

## THE GENUS *SPHACELARIA* LYNGBYE (PHAEOPHYCEAE) IN THE NETHERLANDS

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### SUMMARY

The species of the genus *Sphacelaria* Lyngb. that occur in the Netherlands have been investigated. These species are: *S. plumigera* Holmes, *S. radicans* (Dillw.) Ag., *S. fusca* (Huds.) Ag.

It is suggested that *S. furcigera* and *S. saxatilis* should be regarded as synonyms of *S. fusca*.

It was found that *S. fusca* also forms bifurcate propagulae in contrast to reports in the literature.

Cultures were grown of *S. plumigera*, *S. fusca*, *S. britannica*, and *S. radicans*.

The cultures of *S. fusca*, *S. britannica*, and *S. radicans* exhibited very feebly fixed polarity in contrast to the cultures of *S. plumigera*.

*S. cirrosa* and *S. fusca* are considered to be two different species.

### INTRODUCTION

The taxonomy of the genus *Sphacelaria* as given in various algal floras (van Goor, 1923 a, of the Netherlands; Hamel, 1931—1939, of France: Waern, 1945, and Kylin, 1947, of Sweden; Lund, 1950, of Denmark; Irvine, 1955, of England) is based primarily on the work of Sauvageau (1901—1914), who studied material of world wide distribution and whose investigations are fundamental to the knowledge of this genus. One species of *Sphacelaria*, namely *S. plumigera* which occurs in the Netherlands, has been studied not only by van Goor but also by den Hartog (1954).

A study of the literature indicates that there is considerable difference of opinion with regard to certain aspects of the taxonomy and nomenclature of *Sphacelaria*.

In this report the *Sphacelaria* species that occur in the Netherlands are discussed.

In order to obtain as complete a picture as possible of the various species, a large number of herbarium specimens were studied and in addition living material collected in the Netherlands, unialgal cultures, and where necessary material from abroad (for instance type material of *S. cirrosa*, *S. furcigera*, *S. saxatilis*, and *S. britannica*).

### SPHACELARIA

Lyngbye, 1819, p. 103.

Small brown marine plants, growing in brushes or mats on rocks or on other algae, attached by discs, rhizoids, and stolons from which arise more or less ramified branches. Apical cells large and cylindrical, cut off cells from the basis; the subapical cell divides into a primary and a secondary segment and the secondary segment, in turn, divides into an upper and a lower secondary segment. Laterals generally arise from the upper secondary segment and are of determinate or of indeterminate growth. The secondary segments are divided by longitudinal walls and sometimes by transverse walls of the second order. Reproduction by means of propagulae and/or uni- and/or plurilocular sporangia. In some species the rhizoids form a complete cortication. Chromatophores are disc-shaped, they divide actively, particularly in the apical cell, the primary segment, and the secondary segments near the apical cell.

*Characteristics which can be used to distinguish between species.* The features to be studied are:

1. The mode of branching. Growth of laterals (determinate or indeterminate); when a lateral of determinate growth has reached its maximum length the apical cell generally is no longer rounded but pointed.
2. The width of filaments (not only of the main axes, but also of the laterals). Also the length to width ratio of the apical cells and of the segments.
3. The increasing septation in a basipetal direction, i.e. the maximum number of longitudinal walls and transverse walls of the second order per segment.
4. The absence or presence of secondary thickening.
5. The morphology of the propagulae. These may be bifurcate or trifurcate in some of the species studied and in addition the shape of the arms is distinctive for each species.
6. The size, shape, and site of the sporangia.
7. The size of the chromatophores in the apical cells and in the intercalary cells.

*Material and methods.* Three species, namely *Sphacelaria fusca* (Huds.) Ag., *Sphacelaria radicans* (Dillw.) Ag., and *Sphacelaria plumigera* Holmes, occur in the Netherlands. All the herbarium material, collected in the Netherlands, as well as some samples from abroad and living material were studied. The following abbreviations are used for the herbaria from which material has been borrowed (Lanjouw & Stafleu, Index Herbariorum, 1964): BM — British Museum (Natural History), London; K — The Herbarium and Library, Kew; L — Rijksherbarium, Leiden; WU — Botanisches Institut und Botanischer Garten der Universität Wien.

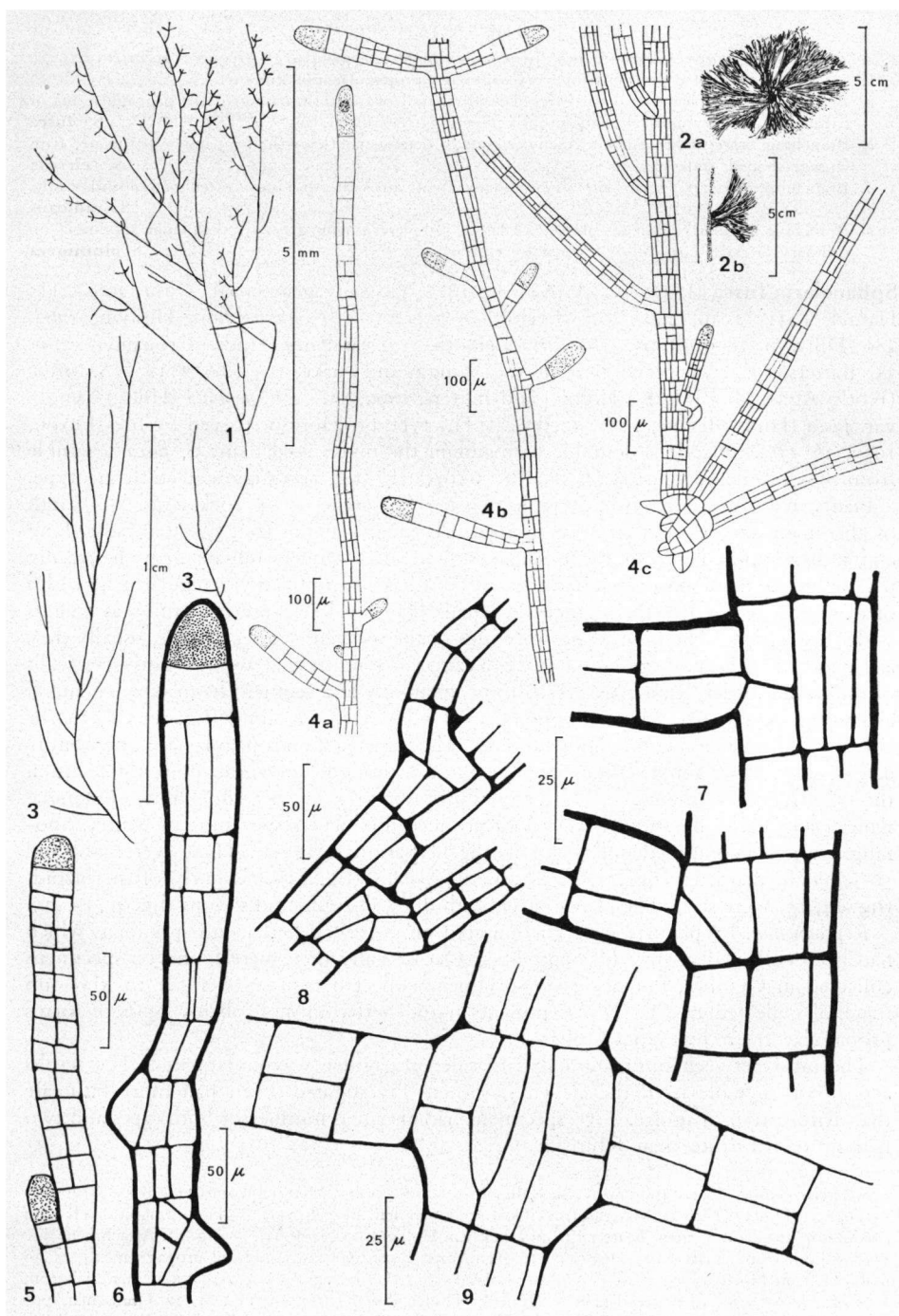
The samples of *Sphacelaria* from the Netherlands which are present in the Rijks-herbarium were mostly collected by J. Th. Koster, C. den Hartog, and C. van den Hoek, for whom the following abbreviations are used: J. Th. Koster — K; C. van den Hoek — v. d. H.; C. den Hartog — C. d. H.

From a number of samples unialgal cultures were grown in culture tubes under relatively constant conditions in order to eliminate the influence of different environmental conditions on the morphological characteristics. The method of van den Hoek (1963) was used, in which unialgal cultures were obtained by cutting off fragments two to six segments long, under a binocular dissecting microscope.

These fragments after a passage through sterile medium contained in two to three watch glasses, were placed separately into tubes containing sterile medium and plugged with cotton wool. Possible algal contaminants were killed by heating the culture-fluid at 100° C. The tubes were sterilized at a temperature of 160—170° C. Erdschreiber-medium was used, the composition of which follows: a basal solution of 500 cc soil extract containing 0.2 g  $K_2HPO_4$  and 1 g  $KNO_3$  was made. In order to prepare one litre of Erdschreiber, 50 cc of the basal solution and 950 cc seawater were mixed and the pH adjusted to 7.5 with 10 % NaOH.

The cultures were grown: 1) on racks, which were placed at a north-facing window, 2) in a constant-temperature room of 12° C, with a light intensity of 2000—3000 lux during daily 16 hours' photoperiods.

*Sphacelaria fusca.* — Fig. 1. Branches with bi- and trifurcate propagulae. Neotype from Roscoff. — Fig. 2a, b. Habit. Plant from Gorishoek, Tholen (28-10-1951). — Fig. 3. Two axes with laterals. Material from Hoek van Holland (15-12-1963). — Fig. 4a, b, c. Apical cells, laterals, basal disc of the same material. — Fig. 5, 6. Apical cells. In 6 two initials of laterals. Same material. — Fig. 7, 8, 9. Laterals, insertion. Same material.



## KEY TO THE DUTCH SPECIES

1. a. Secondary transverse divisions not in every segment; propagulae of frequent occurrence . . . 2  
    b. Secondary transverse divisions in every segment; propagulae not known . . . . . 3
2. a. Branching sparse to rather dense, irregular; all laterals of indeterminate growth; propagulae bi- or trifurcate, arms cylindrical, stalk slightly tapering towards its base . . . . . *S. fusca*  
    b. Branching more or less pinnate; many laterals of determinate growth; propagulae trifurcate, arms sausage-shaped, stalk clavate . . . . . *S. cirrosa*
3. a. Branching sparse, irregular; laterals of indeterminate growth; sporangia often paired and sessile. . . . . *S. radicans*  
    b. Branching regularly pinnate; almost all laterals of determinate growth; unilocular sporangia on ordinary laterals; cortication formed by rhizoids . . . . . *S. plumigera*

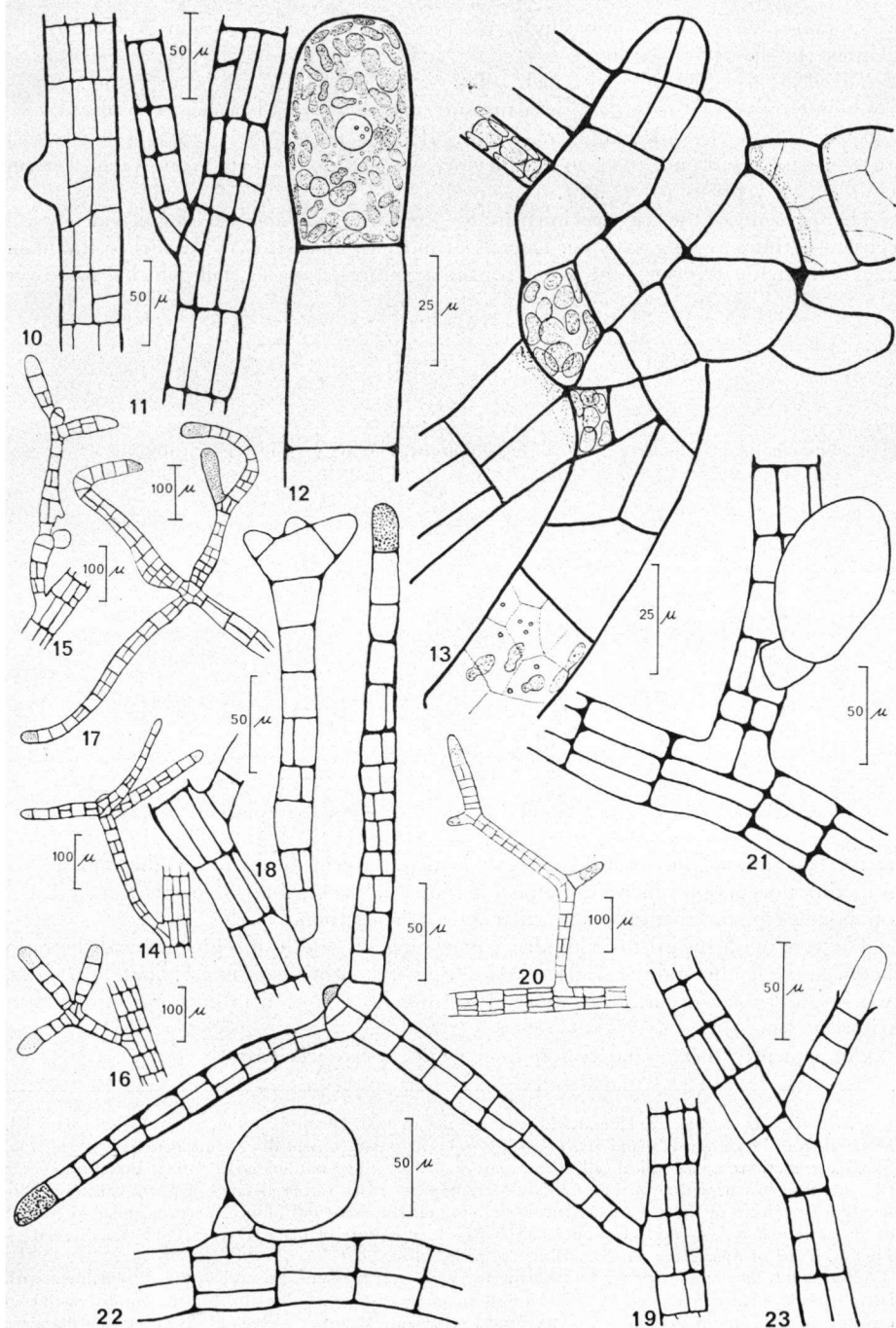
*Sphacelaria fusca* (Huds.) C. A. Agardh, 1828, 34; Sauvageau, 1901—1914, 206—211; Hamel, 1931—1939, 260—261; Taylor, 1957, 120. — *Conserva fusca* Hudson, 1762, 486; Dillwyn, 1809, pl. 95. — *S. cirrosa* (Roth) Ag. var. *fusca* (Huds.) Crouan, 1852, n. 35; Batters, 1902, 39; Newton 1931, 190; Knight and Parke, 1931, 66, 111. — *S. cirrosa* (Roth) Ag. f. *fusca* (Huds.) Holmes and Batters, 1890, 81. — *S. pennata* (Huds.) Lyngb. var. *fusca* (Huds.) Irvine, 1955, 32, 33. — The type probably destroyed by fire (Dixon, 1959, 36—38). Since it is desirable to maintain the much used name *S. fusca*, a sample from Roscoff, Ile Verte, v. d. H. 3695, 30-6-1958 (L) (fig. 1) is suggested as the neotype.

Plants in brushes, 0.5—3 cm, epiphytic on other algae or on rocks (fig. 2). Width of the main axis 25—45  $\mu$ . Few to relatively many laterals (fig. 3), often rather long and indistinguishable from the main axes. Laterals of indeterminate growth, usually parallel to the main axis, often narrower at their base. Ramification irregular. The width of the apical cell and of the segments is equal. The apical cells are 1—3 times as long as wide. (fig. 4, 5, 6). The ratio length to width of the segments varies greatly; usually they are wider than long. Segments usually with 2—6 longitudinal walls. Transverse walls of the second order occur regularly, almost invariably at a segment from which a lateral arises (fig. 4c, 7—11). Chromatophores 4—9  $\mu$  (average 6  $\mu$ ) long (fig. 12, 13). Bi- or trifurcate propagulae with cylindrical arms. The arms of the propagulae are often bifurcate or show other abnormalities (fig. 14—20). Although Sauvageau does not mention the occurrence of sporangia, Dillwyn's illustration of *Conserva fusca* shows sporangia. Knight and Parke mention that *S. fusca* produces unilocular sporangia in winter. Sporangia were encountered only once in the herbarium material. These were oval and 50—60  $\mu$  in diameter (fig. 21, 22). Sometimes hairs (fig. 23) and fairly often rhizoids (fig. 24, 25) were seen. The plants attach with discs, rhizoids, and stolons (fig. 4c, 13, 26).

**Reproduction.** Propagulae were encountered on nearly all herbarium specimens which had been collected in June till September. Occasionally they were found on specimens collected in October, but never on specimens collected from November to May (no material collected in March was present in the herbarium). Probably *S. fusca* forms propagulae from June to October.

The ratio between bifurcate and trifurcate propagulae was investigated. The results are shown in table 1. In the eleven specimens investigated seven had more bifurcate than trifurcate propagulae. Two specimens had an equal number of both types and two had more trifurcate than bifurcate ones.

*Sphacelaria fusca*. — Fig. 10. Transverse walls of the second order. Material from Oude Katse Veer (22-1-1964). — Fig. 11. Lateral. Material from Gorishoek, Tholen (28-10-1951). — Fig. 12. Apical cell with chromatophores and nucleus. Material from Hoek van Holland (15-12-1963). — Fig. 13. Attachment disc with stolons. Same material. — Fig. 14—20. Trifurcate, bifurcate, and abnormal propagulae. 14, 15, 16 material from Norfolk, leg. Batters. 17, 20 material from Bergen op Zoom (6-1937). 18 material from Roscoff (30-6-1958). 19 material from Gorishoek, Tholen (28-10-1951). — Fig. 21, 22. Unilocular sporangia. Material from Norfolk, leg. Batters. — Fig. 23. Hair. Culture of material from Hoek van Holland.



Sporangia were found on a single specimen collected in August in Norfolk by E. Batters (L, sh. 937—714—96).

*Taxonomic notes.* The species which will now be discussed do not occur in the Netherlands but are related to *S. fusca* in a measure that they should be here considered.

*Sphacelaria furcigera* Kützinger, 1855, tab. 91; Sauvageau, 1901—1914, 156; Hamel 1931—1939, 255; Lund, 1950, 29—32; Irvine, 1955, 28, 29. — Type from Karak, Persian Gulf (L, sh. 937—714—72) (fig. 33).

The segments of the type specimen are 25—50  $\mu$  wide, and about as long as wide. Apical cells 1—2 times as long as wide. Laterals of indeterminate growth parallel to the main axes and often narrower at the base. Propagulae bifurcate, with a stalk which is narrower

TABLE 1

Number of propagulae	of those	
	bifurcate	trifurcate
8	5	3
30	27	3
25	23	2
28	16	12
22	12	10
30	20	10
20	10	10
20	13	7
25	13	12
20	8	12
20	4	16

*S. fusca.* Relative occurrence of bifurcate and trifurcate propagulae in material from nature.

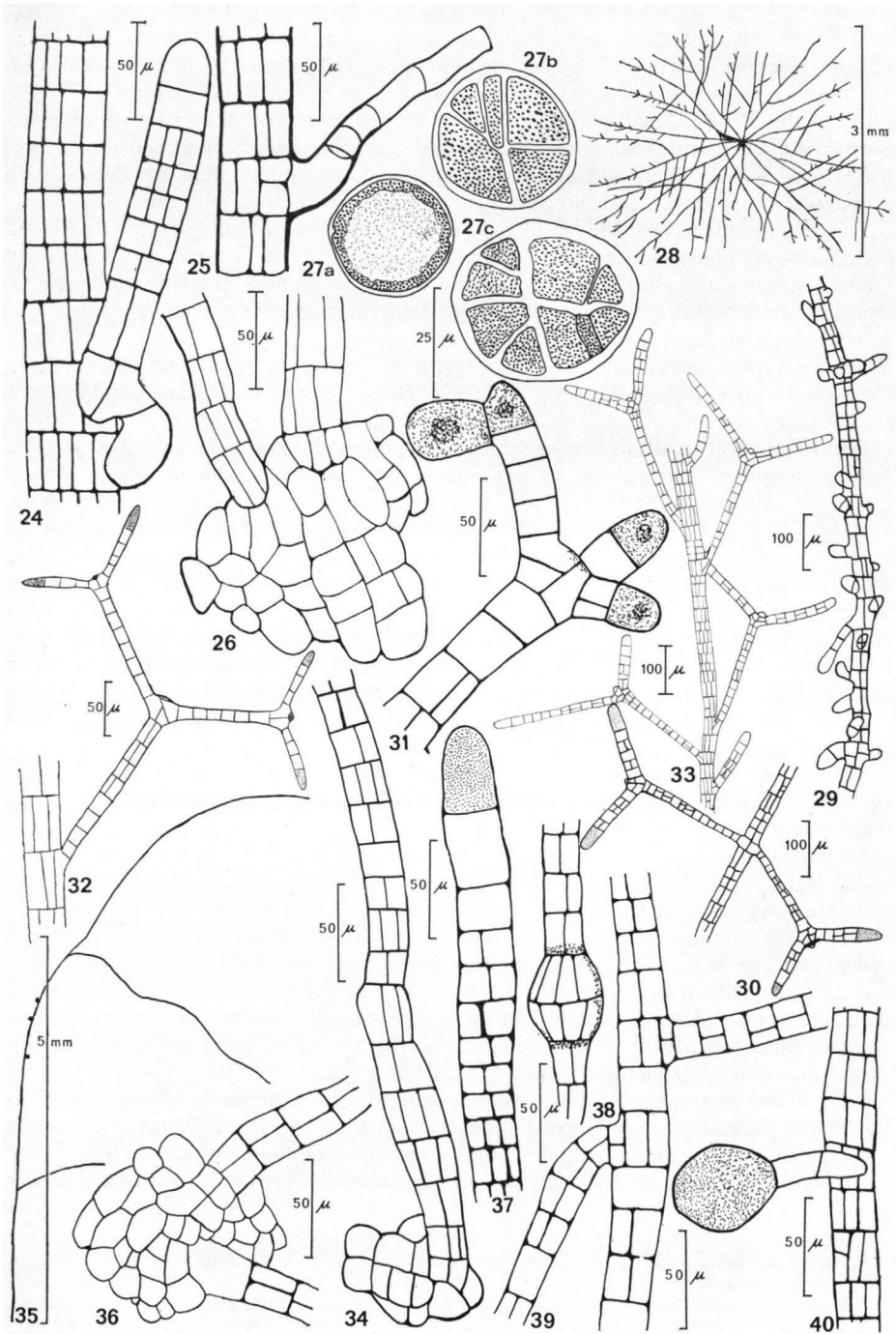
at the base and with cylindrical arms. It is mentioned in the literature that this species sometimes occurs on other algae and sometimes on rocks, that the plants form brushes of about 2 cm, and that only unilocular sporangia are found.

The type with regard to its mode of branching, its width of segments, and the ratio between the length and the width of apical cells and segments, is like *S. fusca*. In *S. fusca*, where propagulae occur, bifurcate ones are found, often even in greater numbers than trifurcate ones.

Consequently there is no reason to separate *S. furcigera* from *S. fusca*.

*Sphacelaria fusca.* — Fig. 24. Lateral with young basal rhizoid. Detail from fig. 4c. — Fig. 25. Rhizoid. Material from Hoek van Holland (15-12-1963). — Fig. 26. Attachment disc. Same material. — Fig. 27a, b, c. Cross sections, a near apical cell, b and c more downwards. Same material. — Fig. 28. Culture after two months growth, with propagule-initials. Material from Hoek van Holland. — Fig. 29. Curious proliferations in culture of the same material. — Fig. 30, 32. Bifurcate and bifurcate propagulae in culture of the same material. — Fig. 31. Abnormal propagule in culture of material from Oude Katse Veer. — Fig. 33. Type of *Sphacelaria furcigera*. Bifurcate propagulae.

*Sphacelaria britannica.* — Fig. 34. Attachment disc with erect filament. Isotype. — Fig. 35. Filament with laterals and unilocular sporangia. Material from Roscoff (21-4-1957). — Fig. 36. Attachment disc with two erect filaments. Same material. — Fig. 37. Apical cell. Same material. — Fig. 38. Swelling in a filament. Same material. — Fig. 39. Ramifications. Same material. — Fig. 40. Unilocular sporangium. Same material.



*S. saxatilis* (Kuck.) Kuck. ex Sauv., 1901—1914, 5, 69, 152. — *S. furcigera* Kütz. var. *saxatilis* Kuckuck, 1897, 373—376. — Isotype from Helgoland (L, sh. 963—584—13).

The description which follows is partly taken from Kuckuck and partly based on a study of the isotype. Small plants which attach themselves to rocks by means of discs. Segments of the vertical filaments are 25—35  $\mu$  wide and sparsely branched. Branching habit as in *S. fusca*. Uni- and plurilocular sporangia. In figure 1 k of Kuckuck (1897) propagulae are shown which are bifurcate with dichotomies in one arm.

This description is very similar to that of *S. furcigera* and *S. fusca*, except that in *S. furcigera* only unilocular sporangia are found. According to the illustrations of Dillwyn (1809) both uni- and plurilocular sporangia are found in *S. fusca*. It seems reasonable to assume that *S. saxatilis* is also synonymous with *S. fusca*.

*Sphacelaria britannica* Sauvageau, 1901—1914, 51—56, 66—69; Hamel, 1938, 251; Waern, 1945, 402—404; Lund, 1950, 22—27; Irvine, 1955, 26, 27; van den Hoek, 1958, 188—190. — Isotype from Berwick on Tweed, *Batters*, 1—1888, herb. Hauck and Richter as *S. radicans* var. *olivacea* (L, sh. 919—335—131) (fig. 34).

Plants consist of small discs from which arise stolons and erect branches (fig. 34, 36). Width of stolons and branches 14—35  $\mu$ . Segments as long as wide or longer. Apical cells 1.5—3 times as long as wide (fig. 37). The few laterals, of indeterminate growth, arise from the upper secondary segments of the main axes and are often parallel to the main axes. Ramification irregular. Often irregular thickening and twisting of the axes, this in association with an easy interchange between rhizoids and ordinary axes (fig. 38). Segments with 0—4 longitudinal walls, occasionally secondary transverse walls, especially where laterals arise (fig. 39). The chromatophores are smaller than those of *S. fusca*, 2—5  $\mu$  (average 3  $\mu$ ). On *S. britannica* no propagulae are found. Sporangia, round or oval, 21—54  $\mu$  in width on a stalk of 1—5 cells (fig. 40—42).

Apart from the isotype, material from Roscoff ('vieux quai du port', level of *Fucus vesiculosus* and *Ascophyllum*, v. d. H. 3516 and 3605, 21-4-1957) was investigated.

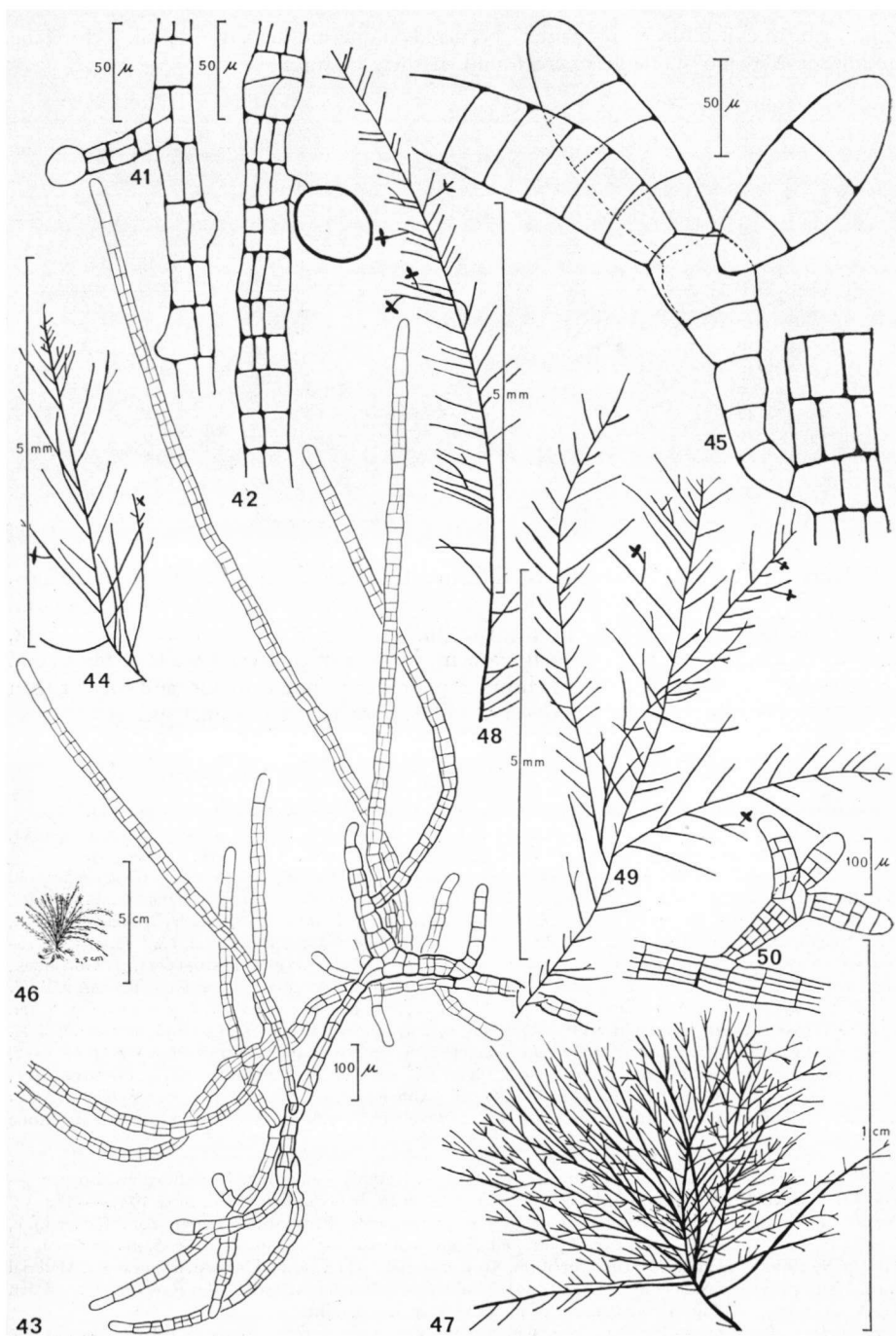
Since *S. britannica* very much resembles small *S. fusca* plants, of which species it might be a high-littoral growth form, comparative unialgal cultures were carried out so as to solve this problem.

**Cultures.** Cultures of *S. fusca* (fig. 27—32) (Hook of Holland, T. Niekerk, 15-12-1963; Oude Katse Veer, Zeeland, T. Niekerk, 22-1-1964). The culture plants exhibited a feeble polarity of growth; they grew in all directions. The width of the cells, manner of branching, number of longitudinal walls, number of transverse walls of the second order, and size of the chromatophores remained constant and characteristic of *S. fusca* during three subcultures. During the first month of the inoculation the plants were dark and remained small. After that, they grew rapidly and became lighter brown. Most cultures began to form propagulae at the beginning of May, that is, one month earlier than in nature. The plants which formed propagulae were 1.5 cm high or slightly longer. Many atypical propagulae were found. The ratio between bifurcate and trifurcate propagulae was investigated. The results which are shown in table II indicate that on plants originating from Oude Katse Veer as well as on those originating from Hook of Holland more bifurcate than trifurcate propagulae occur. It is noteworthy that generally

*Sphacelaria britannica*. — Fig. 41, 42. Unilocular sporangia. Material from Roscoff (21-4-1957). — Fig. 43. Five months' old culture.

*Sphacelaria cirrosa*. — Fig. 44. Pinnate branch-system bearing propagulae. Type. — Fig. 45. Propagule. Type. — Fig. 46, 47. Habit. — Fig. 48, 49. Axes with laterals of determinate growth bearing propagulae. — Fig. 50. Propagule.





either trifurcate or bifurcate propagulae occurred on one and the same lateral. Before the middle or May no sporangia were found in these cultures.

TABLE 2

Number of propagulae	of those	
	bifurcate	trifurcate
17	15	2
40	30	10
230	167	63
7	5	2
47	23	24
20	10	10
27	17	10

*S. fusca*. Relative occurrence of bifurcate and trifurcate propagulae in cultures.

Cultures of *S. britannica* were isolated from one sample from Roscoff (M. Th. Halos, 'vieux quai du port', 4-4-1964). After five months were the plants 6-8 mm long and looked like radiating fluffs. No propagulae (fig. 43). The width, measure of branching, number of longitudinal walls in each segment, number of transverse walls of the second order in each segment, and size of chromatophores remained constant, and smaller than in *S. fusca*. So it is clear that *S. britannica* and *S. fusca* are two distinct species.

#### *Distribution of S. fusca in the Netherlands, based on herbarium specimens.*

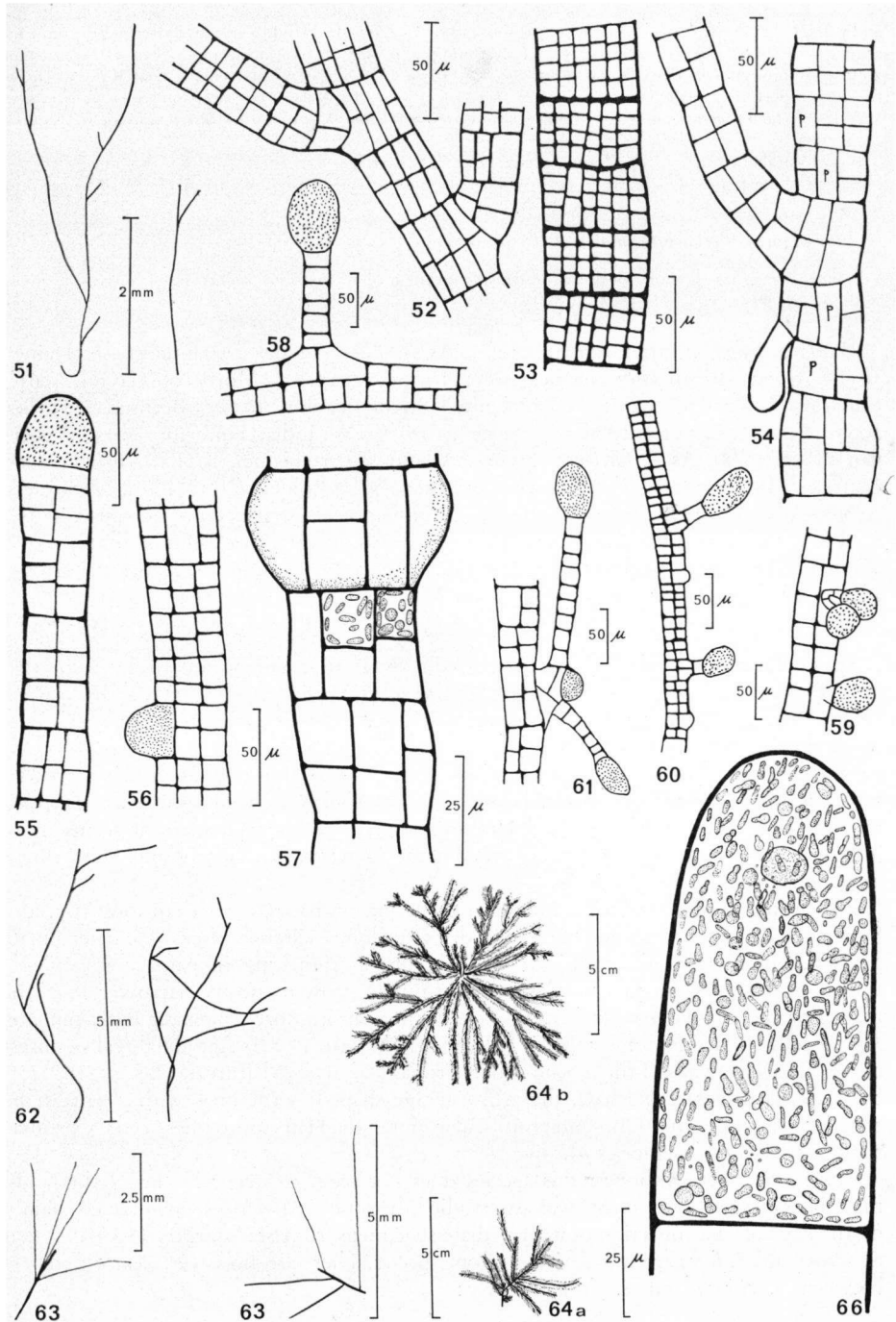
Noord-Holland: Amsteldiep, dike, on algae and on stone, C. d. H. 1328, 13-11-1952 (L).

Zuid-Holland: Hook of Holland, north side of piles among *Pilayella littoralis*, v. d. H. 1151, 23-1-1954, det. as *Sphacelaria britannica* (L); idem, v. d. H. 3497, 7-4-1958; idem, T. Niekerk, 15-12-1963.

Zeeland: Schouwen Duiveland. Zierikzee. Havenkanaal on stone and epiphytic on *Cladostephus* and *Ascophyllum*, C. d. H. 1240, 22-7-1952 (L). — Tholen. Gorishoek, epiphytic on *Fucus serratus* and on stones, C. d. H., 20-10-1951 (L, sh. 937-117-376); Gorishoek, epiphytic on *Fucus serratus*, in *Ascophyllum* association, C. d. H. 505, 28-10-1951 (L); Gorishoek, on stone in *Ascophyllum nodosum* association, C. d. H. 506, 28-10-1951 (L); Gorishoek, epiphytic on *Fucus serratus* and on stone, C. d. H. 1003, 28-10-1951 (L); Gorishoek, epiphytic on *Codium fragile*, C. d. H. 1004, 28-10-1951 (L); Gorishoek, epiphytic on *Fucus serratus*, v. d. H. 2053c, 7-7-1954, det. as *Sphacelaria cirrosa* (L); Strijenham, epiphytic on *Ascophyllum nodosum*, v. d. H. 2381, 9-8-1955 (L); Strijenham, low-littoral in *Fucus serratus* zone, epiphytic on *Fucus* and on stone, v. d. H. 3138, 15-5-1956 (L); Strijenham, under *Fucus serratus* zone, epiphytic on *Chondrus crispus*, v. d. H. 3150, 15-5-1956 (L); Strijenham, east-exposed slope, epiphytic on *Chondrus crispus*, K. 5910, 15-5-1956 (L); Strijenham, on stones, v. d. H. 2519, 19-9-1956 (L); Koffiehoek, on stone in the *Ascophyllum nodosum* association, C. d. H. 502, 27-10-1951 (L). — Noord-Beveland. Kortgene, *Ascophyllum* zone on sandstone

*Sphacelaria radicans*. — Fig. 51. Filament with laterals. Isotype. — Fig. 52. Ramifications. Isotype. — Fig. 53. Transverse walls of 2nd order. Material from Roscoff, leg. van den Hoek, 21-4-1957. — Fig. 54. Branch and rhizoid, arising from two neighbouring segments. Pericysts. Material from Kattendijke, Zuid-Beveland (1-1964). — Fig. 55. Apical cell. Same material. — Fig. 56. Pericyst. Same material. — Fig. 57. Swelling in filament. Chromatophores. Same material. — Fig. 58, 59. Unilocular sporangia. Material mixed with isotype of *S. saxatilis*. — Fig. 60, 61. Unilocular sporangia. Material from Roscoff, leg. van den Hoek, 21-4-1957. — Fig. 62, 63 Culture of material from Kattendijke.

*Sphacelaria plumigera*. — Fig. 64a, b. Habit, a from Vlissingen, b from Joppa (Scotland). — Fig. 66. Apical cell. Material from Vlissingen.



and piles, *C. Brakman*, 14-2-1941 (L, sh. 939-69-1188). — Zuid-Beveland. Yerseke, oyster ponds, on stone at low water, *C. d. H.* 736, 25-10-1951 (L); Kattendijke, n. side of dike, on stone in *Ascophyllum nodosum* zone and epiphytic on *Ulva lactuca*, *K.* 5876, 15-5-1956 (L); Dike of Oosterschelde near Kattendijke, in the lower part of *Ascophyllum* zone, *v. d. H.* 3152, 15-5-1956 (L); Katse Veer, dike, under *Fucus vesiculosus* and *Ascophyllum nodosum*, on stone among *Rhodochorton floridulum*, *K.* 7135, 9-9-1963 (L); idem, *T. Niekerk*, 21-1-1964.

Noord-Brabant: Bergen op Zoom, oyster pond, *D. Korringa*, 6-1937 (L, sh. 951-152-113).

Except those places den Hartog (1959) collected *S. fusca* from Tessel and from the Waddenzee.

### *Investigated herbarium material from abroad.*

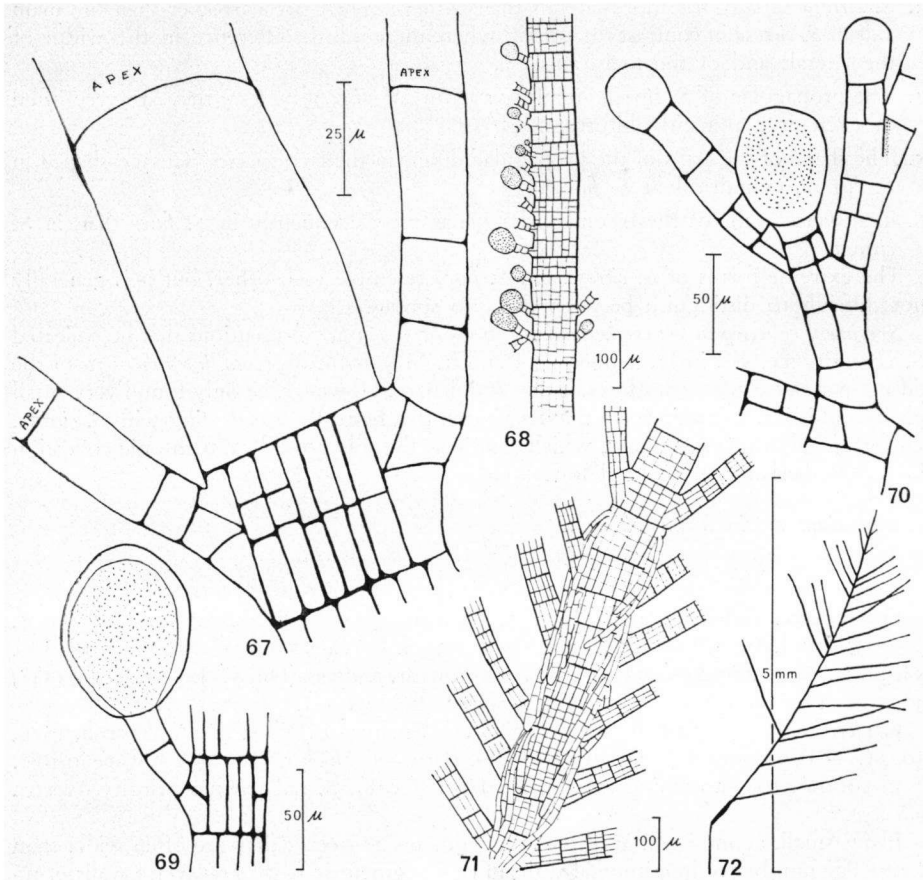
France. Bretagne, Roscoff, Ile Verte, north side on the level of *Fucus vesiculosus* and *Ascophyllum*, mixed with *S. britannica*, *v. d. H.* 3695, 30-6-1958 (L).

*World distribution*, after the literature. As *S. fusca*: France, Atlantic coast (Hamel, 1931-1939); British Isles (Irvine, 1955; Børgesen, 1926); Morocco (Gayral, 1961); Canaries (Børgesen, 1926); N.W. United States (Taylor, 1957); Bermuda (Taylor, 1960); Pacific coast of N. America (Scagel, 1957); S.W. India, Timor, Celebes (Weber-van Bosse, 1928). As *S. furcigera*: France, Atlantic coast (Hamel, 1931-1939); Faeroes, Canaries (Børgesen, 1926); Florida, Bermuda, N. Carolina, Costa Rica, Venezuela, Antilles (Taylor, 1928, 1960); California (Smith, 1944); Persian Gulf (Kützing, 1855); Red Sea, Indian and Pacific Oceans (Lucas, 1936); Indian, Ceylon (Durairatnam, 1961); Vietnam (Dawson, 1954); Sumba, Celebes, Timor, New Guinea (Weber-van Bosse, 1928); Australia (Lucas, 1936); Japan (von Martens, 1866; Durairatnam, 1961).

***Sphacelaria cirrosa*** (Roth) C. A. Agardh, 1824, 164; Sauvageau, 1902-1914, 173, 227; Hamel, 1931-1939, 258-260. — *Conferva cirrosa* Roth, 1800, 214. — *S. pennata* (Huds.) Lyngb. var. *cirrosa* (Roth) Irvine, 1955, 29, 30. — Type material present in the Wulfen collection (WU, sh. 1261) (fig. 44, 45) corresponds to the general usage of the name *S. cirrosa*. According to Irvine (1955) *C. pennata* Hudson has priority over *C. cirrosa* Roth, but since the material collected and described by Hudson was destroyed by fire (Dixon, 1959, 36-38) and Hudson's description is inadequate, it seems more justifiable to maintain the adequately typed name *S. cirrosa*, particularly since this name is in general use.

Plant mostly epiphytic, sometimes also occurring on rocks, 0.3-4 cm long (fig. 46). Segments 45-91  $\mu$  wide and mostly wider than long. Laterals often of indeterminate growth, but mostly of determinate growth, often originating in pairs from a single upper secondary segment; laterals of determinate growth mostly narrower than the main axis and 25-60  $\mu$  wide (fig. 47-49). Ramification more or less regularly pinnate. Apical cells 1-2 times longer than wide. Segments with 1-6 longitudinal walls; almost never transverse walls of the second order. Propagulae always trifurcate (fig. 45, 48-50); the stalk narrower at the base, the arms sausage-shaped; sometimes with a hair at the centre of the three arms. Uni- and plurilocular sporangia. Hairs sometimes occur. Chromatophores 3-8  $\mu$  (average 5  $\mu$ ).

*Taxonomic notes.* Although this species does not seem to occur in the Netherlands, material from European coasts was also studied, because Irvine (1955) maintained mainly on the basis of one collection of intermediate specimens from St. Andrews, (Scotland) that *S. cirrosa* and *S. fusca* are two varieties of one species. There are, however, clear differences between *S. cirrosa* and *S. fusca*, namely:



*Sphacelaria plumigera*. — Fig. 67. Apex just below apical cell. Material from Vlissingen. — Fig. 68. Lateral bearing unilocular sporangia. Material from Joppa, Scotland. — Fig. 69, 70. Unilocular sporangia. Same material. — Fig. 71. Secondary thickening by rhizoidal cortication. Material from Vlissingen. — Fig. 72. Culture of material from Vlissingen.

1. The habit of *S. cirrosa* differs markedly from that of *S. fusca* (pinnate versus irregular ramification).
2. Most laterals in *S. cirrosa* are of determinate growth; those of *S. fusca* are of indeterminate growth.
3. *S. cirrosa* usually has more laterals than *S. fusca*. These are narrower than the main axis in *S. cirrosa* in contrast to *S. fusca*, where there is little difference in the width of the laterals and of the main axis.
4. The propagulae of *S. cirrosa* are always trifurcata and of *S. fusca* they are very often or even predominantly bifurcate.
5. The shape of the arms of the propagulae differs in the two species (sausage-shaped in *S. cirrosa*, cylindrical in *S. fusca*).
6. Transverse walls of the second order occur more frequently in *S. fusca* than in *S. cirrosa*.

The extreme forms of *S. cirrosa* and *S. fusca* resemble each other, but it is generally not difficult to distinguish between the two species.

*Specimens collected in the Netherlands.* Van Goor (1923 a, 79) mentions that he collected *S. cirrosa* twice, viz. in December 1915 and in May 1916, on *Corallina rubens* from the deeper parts of *Zostera*-meadows of the Waddenzee. However, he only found very small plants and it is not certain from the description that he really was dealing with *S. cirrosa*. Unfortunately these specimens, which represent the sole possible autochthonic collection in the Netherlands, have been lost.

*Herbarium specimen investigated.*

Huisduinen, epiphytic on washed-up *Himanthalia*, C. Swennen, 24-9-1950 (L).

***Sphacelaria radicans*** (Dillw.) C. A. Agardh, 1824, 165; Sauvageau, 1901—1914, 51—65; Lund, 1950, 17—22; Irvine, 1955, 38, 39. — *Conferva radicans* Dillwyn, 1809, 58, pl. C. — *S. olivacea* (Dillw.) C. A. Agardh var. *radicans* (Dillw.) J. G. Agardh, 1848, 31. — Isotype in BM, sh. 142 832, Hutchins (fig. 51, 52).

*Conferva olivacea* Dillwyn, 1809, 57, pl. C. — *S. olivacea* (Dillw.) C. A. Agardh, 1828, 30, 31. — Type from Papa Westra, Orkneys, Borrer and Hooker, 1849 (K). Isotype in BM.

In contrast to the opinion of van den Hoek (1958), *S. radicans* has priority over *S. olivacea*.

Plants small, about 1 cm. Width of the segments 28—60  $\mu$ , they are often wider than long. The number of longitudinal walls in each segment is 3—7. Transverse walls of up to the third order were found (fig. 53). Rather few laterals, of indeterminate growth (fig. 51, 52, 54). Ramification irregular. Attaches itself to rocks with discs, rhizoids, and stolons. Chromatophores 2—6  $\mu$  (average 3.5  $\mu$ ). Dark coloured pericysts<sup>1</sup> occur in upper secondary segments (fig. 55, 56). Occasional thickening (fig. 57) of the axes, this in association with an easy interchange between rhizoids and ordinary axes. Propagulae unknown. Unilocular sporangia sessile or on few-celled stalks, often in pairs, round or oval (fig. 58—61). Plurilocular sporangia not observed but mentioned by Kuckuck (1897).

<sup>1</sup> Pericysts (i. e. lateral-initials) also occur in other *Spacelaria* species investigated but are not as obvious as in *S. radicans* because these other species do not form secondary transverse walls in every segment.

*Cultures* (fig. 62, 63). Cultures were isolated from material collected at Kattendijke, Zeeland (T. Niekerk, 20-1-1964) and from material from the 'vieux quai du Port' at Roscoff (M. Th. Halos, 4-4-1964). In cultures of three to four months the plants maintained their natural morphology and exhibited little polarity. No sporangia have as yet been observed.

*Distribution in the Netherlands.* *S. radicans* was found for the first time in the Netherlands by T. Niekerk at Kattendijke, Zeeland, in January 1964.

*World distribution*, according to the literature. Arctic coasts of Europe (Zinova, 1953); Iceland (Jónsson, 1912); S. coast of Norway (Sundene, 1947); W. coast of Sweden (Kylin, 1907, 1947); Denmark (Lund, 1950); British Isles (Irvine, 1956); Bothnian Sea (Waern, 1952); Helgoland (Hauck, 1885); Kieler Förde (Reinbold, 1891); France, Atlantic coast (Hamel, 1931-1939); N.E. United States (Taylor, 1957).

***Sphacelaria plumigera*** Holmes, 1883, 141; Waern, 1945, 405; Kylin, 1947, 30; Lund, 1950, 50-54; Irvine, 1955, 40. — Type from Eastbourne, *Borrer*, 1808 (BM).

Plants up to 10 cm long, growing attached to rocks (fig. 64). Laterals of determinate growth, arising in pairs from each upper secondary segment (fig. 67). Occasionally a lateral of indeterminate growth occurs. Ramification regularly pinnate. Width of segments of the main axes 80-450  $\mu$  and of the laterals 40-60  $\mu$ . Segments of the main axis 1-4 times as wide as long; segments of the laterals 1-2 times as long as wide. Main axes with 4-9 longitudinal walls in each segment. Transverse walls of the second order always present, sometimes transverse walls of the fourth order. Chromatophores 2.5-5  $\mu$  (average 3  $\mu$ ) (fig. 66). Sporangia round or oval, 26-60 by 30-74  $\mu$  (fig. 68-70), on the laterals of determinate growth, single and terminal on a 2-5 celled stalk, or united into small racemes of 2 to 5 sporangia. Secondary growth by means of rhizoids which surround the whole main axis and which arise at 20-30 segments from the apical cell, each from the upper half of a lower secondary segment, in the same plane as the laterals. It is through this rhizoidal secondary growth that the axes achieve such an enormous width (fig. 71).

*Taxonomic notes.* *S. plumigera* is frequently confused with *Chaetopteris plumosa* (den Hartog, 1962). The differences between *S. plumigera* and *C. plumosa* are:

1. In *S. plumigera* the unilocular sporangia occur on the laterals of determinate growth; in *C. plumosa* they occur on special short laterals, stichidia, which arise from the rhizoidal cortex around the main axis.

2. In *S. plumigera* the rhizoidal cortex consists of rhizoids growing downwards and which have their origin in cells situated diametrically opposite each other. In *C. plumosa* all cells around the main axis contribute to the formation of the cortex.

*Cultures.* Cultures were isolated from plants collected by M. Donze at Vlissingen on 15-1-1964. The plants in four months grew much more slowly than *S. fusca* and *S. radicans*. The growth is very obviously polarized. The resulting plantlets exhibited the characteristic morphology of *S. plumigera* (fig. 72).

*Distribution in the Netherlands*, based on herbarium specimens.

Schouwen. Westbuit, on stone, *C. d. H.* 746, 23-8-1950 (L); Dike near Kistersinlaag, on stone, *C. d. H.* 716, 28-8-1950 (L); idem, *C. d. H.* 700, 29-8-1959 (L). — N. Beveland, near Kats, low-littoral on basalt, *Holt*, 28-3-1964 (L, sh. 963-337-084). — Walcheren. Vlissingen, Nollédijk, on stone and wood, *C. d. H.* 1762, 4-4-1954 (L).

*Investigated herbarium material not from the Netherlands.*

Type, as *Sphacelaria plumosa* Engl. Bot., Eastbourne, Beachy Head in pools left by the tide, *W. Borrer*, 2-10-1808, herbarium Catherine Cutler (BM). Scotland, Joppa, *W. Traill*, 11-4-1880, 4-6-1880, 12-1-1881 (L. sh. 937-71-751).

*World distribution according to the literature.* Swedish W. coast, Gulf of Finland, Bothnian Sea (Waern, 1948, 1952); Oslofjord, Norway (Sundene, 1953); N.W. Jutland, Baltic (Lund, 1950); 'Abundant on some places of British Isles' (Irvine, 1955); N. coast of France (Chalon, 1905); NE. United States (Taylor, 1957).

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