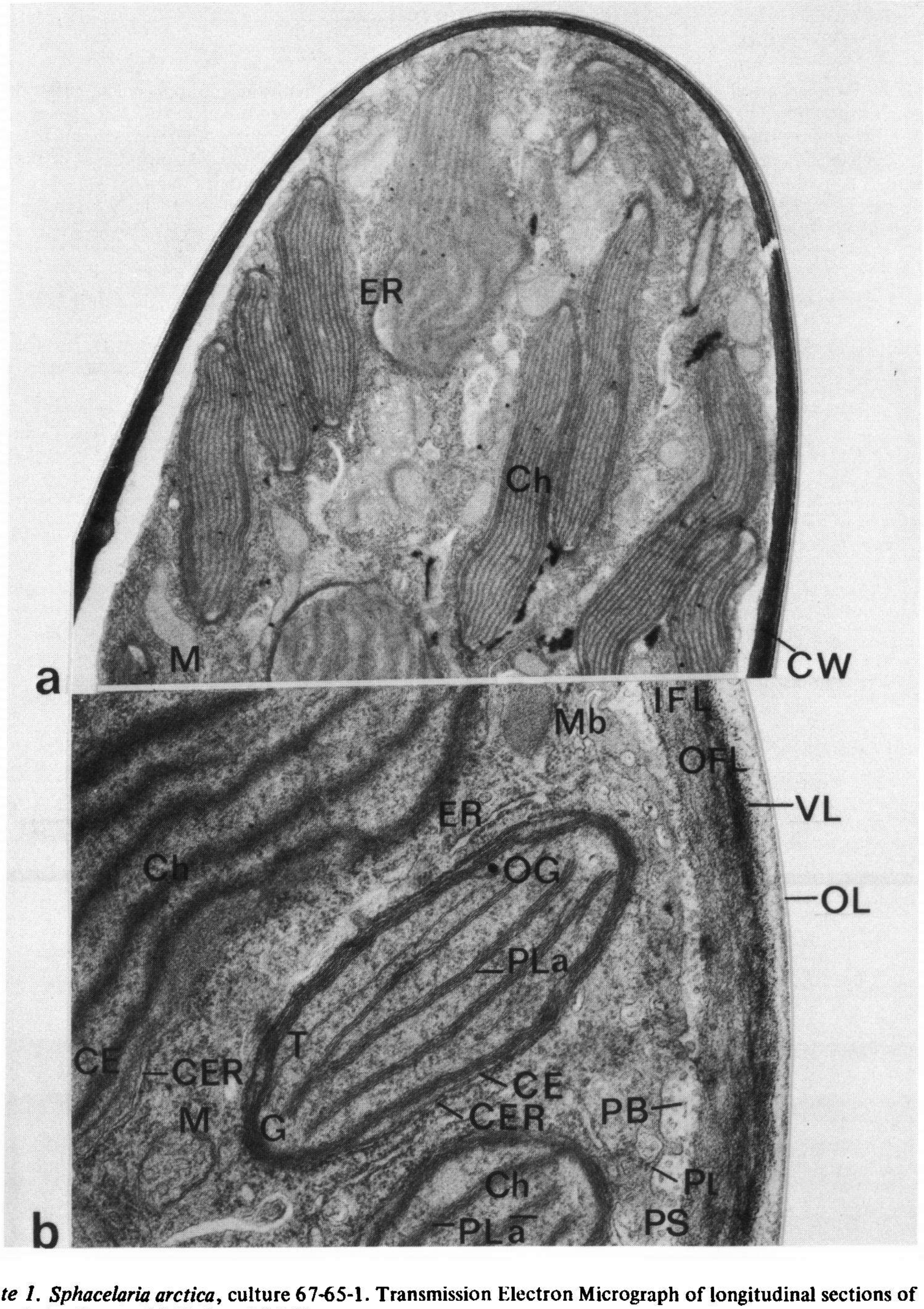

Plate 1. Sphacelaria arctica, culture 67-65-1. Transmission Electron Micrograph of longitudinal sections of an apical cell. a. × 9,900; b. × 29,700.

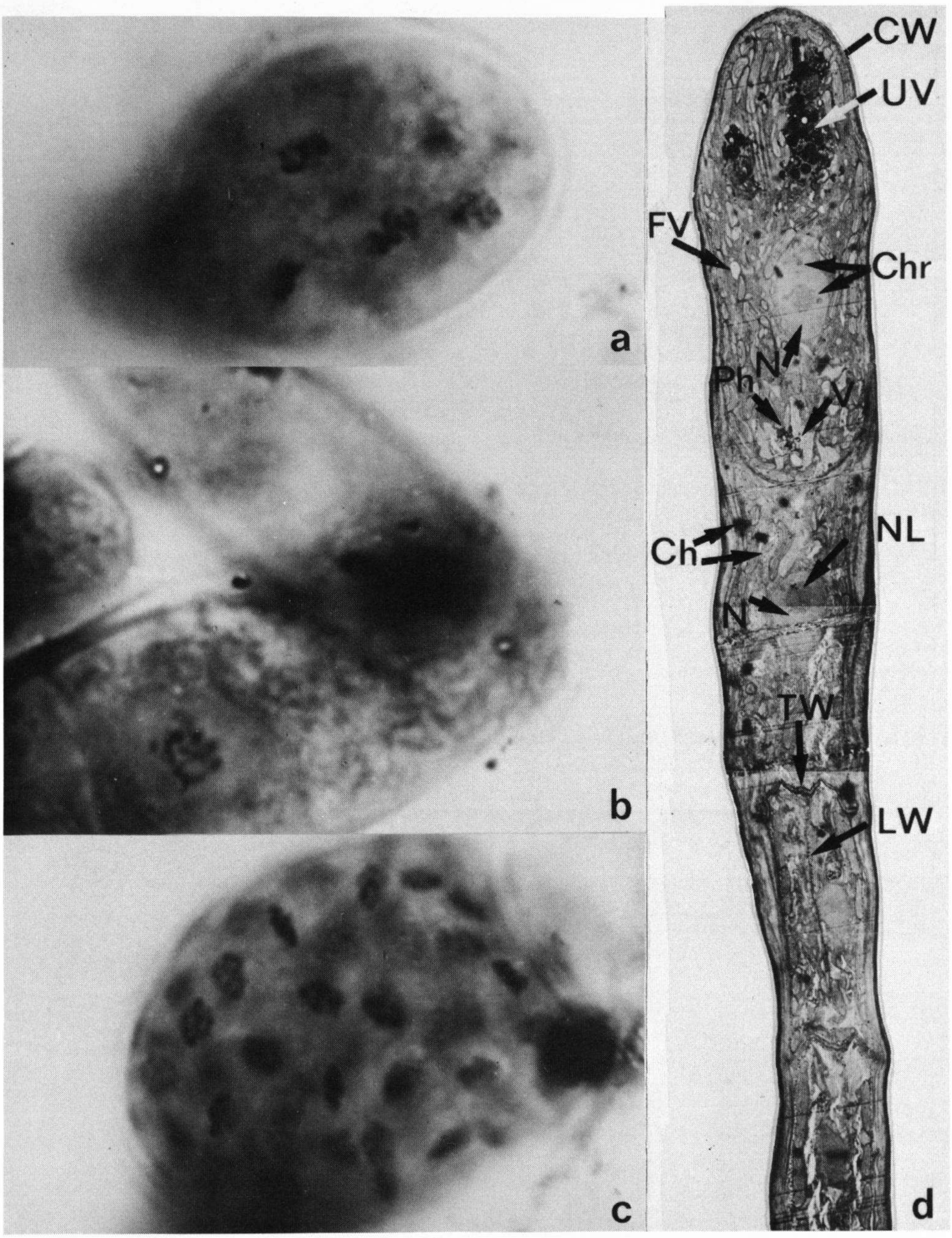

Plate 2. a–c. ***Sphacelaria mirabilis*****,** St. Andrews, ***Prud'homme van Reine 71-17.*** a. Mitosis-metaphases or early anaphases in a young unilocular zoidangium, × 2,200; b. Meiosis-diakinesis in an initial of a unilocular zoidangium, × 1,840; c. Simultaneous mitotic division in a young unilocular zoidangium, × 2,080; d. ***S. nana*****,** culture 67-34-3. TEM of longitudinal section of an erect filament, × 1,750.

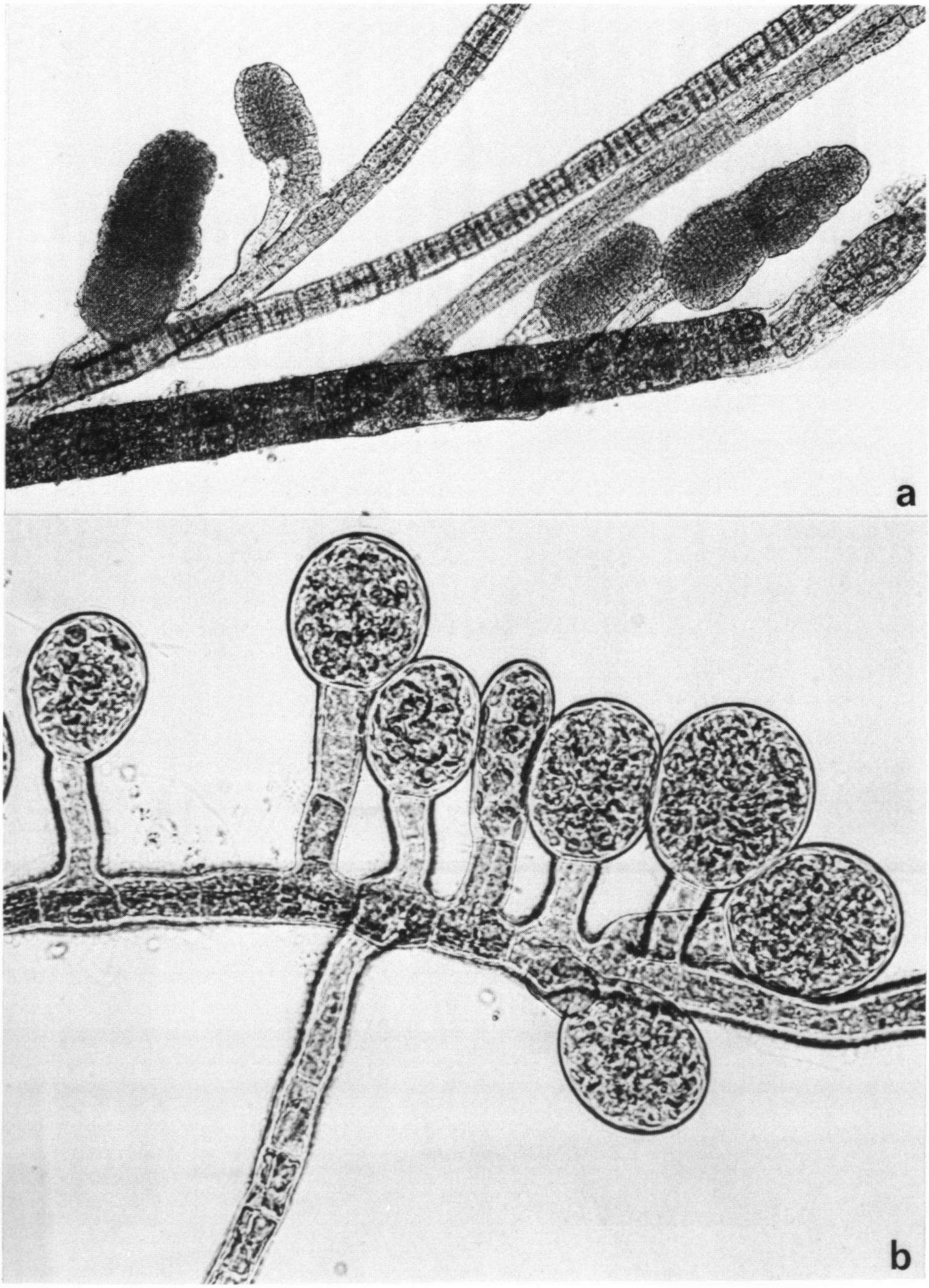

Plate 3. a. ***Sphacelaria radicans***, culture 67-62-6. Plurilocular zoidangia, × 215; b. ***S. nana***, culture 66-3-5. Unilocular zoidangia, × 520.

Plate 4. Sphacelaria nana, culture 67-31-1. Plurilocular zoidangia, × 59.

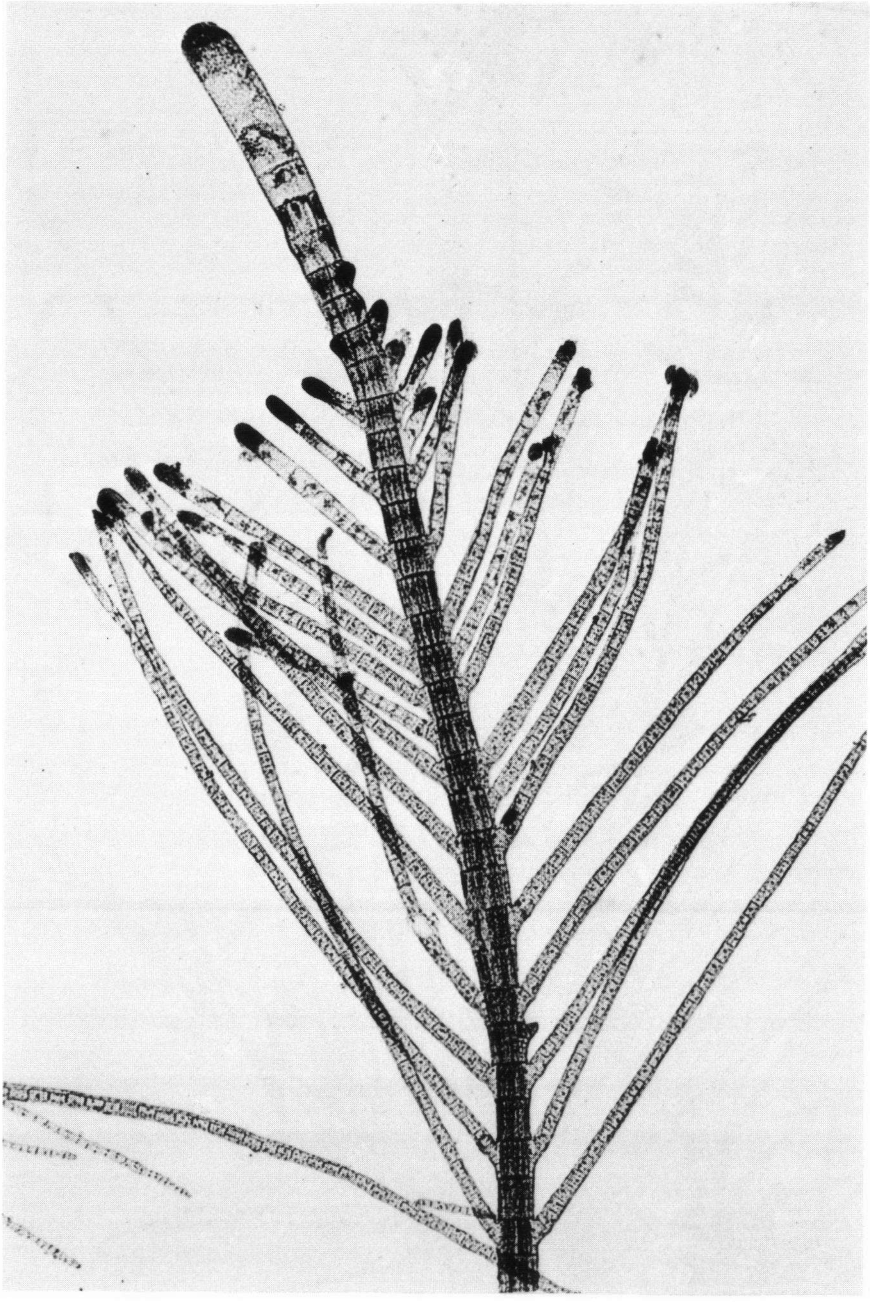

Plate 5. Sphacelaria plumula, Banyuls-sur-Mer, *Prud'homme van Reine 67-144B*, coloured with aceto-carmine. Apical part of an erect filament, × 76.

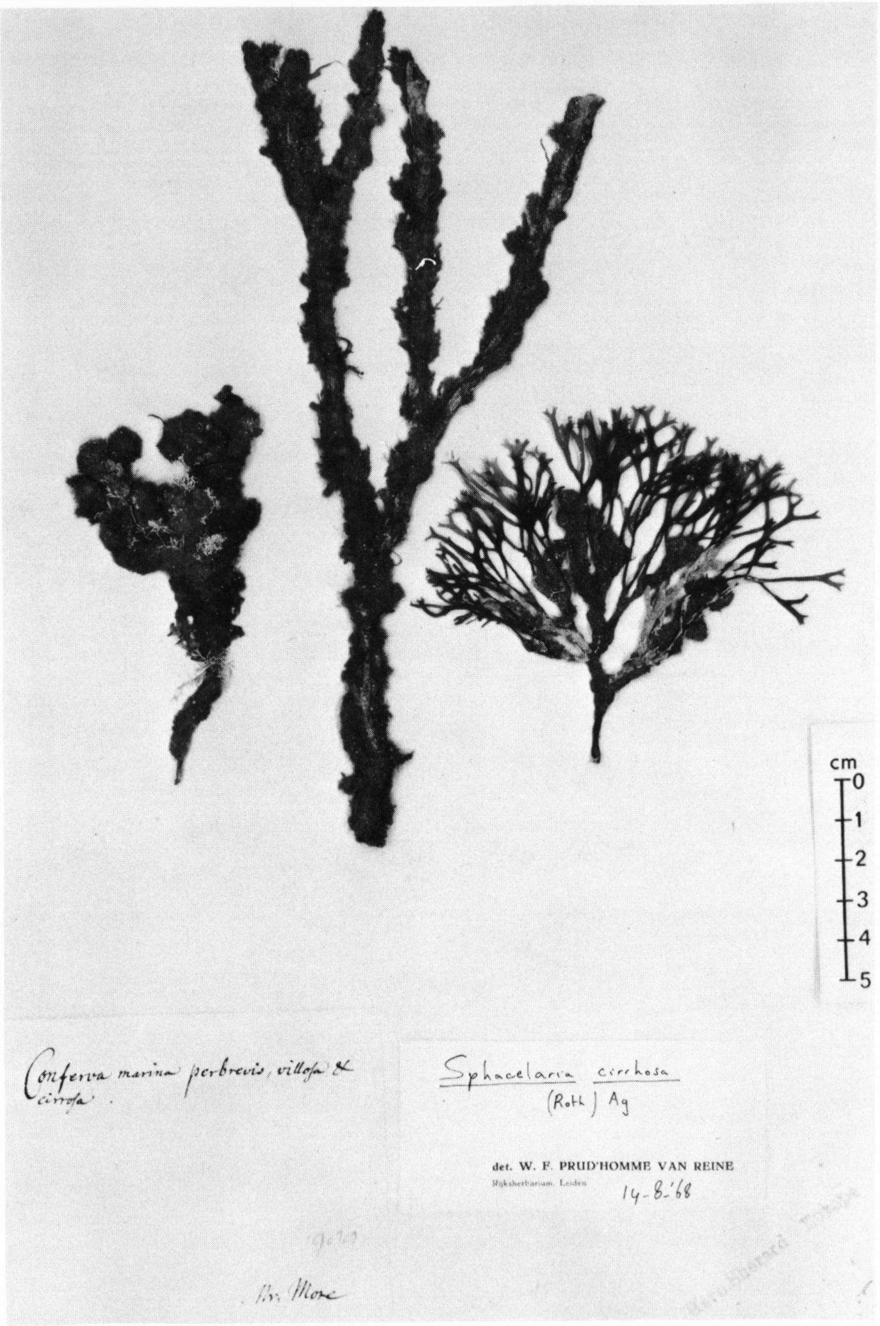

Plate 6. Type of *Conferva marina perbrevis villosa et cirrosa* Dillen. The specimen on the left has probably been figured by Dillen.