THE MARINE ALGÆ OF DENMARK

CONTRIBUTIONS TO THEIR NATURAL HISTORY

PART IV

RHODOPHYCEÆ IV.

(GIGARTINALES. RHODYMENIALES. NEMASTOMATALES)

BY

L. KOLDERUP ROSENVINGE

WITH ONE PLATE

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INTRODUCTION

Though a comparativety small number of species, belonging to the *Gigartinales, Rhodymeniales*, and *Nemastomatales*, are treated in the present part, seven years have been spent in completing it. This is partly due to the fact that some of the species offered problems that demanded thorough investigations. Two of these problems have been treated in particular papers, viz. (1) the question of the reproduction of *Phyllophora Brodiæi* and the nature of *Actinococcus subcutaneus*[1]), and (2) the question of the reproduction of *Ahnfeltia plicata*[2]).

In the years elapsed since the publication of the third part of this work, numerous gatherings have been made in several places on the coasts, and dredgings have been made in many new stations which are recorded below. Many new localities have been stated for species recorded in the foregoing parts, but these are not named here; only a few species belonging to the orders treated in the foregoing parts but not named there are mentioned here under *Addenda*.

List of new Dredging Stations arranged according to the different Waters.

Kattegat, Northern Part. (Kn)

gR. $^{17}/_{7}$ 29. Midway between Hirsholm harbour and Kølpen. — 8 m. — Boulders (picked up). On the upper side mostly *Halidrys siliqu.*, on the other sides many others, e. g. *Deless. sangu., Polys. viol., Phylloph. membr., Codium toment.*, (young plants), *Rhodym. palm., Bryopsis plum.* and many others.

gI. $^{5}/_{7}$ 28. Midway between Hirsholm and Deget. 7.5 m. — Soft bottom with stones. — Scarce vegetation: *Desmarestia aculeata, Acrothrix gracilis, Desmar. viridis.*

gK. $^{5}/_{7}$ 28. Hirsholm light-house in N.W., Frederikshavn Church in W. S. W., 19 m. — Soft bottom, no Algæ.

gQ. $^{15}/_{7}$ 29. East end of Hjellens Rev by Frederikshavn. — 4—6 m. — Stones. — Abundant vegetation: *Halidrys siliqu.*, the three *Laminaria* species, *Fuc. serratus, Furcellaria, Laurencia pinn., Polyides, Ahnfeltia, Corallina offic.*

[1]) L. Kolderup Rosenvinge: Phyllophora Brodiæi and Actinococcus subcutaneus. K. D. Vid. Selsk. Biolog. Meddel. IX, 4, 1929.

[2]) L. Kolderup Rosenvinge: The Reproduction of Ahnfeltia plicata. K. D. Vid. Selsk. Biolog. Medd. X, 2, 1931.

gL. $^{25}/_{7}$ 28, $^{22}/_{5}$ 29, $^{19}/_{9}$ 29. Off Friis' Sten W. side of Læsø. 2—3 m. — Sand with stones. — *Fucus serratus, Fuc. vesic., Phylloph. Brodiæi,* further *Brongniartella, Zostera, Phylloph. membranifolia.*

gK^{1}. $^{25}/_{7}$ 28. Vesterø harbour in S. E. by E. 10—11 m. — Sand. — *Acrothrix gracilis, Striaria* and others on dead *Zostera* leaves.

Samsø area. (Sa)

fN. $^{5}/_{8}$ 25. Off Ballen, east side of Samsø.
1) East of the channel, 13 m. — Stony bottom — *Laminaria saccharina, Lithothamnion glaciale, Corallina off., Ectocarpus silicul., Brongniartella byss.*
2) In the channel, 22.5 m. — Soft bottom with stones. — *Lithothamn. glaciale.*
3) Within the channel, 13.5 m. — Sand.

gT. $^{27}/_{5}$ 30. Paludans Flak, near the broom. — 10—11 m. — Sand with small stones. — *Fucus serratus, Lamin. digit., Furcell. fast., Polys. viol., Chondrus crispus.* — 6—8 m, further *Ahnfeltia plicata, Corallina off.* and many others.

gH. $^{1}/_{8}$ 27. South side of Hesbjerg Grund, near land, 3 m. — Gravel. — *Furcellaria fast., Zostera, Ascophyllum nodosum scorpioides, Halidrys sil.* loose, *Asperococcus echinatus, Ectocarpus conferv., Rhodomela subfusca, Chorda Filum.*

The South Fyen Waters. (Sf)

fX. $^{15}/_{8}$ 25. South side of Svelmø. 7,5 m. — Soft bottom. — Broad-leaved *Zostera.*

— Same place, nearer to land, 4 m. — Narrow-leaved *Zostera marina, Potamogeton pectinatus, Cladophora.*

fV. $^{15}/_{8}$ 25. At the East side of Avernak Ø, near land, 3—4 m. — Stones with *Fucus vesicul.* and *Chorda Filum.*

Great Belt. (Sb)

gU. $^{27}/_{5}$ 30. East side of Lille Grund, North of Hindsholm. — 10—11 m. — Sand with stones. — *Fucus serratus, Fuc. vesic., Furcellaria, Laminaria digit., Phylloph. Brod.* and *Ph. membranif., Corallina off., Ahnfeltia plic.* and many others.

gS. $^{19}/_{11}$ 29. Elefant Grund, north side and middle. — 6—7.5 m. — Stones and *Mytilus edulis* abundantly. — *Phylloph. Brodiæi, Rhodomela subfusca, Ahnfeltia plic.* etc.

gV. $^{27}/_{5}$ 30. At the broom S. E. of Romsø, 11 m. — Stones. — *Laminaria digitata, Furcellaria fast.*

(LP) $^{18}/_{5}$ 27. Off Stavreshoved, 7 m. — Stones. — *Fucus serratus, Fuc. vesicul., Laminaria digitata, Lam. sacchar.,* several Florideæ.

gX $^{27}/_{5}$ 30. Off Stavreshoved. — 8 m. — Sand with spots of *Zostera* vegetation. — *Fucus serratus, Laminaria sacch., Furcellaria, Halidrys.*

gY. $^{27}/_{5}$ 30. Møllegrund. — 8 m. — Sand with stones. — *Laminaria digitata, L. sacch.*

gG. $^{18}/_{5}$ 27. Off Bovense, 6.5—8 m. — Stones. — *Laminaria digitata, Furcellaria fast., Phylloph. membranifolia* and many others.

gF. $^{18}/_{5}$ 27. Off Teglværksskoven, 7.5—10 m. — Stones. — *Laminaria saccharina, Lam. digit., Fucus serratus,* several Florideæ e. g. *Phycodrys rubens, Cystoclonium purp.*

fY. $^{24}/_{11}$ 25. Sprogø light-house in N. W. $^{3}/_{4}$ W., Halskov Rev light-ship in N.E., 9—10 m. — Stones. — *Furcellaria, Fucus serratus, Laminaria digitata,* several Florideæ.

fY^{1}, — near the foregoing place, 12—14 m. — Stones. — Same vegetation.

fZ. $^{24}/_{11}$ 25. Sprogø light-house in N.W. $^{1}/_{4}$ W., Halskov Rev light-ship in N. E. $^{3}/_{4}$ N. — 20 m. — Soft bottom, stones. — *Phyllophora Brodiæi, Delesseria sanguinea, Phycodrys rubens, Furcellaria, Phylloph. membranifolia.*

gA. $^{24}/_{11}$ 25. Sprogø light-house in N. E. $^{1}/_{2}$ N., Gjellegrund light-beacon in S. E. $^{1}/_{4}$ E. — *Mytilus edulis,* few Algæ: *Laminaria digitata, Furcellaria fast.*

gC. (= NS) 24/11 and 25/11 25. Between Knudshoved and Slipshavn. 5—6 m. — Stones. — *Fucus serratus, Chorda Filum, Fucus vesic., Phycodrys rubens, Laminaria digitata, Halidrys siliqu.* fructiferous.

gB. 24/11 25. Vresens Puller, the broom in E. by N. 1/2 N., 0.4 mile to 0.2 mile. — 7 m. — Stones. — *Fucus serratus, Halidrys siliqu., Laminaria digitata.*

gD. 25/11 29. The double broom for Kobberdyb in N. by E. 3/4 E. 1.0 mile. — 9 m. — Soft bottom (?) — *Phyllophora Brodiæi* f., *Furcellaria fastig.*

gE. 25/11 25. Stokkebæks Flak. 5—7 m. — Stones. — *Zostera, Fucus serratus, Chorda Filum.*

fP. 13/8 25. 1/2 mile E. of Hov light-house, 5.5 m. — Coarse sand with scattered stones, and firm clay. — *Zostera* leaves and abundant, partly loose Algæ: *Fucus vesicul., Furcellaria, Rhodomela, Phyllophora Brodiæi* and *Phyll. Bangii.*

fO. 13/8 25. S. S. E. of Vresen, E. of Langesand. 7,5 m. — Bottom? with a few stones. — Dead *Zostera* leaves, *Ascophyllum nodosum* f. *scorpioides,* loose *Furcellaria.*

fQ. 14/8 25. Off Spodsbjerg, 19 m. — Bottom with stones. — Mostly *Delesseria sanguinea,* further *Laminaria saccharina* and *digitata, Phycodrys rubens.*

fR. 14/8 25. Off Hjortholm Skov, Kjelsnor light-house in W. by N., 5/6 mile from land, 21 m. — Stones. — *Laminaria digitata, Delesseria sanguinea, Phycodrys rubens, Brongniartella byss., Laminaria saccharina.*

fS. 14/8 25. East of Kjelsnor light-house, 5/6 mile, 9.5 m. — Sand with stones, gravel. — Mostly *Furcellaria,* further *Laminaria digit., Mytilus edulis* abundant.

— Same place, 11.5 m. — Stones. — Similar vegetation, mostly *Furcellaria,* further *Rhodomela, Deless. sangu., Polysiph. elongata, Brongniartella byss., Phycodrys rubens.*

The Sound (Øresund). (Su)

gM. 25/6 29. Taarbæk Rev. One mile W. of the bell buoy. 8—9 m. — Stones and *Mytilus.* — In particular brown Algæ, *Ectocarpus silicul., Chorda Filum, Stictyosiphon tort., Rhodomela subf., Polysiph. nigr., Dumontia incrassata* etc.

gM1. 25/6 29. Just outside the bell buoy. 12 m. — Stones. — *Laminaria saccharina, L. digitata, Rhodymenia palmata, Fucus serratus,* etc. as in the foregoing place.

gM2. 25/6 29. Same place, 500 m N. E. of the bell buoy. 15 m. — *Striaria attenuata, Rhodymenia palmata, Ceramium Areschougii.*

gN. 25/6 29. Taarbæk Rev, 2 1/2 miles N. by W. of Middelgrundsfort. — 7 m. — Sand with scattered stones. — *Chorda Filum, Ectocarpus, Polysiph. violacea, P. urceolata, Dumontia incrassata.*

gP. 25/6 29. 2 1/2 miles E. of Skovshoved. — 11 m. — Sand with stones. — *Mytilus. Desmarestia viridis, Polysiph. nigrescens, Laminaria sacch.* etc.

gO. 25/6 29. Skovshoved in W. by N. 3 miles. 14 m. — Clay-mud. — *Mytilus. Laminaria sacchar., Desmarestia aculeata.*

Baltic, Western Part. (Bw)

fT. 14/8 25. South of Marstal, Fakkebjerg light-house in S. E. by E. 5 1/2 miles. 7.5 and 11 m. — Gravel. — *Fucus vesicul., Chorda Filum, Rhodomela subfusca, Zostera.*

fU. 14/8 25. South of Ærø, off Drejet. 7 m. — Gravel with stones. — *Fucus vesicul., Fuc. serratus, Furcellaria, Rhodomela subf., Phylloph. Brodiæi* and *membranifolia,* numerous loose forms of *Phylloph. Brodiæi,* and *Phyll. Bangii.*

V. Gigartinales.

Fam. 15. Gigartinaceæ.

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P. Kuckuck (Bemerk. I. 1894): Bemerkungen zur marinen Algenvegetation von Helgoland. Wissensch. Meeresuntersuch. Neue Folge I. Band. Kiel und Leipzig 1894.

— (Bemerk. II. (1897): — II. Ibid. II. Band, Heft 1.

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— (1928), Entwicklungsgeschichtliche Florideenstudien. Lunds Univ. Årsskrift. N. F. Afd. 2. Bd. 24 No. 4.

H. C. Lyngbye (1819), Tentamen hydrophytologiae danicae. Hafniae.

R. W. Phillips (1925), On the genera Phyllophora, Gymnogongrus and Ahnfeldtia and their parasites. The New Phytologist, Vol. 24, No. 4.

Henrik Printz (1926), Die Algenvegetation des Trondhjemfjordes. Skrifter utgitt av d. Norske Videnskaps-Akademi i Oslo. Math. naturv. Kl. 1926. No. 5. Oslo.

Fr. Schmitz (1893), Die Gattung Actinococcus Kütz. Flora 1893.

See further pp. 79, 297, 465.

Harveyella Schmitz and Reinke.

1. **Harveyella mirabilis** (Reinsch) Schmitz et Reinke.

Reinke Algenfl. westl. Osts. 1889 p. 28; Buffham (1893), p. 292, Pl. XIII figs. 3, 4, Pl. XIV figs. 40—42; Kuckuck, Bemerk. II, 1897, p. 395. H. H. Sturch, Harveyella mirabilis. Annals of Botany, Vol. 13, 1899, p. 84 Pl. III, IV; id, on the life-history of Harveyella pachyderma and H. mirabilis. Ann.

of Botany, Vol. 38, 1924 p. 27. Kylin (1923) p. 134. E. Chemin, Sur le développement des spores et sur le parasitisme d'Harveyella mirabilis Schmitz et Reinke. Comptes rendus d. s. de l'Acad. d. sc. Paris t. 184, p. 1187, 1927.

Choreocolax mirabilis Reinsch, Contrib. 1875 p. 63, Taf. 53 et 54.

Choreocolax albus Kuckuck, Choreocolax albus n. sp., ein echter Schmarotzer. Sitzungsber. d. K. preuss. Akad. d. Wiss. 1894.

Although not described until 1875, this interesting parasitic alga was already observed by LYNGBYE. In Tent. Hydr. (1819, p. 47 tab. 11 B) he mentions and gives a drawing of some warts seated laterally on the branchlets of *Gigartina subfusca γ, tenuior* (*Rhodomela subfusca*). The "*puncta nigra*" mentioned (l. c. p. 48) which "potius pro massa interna hic illic magis condensata, quam pro seminibus sumenda sunt", were probably the large inner cells rich in starch-grains. Specimens in Herb. LYNGBYE of the named host-plant from Svinøer, Norway, collected by LYNGBYE in October 1817, bear several of these warts which are mentioned in the label in similar terms as in Tent. Hydr.; they proved on microscopical examination to be sexual specimens of *Harveyella mirabilis*, one with procarps and a young gonimoblast, another perhaps a young male specimen. LIEBMAN also met with this species in December 1838 at Helsingør but referred it to *Corynephora marina* (*Leathesia difformis*).

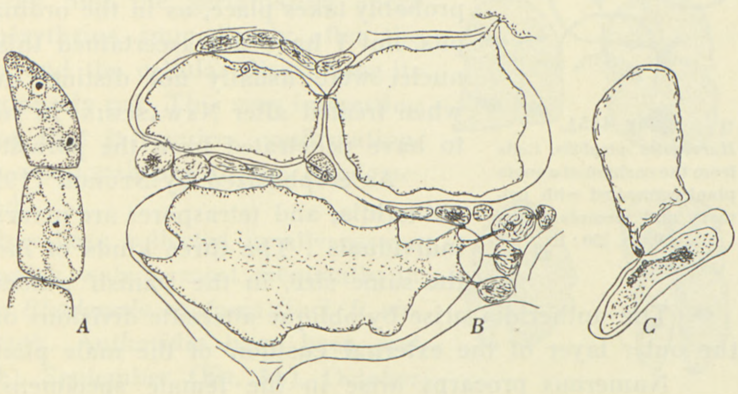


Fig. 454.
Harveyella mirabilis. *A*, end of intramatrical filament (May); the last cell in beginning division (to the right). *B* and *C*, longitudinal sections of Rhodomela with intercellular filaments of Harveyella, pit-connections between the host and the parasite. *A*, 560 : 1, *B*, *C* 350 : 1.

Our knowledge of the structure and development of this plant is principally due to the researches of SCHMITZ, KUCKUCK and STURCH cited above. The colour of the plant may be pure white in the living state, in particular in the large tetrasporiferous specimens collected in May, but other specimens were feebly rosy or yellowish, apparently owing to the isolated cells of the host plant interspersed among the cells of the parasite.

As pointed out by KUCKUCK, the cells are devoid of chromatophores; it would be of interest to ascertain whether leucoplastids are also wanting. The cells represented in fig. 454 A after treatment with NAWASHIN's mixture[1], showed filamentous bodies which are probably leucoplastids. The cells contain one nucleus as shown by STURCH

[1] See Karpechenko, The production of polyploid gametes. Hereditas IX, 1927, p. 349.

(comp. fig. 454 *A*, *B*). Floridean starch-grains are often very abundant, in particular in the inner large cells of the globular thallus. The statement of Sturch that there are no secondary connections between the cells of the gametophyte does not agree with my observations as I have repeatedly met with secondary pit-connections between the cells situated a little within the antheridia-producing cells (fig. 455).

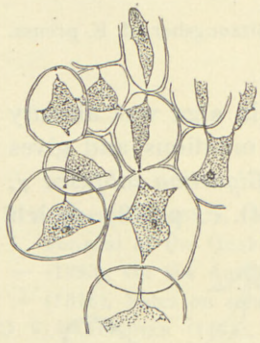


Fig. 455.
Harveyella mirabilis. Cells from the cushion of a male plant connected with primary and secondary pits (May). 350 : 1.

According to Schmitz (1889, p. 29), the cells of the intramatrical filaments are here and there connected with the cells of the host-plant through secondary pits. An immigration of a nucleus from the parasite into the host-plant or vice versa probably takes place, as in the ordinary formation of secondary pits, but I have not ascertained this with full certainty, as the nuclei were usually not distinct in the specimens examined when treated after Nawaschin. In some cases a nucleus seemed to have penetrated from the parasite into the host-plant.

As emphasized by Sturch (1924, p. 39), "the cystocarps, antheridia, and tetraspores are invariably developed on separate individuals". The three kinds of individuals may attain about the same size, in the Danish waters scarcely exceeding 1 mm.

The antheridia arise by oblique alternate divisions of elongated cells composing the outer layer of the external cushion of the male plants (Sturch 1924, fig. 20).

Numerous procarps arise in the female specimens, but one cystocarp only is produced, which occupies most of the cushion. As to the details of the development of the cystocarp, reference may be made to Sturch's papers. It shall only be stated that I found a four-celled carpogonial branch in accordance with Sturch. According to Sturch, the cystocarpial wall is composed of branched cell-filaments consisting of fairly short cells. In a cystocarp collected by Liebman December 1838 I found the filaments feebly branched and consisting of long cells (fig. 456).

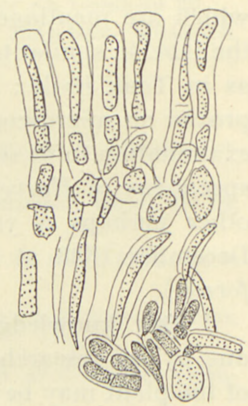


Fig. 456.
Harveyella mirabilis. Helsingør, December. Section through the cystocarpial wall; below, cells of the gonimoblast. 350 : 1.

The tetrasporangia are cruciately divided, as shown by Kuckuck and Sturch. In specimens preserved in spirit the nuclei in the dividing sporangia sometimes showed irregular lobed features that may perhaps be due to the imperfect state of preservation (fig. 457). This picture shows, moreover, that the division of the tetrasporangium does not consist in two consecutive bipartitions but that the transverse and the longitudinal divisions proceed almost simultaneously from the periphery towards the centre of the sporangium.

The relationship of the genus *Harveyella* is doubtful. Schmitz (Engler a. Prantl. I. 2, 1897 p. 344) classed it among the *Gelidiaceæ*, whilst Sturch referred it to the *Gigartinaceæ*. As emphasized by Kylin (1923, p. 124) it is not in accordance with the latter family, from which it differs among other things by a four-celled carpogonial filament and by the first gonimoblast-cell being cut off on the outer side of the auxiliary cell. In these characters it agrees better with the *Rhodomelaceæ*, but as, on the other hand, it differs very much from this family in the structure of the frond, it seems impossible to refer it to it[1].

E. Chemin in 1927 made the surprising communication that he had obtained the germination of the tetraspores of *Harveyella mirabilis* on a glass-plate. The ripe spores were without the slightest trace of pigment; they surrounded themselves with a membrane and were divided in 48 hours by successive bipartitions into a parenchymatous disc much resembling that of *Chondrus crispus*. The French author remarks that the germinating spore begins to produce phycoërythrine immediately after the fixation on the substratum, and the cellular disc taking its rise from it is coloured intensely red. This very interesting statement is so unexpected that it requires confirmation. If this can be obtained, a relationship with the *Rhodomelaceæ* is decidedly excluded[2].

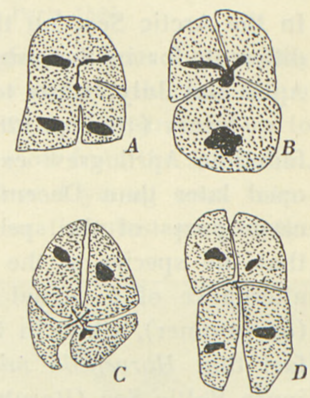


Fig. 457.
Harveyella mirabilis. Tetrasporangia in various stages of division. 835 : 1.

Harveyella mirabilis has been collected in all seasons in nearly all the inner Danish waters, most frequently in spring, always growing on *Rhodomela subfusca* (incl. *R. virgata*) at 4—26 metres' depth. Antheridia have been met with in July (**Bm** and **Bb**), September (**Kn**, **Lb**), October (**Ke**, **Su**) and once in January (**Kn**). Procarp-bearing specimens may probably be sought in autumn; I met with them once in October (**Su**) and once in April in one specimen together with tetrasporiferous ones, probably a retarded abortive specimen. Cystocarps were met with in December and January. Tetrasporiferous cushions were frequently found in April to June, in July once only in the Northern Kattegat, but several specimens at Bornholm, and finally once in August in the Great Belt and once in October in the Sound. The species is most frequently met with in spring (May) and then always with tetrasporangia.

It would be of interest to compare this occurrence with that on other coasts

[1] It is remarkable that Sturch in 1924 described another species, *H. pachydermus*, parasitic on *Gracilaria confervoides*; it differs by having a two-celled carpogonial branch and by numerous fusions of the ooblastema with cells of the gametophyte. As the number of cells in the carpogonial branch as a rule is a good systematic character, it ought to be examined 1) whether this number is really constant and 2) whether this species is rightly referred to the genus *Harveyella*.

[2] To verify the statement of Chemin, I searched for specimens with ripe tetrasporangia in May 1929 and in June 1930, but in vain. In June 1930 the season of fructification seemed to be closed for that year, for although I dredged in several places where I might reasonably expect to find fructiferous specimens of *Harveyella*, only few specimens were met with and none with well developed ripe tetrasporangia, and the examination of the germination of the spores could not, therefore, be made.

of North Europe. The cystocarps have everywhere been met with only in winter (Plymouth December to February, west coast of Sweden December (Kylin), west coast of Holstein December (Reinke), Færöe Islands November (Børgesen)). The tetrasporangia were met with only in February and March at Plymouth (Sturch). At the Faröe Islands (Børgesen), in Kristiania Fjord (Gran) and at the coast of Bohuslän, Sweden (Kylin) they were met with in April or May, at Helgoland (Kuckuck) at the end of May, at the coast of Halland sparingly in June and July (Kylin), and at Gotland in the Baltic Sea at the end of June (Svedelius). The sporangia thus generally develop on the North-European coasts in late spring, at Plymouth earlier, and in the inner Danish waters partly a little later (June, July, once in October). In the Arctic Sea, on the other hand, the biology of the species seems to be very different, for in Scoresby Sound (East Greenland) it was found with cystocarps in April and July, while tetrasporiferous plants were not met with at all.

Kylin (1907 p. 128) has emphasized the fact that the tetrasporiferous specimens found in April grew exclusively on branchlets of the host-plant which had developed later than December and concludes that they must have arisen from the carpospores of the specimens occurring in December. It must really be supposed that the species at the coasts of North Europe offers a rare example of a regular alternance of a sexual generation in winter and a tetraspore-generation in spring (or summer), while in the Arctic Sea one sexual generation only is produced. The fact that *Harveyella mirabilis* has only been observed with tetrasporangia in the inner Baltic Sea (Bornholm, Gotland) must perhaps be explained by the lack of dredgings during the winter in these waters.

Localities. Not observed in **Ns**, **Sk** and **Lf**. — **Kn:** KA, Aalbæk Bugt, 13 m (+ 5[1]); TX, North of Hirsholm, 9 m (♂ 1); TL, West of N. Rønner, 7.5 m (♂ 9); FE, Læsø Trindel 9—11 m (+ 7). — **Ke:** fH, east of Fladen light-ship, 17 m (♂ 10). — **Ks:** OS[1], Hastens Grund, 16 m (+ 4): at Hesselø (+ 5); aU Lumbsaas mill in South 32° West, 13 m. — **Sa:** KM, east of Øreflippen, 9—17 m (+ 5); DK, Bolsaxen, 13—15 m (+ 5) — **Lb:** OB, at Stavrshoved, 9—11 m (unripe + 3); DF, Remmen east of Bogø, 5.5 m (+ 5); DE, by the broom at Thorø Rev, 5.5 m (+ 5); dH, east of Hesteskoen, 15 m (+ 6). — **Sf:** CC, south side of Hornenæs, 7.5 m (♂ 9); UV, north of Ærø, 13 m (+ 5). — **Sb:** gY, Møllegrund, 8 m; cL, NE of Sprogø, 25—27 m (+ 6); NN, Sprogø light-house i NE 3/4 E 3 1/3 miles 19 m (◯ 1); AB north of Nyborg, 7.5 m (+ 8); Nyborg (Lyngbye); UE, by the buoy of Vresens Puller, 7 m (+ 5); UF, by Hov Sand, 8.5 m (+ 5); UT, Langelands Belt, 19 m (+ 5); UJ, near Onsevig, 7.5 m (+ 5); DR, by the broom of Albu Triller, 8.5 m (+ 5). — **Su:** Off Hellebæk (+ 4); near Helsingør (Liebman), (◯ 12); OJ, Nivaa Flak, 6 m (+ 4, one sp. with ♀); OG, by Taarbæk Rev, 6 m (+ 4); east of Taarbæk Flak 12.5 m (S. Lund, + ♂ ♀ 10); Charlottenlund (Hoffmeyer). — **Bw:** dM, Flensborg Fjord, east of the broom at Krage Sand, 14 m (+ 6); dK, Pøls Rev south of Als, 6—7 m (+ 6); UL, Femerbelt, Øjet, 20 m (+ 5). — **Bm:** VJ, off Hjelm, Møen, 6 m (+ 5); VG and QS north of Møen (+ 5 and ♂ 7); VD at Bøgestrømmen, 7.5 m (+ 5). — **Bb:** Davids Banke, 15 m (♂ 7), 19—21 m (+ 7); near Salthammer Rev, 24.5 m (+ 7).

[1] + designates tetrasporangia, ♂ antheridia, ♀ carpogonia, ◯ cystocarps, the number added being the number of the month.

Chondrus Stackh.

1. Chondrus crispus (L.) Stackh.

Lyngbye, Hydr., 1819, p. 15, tab. 5, A, B; Greville Alg. Brit. 1830, p. 129, pl. 15 (cystocarp); Kützing, Phycol. gen. 1843, p. 398, tab. 73 III; Harvey Phyc. Brit. III, 1846, pl. 63; J. Agardh, Sp. g. ord. Vol. II, I, 1851, p. 246; Kützing, Tab. phyc. Bd. 17, 1867, tab. 49; Schmitz, Befr. d. Florideen 1883, p. 238; Wille, Beitr. 1887, p. 82, Taf. VII, figs. 70—71; Buffham, Notes 1896, p. 183; Darbishire, Chondrus, Liverpool Marine Biology Committee. Memoirs IX. London 1902; Oltmanns, Morph. u. Biol., I, 1904, p. 549; Kylin, Studien 1907, p. 123; id. Keim. ein. Florid., Arkiv för Botanik, Bd. 14, No. 22, 1917, p. 12; id. Entwickl. 1923, p. 19; Violet Grubb, The Male Organs of the Florideæ, Linn. Soc. Journal. Botany, Vol. 47, 1925, pp. 184—187.

Fucus crispus Linné Mantissa plant. 1767, p. 134.

Fucus polymorphus Lamour. Diss. sur plus. espèces de Fucus. I. Agen et Paris 1805.

The fronds arise from a flat expanded disc which originates from the primary cushion-shaped stage of the germling. It is in older plants a nearly orbicular rather thin plate with irregularly lobed margin, densely attached to the substratum up to 1 or 2 cm in diameter. Several upright shoots may be given off from the same disc, e. g. 30—40, and these shoots are of very different age, old and young ones intermixed without any distinct order, the youngest, however, for the most part at the periphery. The disc itself may attain an age of several years. In specimens collected in summer upright shoots from the foregoing year or perhaps older are found together with numerous shoots produced after the last winter, and the latter have evidently arisen at various times during the last period of vegetation, for all gradations are to be found from well developed repeatedly branched shoots to quite small ones, a few mm long only.

Owing to the fact that the upright shoots produced in the last period of growth are in very different stages of development when the growth is arrested in winter, it is not always easy to distinguish the portion of an older shoot which was produced in the last year from that existing already in the foregoing year. A difference in the colour, however, is often very significant, in particular in spring and the first part of the summer, the new portions of the frond showing a brighter colour. But the difference often becomes more striking by the epiphytes covering more or less densely the portion of the frond produced in the foregoing year, whereas the new segments are destitute of epiphytes or bear only very young specimens of such (comp. fig. 458).

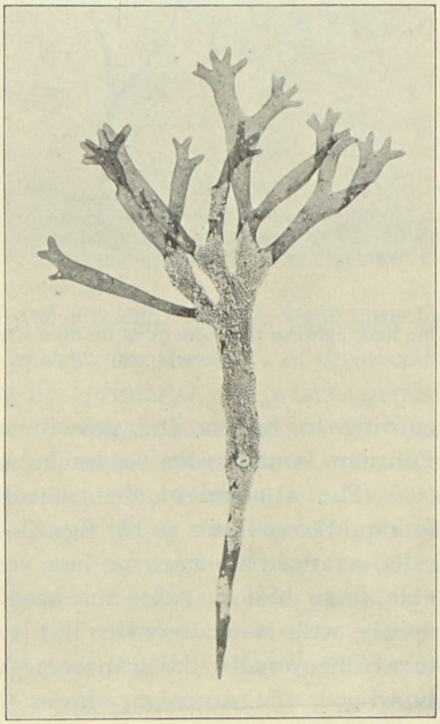


Fig. 458.
Chondrus crispus. Northern Kattegat at Læsø Trindel, about 10 m depth, July. Photo, nat. size.

The upright fronds ordinarily attain an age of two years, and sometimes they continue growing in the third year. This seems to be the case with the specimen represented in fig. 459 which was gathered in May. This frond has probably in the first year produced the first system of fans, in the second year the branches of these have produced a new system of fans, and in the year when the plant was gathered some of the branches have continued growing but have only caused a slight prolongation of the frond, 1 cm at most; the growing power of this frond was evidently exhausted. In the cases where the frond has arisen late in summer and therefore has only a small size at the end of the first season, the chance for a considerable growth in the third year may probably be greater. The period of growth begins in spring in the Danish waters and ceases towards the end of summer. The old fronds finally decay and are thrown off, probably as a rule in autumn and winter; they are separated at the very base, leaving scars that are a little deepened and have a slightly elevated border. An attachment disc, gathered in spring, showed some 30 such scars and a few upright shoots. According to Printz the growth of the frond begins in Trondhjem Fjord about February and mostly ceases in August and September.

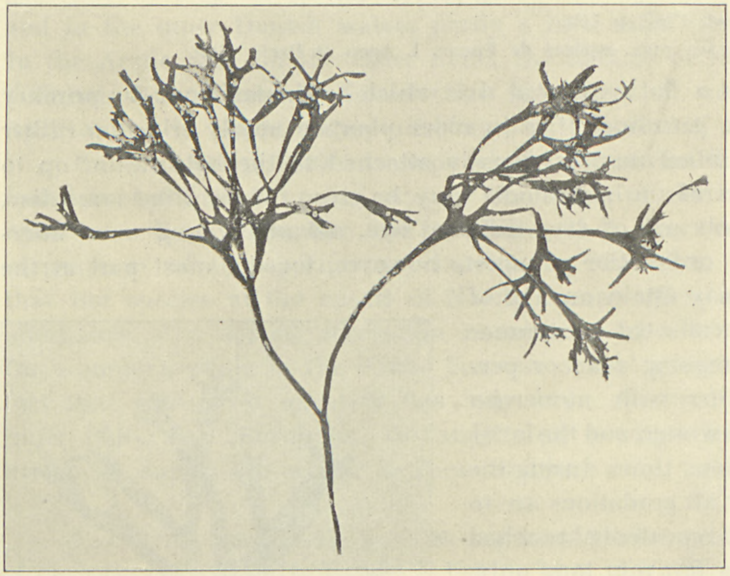


Fig. 459.
Chondrus crispus. Krageskovs Rev, 4 m, May. The short streaks above indicate the limit between the portions of the frond formed in the foregoing and the present year. Photo, 3/4 nat. size.

The attachment disc has a parenchymatous structure of firm consistence (comp. Darbishire p. 15, figs. 9—11), being built up of approximately quadrangular cells arranged in more or less vertical rows. The height of the cells is rather variable, from half to twice the breadth. The cell-walls are firm, not gelatinous, staining deeply with hæmatoxylin. The outer wall is very thick, showing a lamellate structure. The pits in the transverse walls are scarcely discernible except in the neighbourhood of the upright shoots. A stratification due to the periodical growth of the crust appears in older crusts, but it is rather irregular, probably depending on the production of the upright shoots. The cells are filled with starch grains.

The upright fronds arise as outgrowths from the basal disc. A vertical section of the lowermost portion of the frond issuing from the disc shows a marked difference between the frond and the disc. In the neighbourhood the cell-rows of the disc are bent outwards, the cell-walls, which in the normal disc are firm, swell, the intercellular substance becoming much developed and gelatinous, and numerous transverse secondary pits appear between the cells of the originally vertical cell-rows (Fig. 460). These cell-rows gradually pass into the cortical cell-rows of the upright shoot, where the transverse secondary pits are also numerous and very long. These secondary pits enable a more intense longitudinal conductive power between the frond and the disc.

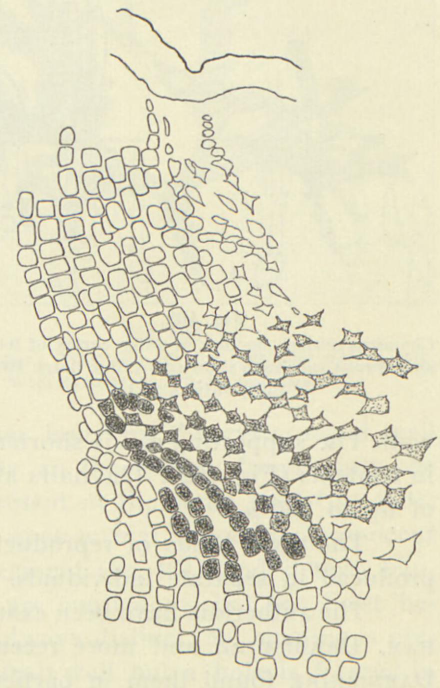


Fig. 460.
Chondrus crispus. Longitudinal section of an attachment disc at the base of an upright shoot; the latter issued to the right. 350 : 1.

The structure of the upright frond has repeatedly been described and pictured (KÜTZING 1843, WILLE, DARBISHIRE, OLTMANNS, KYLIN 1923). The tip of the frond has the structure designed by OLTMANNS as the fountain type (Springbrunnentypus) (KYLIN 1823, p. 20, fig. 10 a). The medullar or conducting tissue is built up of elongated cells arranged in longitudinal rows, 7—16 μ in inner diameter, connected with small pits in the end-walls and here and there also by transverse pits of secondary origin. The longitudinal cell-rows may be more or less bent, especially in the older parts of the frond. WILLE (1887, p. 83) thought that this might be explained by the supposition that the ends of the long cells slide past each other much as the bast-cells of the Phanerogams. This view, however, cannot be upheld, for the ends of these cells are connected by (primary) pits which persist and do not permit of such a sliding growth. The cells of the outer longitudinal cell-rows are much shorter than the inner ones, and gradually pass into the cortical layer which consists of branched cell-rows that are outward-directed and not unfrequently connected with secondary pits. The inner part of these cell-rows forms the storage tissue. The last 2 or 3 cells in the cortical cell-rows are very narrow and contain no starch, whereas the inner cells are more or less filled with starch-grains. For further details of the anatomy and cytology see the authors quoted, in particular DARBISHIRE. According to this author each cell contains only

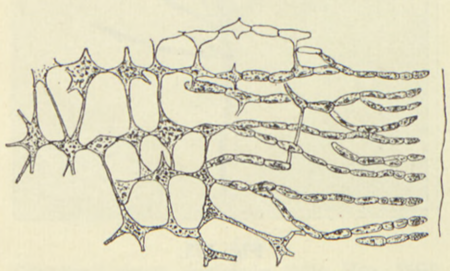


Fig. 461.
Chondrus crispus. Vertical section of the cortex at the base of an upright shoot. 560 : 1.

one chromatophore. In the outermost, assimilating cells it forms a plate lining the cell-wall, in the storage-cells the plate is divided into branched ribbons. According to the same author, the conducting cells of the medulla contain several leucoplastids.

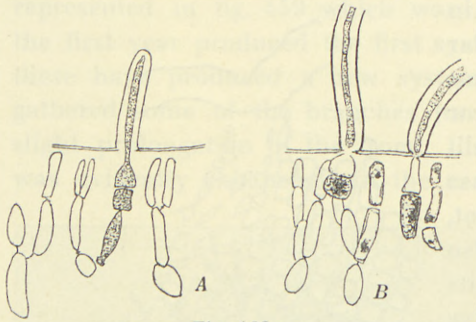


Fig. 462.
Chondrus crispus. Section of outer cortex of tetrasporiferous specimen showing hyaline hairs. Hirtshals, July. 835 : 1.

In 1911 (Hyaline hairs, p. 205) I have ranged this species among those which are devoid of hyaline hairs. I have, however, recently found such hairs in tetrasporiferous specimens collected at Hirtshals, Skagerak, in July 1914 and preserved in alcohol. They occurred scattered in the upper part of the frond. The basal portion of the hair-cell is swollen and sunk in the frond; this swelling is emptied when the hair has grown out, but still contains a thin layer of protoplasm lining the wall. The supporting cell is shorter and thicker than the surrounding cells and richer in contents (Fig. 462). The hairs attained a length of up to 250 μ.

The three kinds of reproductive organs are produced in separate individuals.

The antheridia have been examined by Buffham, Darbishire and more recently by Grubb. Darbishire found them in particular small and narrow white leaves (spermophores), while Miss Grubb describes them as whitish-pink patches or sori on the upper parts of the thallus of an otherwise normal vegetative plant. Buffham and Darbishire found them ripe in September and October, while Grubb found the material examined fully fertile in the spring, and she suggests that there are two seasons of spermatial production, spring and autumn. The outermost cortical cells, according to this author, give rise to two antheridial mother-cells from which two antheridia spring. For more details see Grubb's paper.

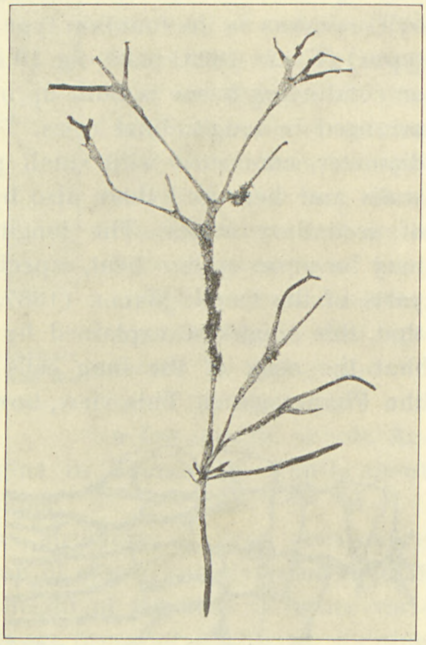


Fig. 463.
Chondrus crispus. North of Læsø, 9,5 m, January. With cystocarps (above). Photo, 3/4 nat. size.

The procarp was first described by Schmitz (1883, p. 238), later by Darbishire and recently by Kylin (1923, p. 20) who also followed the development of the gonimoblast. The three-celled carpogonial branch is borne on a large cell rich in protoplasm, which is the auxiliary cell.[1] After

[1] According to Darbishire, the large basal cell has a small cell cut off that is the auxiliary cell, l. c. p. 28.

fertilisation and fusion of the carpogonium with the auxiliary cell the latter gives off several sporogenous filaments penetrating between the vegetative cells of the frond and finally forming a large gonimoblast producing numerous carpospores. The ripe gonimoblast is composed of a number of more or less distinct glomeruli separated by shrunken hyphæ, as shown by KÜTZING (Tab. phyc. 17 Tab. 49 b). The whole cystocarp appears as an oblong or round swelling, up to 2 mm long, prominent on one or sometimes on both faces of the frond; in the first case the not swollen face of the frond may be concave. The cells of the inner layers of the cystocarpial wall are all connected transversally with secondary pits. In the narrow fronds only one cystocarp is present at the same level (fig. 463); in the broader ones several cystocarps may occur in the same segment (fig. 464), and it then happens that two are contiguous, but the limit between them is always distinct. No opening is preformed in the fruit wall but a hole is formed in the middle of the convex fruit wall by disintegration of the cells.

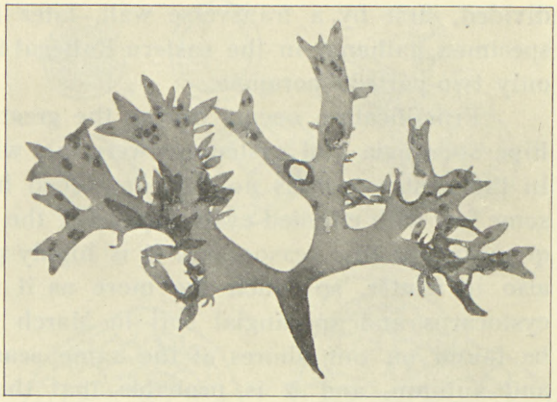


Fig. 464.
Chondrus crispus. West side of Hirtshals, low water, July. With cystocarps. Photo, nat. size.

The tetrasporangial sori appear as dark-red elongated spots, slightly bulging on both faces of the frond, in particular in a dried condition; they are usually smaller, more irregular in outline and more numerous than the cystocarps and often confluent, and no limit can then be drawn between the fused sori. They occupy the younger portions of the frond, also the adventitious shoots, but may sometimes, in specimens growing near low-water mark, be met with in most parts of the frond (fig. 465). The production of the sporangial sori may persist during a long period and the development then proceeds from the base towards the top. Emptied sori may be met with in the middle of the frond or lower, while young sori are still in development at the top. The sporangia arise in branched cell-rows produced by the medullar cells, not only in the end-cells, but also from the intercalary ones. They are cruciately

Fig. 465.
Chondrus crispus. Hirtshals, mole, May. With tetrasporangial sori. Photo, nat size.

divided, first by a transverse wall, later by two longitudinal ones (fig. 466). In a specimen gathered in the eastern Kattegat in October I met with a sorus containing only two-parted sporangia.

Fructification occurs during the greater part of the year at the Danish coasts. Ripe sporangia and cystocarps were met with in all the months of March to October. In the winter months no well developed fructiferous specimens were met with, but some few with emptied cystocarps; but the species has only been gathered in small quantities at this season, and it is highly probable that it will be found fructiferous also in winter, so much the more as it may occur with ripe and partly emptied cystocarps and sporangial sori in March and April. The antheridia will probably be found on our shores at the same season as on the British coasts viz. spring and autumn, and it is probable that the development of the cystocarps usually begins in the autumn; it then continues through the following year. The production of the tetrasporangia has apparently a similar course. At the west coast of Sweden the fructification seems to take place at the same seasons as at the Danish coasts (comp. ARESCHOUG Phyceæ, p. 86, KYLIN 1907, p. 123). On the British coasts it has not, according to BATTERS and DARBISHIRE, been recorded with fruit in the summer months, but that is perhaps only accidental, and will probably not be confirmed by further investigation, for it has been gathered with cystocarps at the Færöes in June and September by BØRGESEN (Mar. Alg. Fær. 1902, p. 357). According to PRINTZ the cystocarps and the tetrasporangia begin to appear in August and September in Trondhjem Fjord, and the fructification continues during the winter and mostly ceases in early spring; he adds, however, that the species shows great power of variation as to the incidence of fructification.

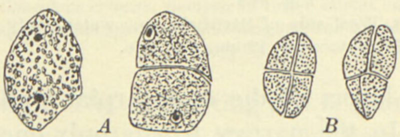


Fig. 466.
Chondrus crispus. Tetrasporangia. Hirtshals mole, *A* July, *B* August. 520 : 1.

The germination of the tetraspores has been shortly described and illustrated by DARBISHIRE and KYLIN (1917). I have observed the germination of the tetraspores and the carpospores in summer (July, August); they present the same features. The spore-cell is first divided by a perpendicular wall and then by rather irregularly orientated walls in a number of cells that are much smaller than the spore-cell. The germling is then hemispherical or cushion-shaped with a fairly regular outline, and increases slowly without changing in shape, or it becomes more flat, the vertical radius increasing less than the transverse ones. Sometimes one or two filaments are given off from the border; these filaments consist of a single cell-row rarely divided by a longitudinal wall (fig. 467, comp. DARBISHIRE, fig. 29, KYLIN, figs. g—i). Most of the sporelings in my cultures, however, were without such filaments. When two sporelings are developing close together, they may fuse together without any distinct limit. The oldest germlings in my cultures, 24 days old, showed no upright shoots. The young plants arising from germinating spores in summer probably only attain a small size before the following winter.

The variability of *Chondrus crispus* is well known, but it is impossible to draw any distinct limits between the numerous forms that may be met with. The most frequent and characteristic forms in the Danish waters are here recorded.

A. Forms occurring near low-water mark, down to 2 or 3 metres' depth. The uppermost specimens growing on stony reefs or moles left dry at low-water. Frond proportionally broad.

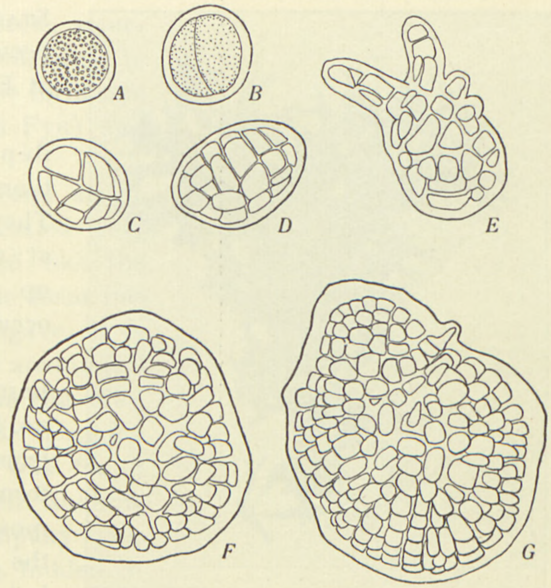


Fig. 467.
Chondrus crispus. Germination. *A—D*, germinating carpospores, 6 days old ($^{31}/_{7}$—$^{6}/_{8}$ 1928). *E*, germling from carpospore $^{13}/_{7}$—$^{25}/_{7}$ 1914. *F*, *G*, germlings from tetraspores, Hirtshals $^{9}/_{7}$—$^{2}/_{8}$ 1914. 625 : 1.

F. *typica*. The most common form near low-water mark. Frond regularly dichotomously divided, sometimes with proliferations, up to 14 (18) cm long, 6—10 mm broad, deep brown-red with a blue lustre. (Lyngbye Tent. Tab. V A, Lamouroux, figs. 2—5, 8). The best developed specimens were found at Hirtshals, Skagerak, where the fronds are usually regularly flabellate and broad without proliferations (figs. 464, 465).

F. *abbreviata* Kjellman. Kylin 1907. Only different from the foregoing by smaller dimensions. Frond up to 9 (13) cm long, up to 4 (6) mm broad. Same occurrence as the foregoing, in particular in the inner waters, on moles and stony reefs.

Fig. 468.
Chondrus crispus f. *densa*. Shallow water. Frederikshavn, July. Photo, nat. size.

F. *densa*. The frond short, broad, much branched, often taking a nearly globular form. The ramification may be apical (fig. 468) or, more frequently, chiefly marginal; in the latter case the frond is very broad and bears a very great number of longer or shorter, branched or unbranched marginal shoots. The number of branches and shoots is so great that the tips of the shoots point in all directions in the globular forms (fig. 468). This form grows on stones in shallow water protected against the waves, for instance at Frederikshavn at the north-side of the harbour. A less dense form with numerous proliferations is depicted in Flora Danica under the name of *Ch. crispus* var. *ciliatus* Suhr. It seems to be common at the isle of Föhr at the west coast of Slesvig, and has also been collected at Blaavandshuk. (Specimens with numerous narrow branches or proliferations at the upper margin of a short broad thallus may be named f. *stellata*

Fig. 469.
Chondrus crispus, f. *densa* (*ciliata* Suhr). Shallow water, Frederikshavn, July. With tetrasporangial sori. Photo, nat. size.

Stackh., Lyngbye). Similar specimens have been met with in shallow, protected water at Frederikshavn (fig. 469).

B. The specimens growing at greater depths, more than 3 metres, are less variable than those growing near low-water mark. They are proportionally narrow, being usually at most 2—4 mm broad, and fairly long, up to 16 cm. Proliferations do not usually occur. The colour is more reddish.

F. *æqualis* Lyngb., Tent. Tab. 5 B, Lamour., figs. 12, 16, 22, Areschoug Exsicc. no. 156. Figs. 458, 463. Most of the specimens from deeper water may be referred to this form, characterized by the frond having almost a uniform breadth. The specimens from the greatest depths (13—20 m) are thinner but not otherwise different; they might be named f. *membranacea*.

F. *polychotoma* Kjellman, Kylin 1907, p. 123, Lamouroux tab. XII, figs. 31, 32. This form is represented by two year old fronds, with numerous branches in the upper part of the frond. Two systems of fan-shaped ramifications from two consecutive years may be found (fig. 459).

C. Specimens lying loose on the bottom. Fronds disengaged from the attachment disc may maintain life in the loose condition for a shorter or longer time. Such specimens may keep the original form for some time (usually f. *æqualis*); but upon continued life in a loose condition the shape of the frond becomes altered. The specimens that have lived for some length of time lying loose on the bottom and are carried along by the currents often show a swelling at the lower end where they have been loosened, like a feeble callus disc (fig. 470). The loose specimens are always sterile. They are only met with in sheltered localities in the inner waters.

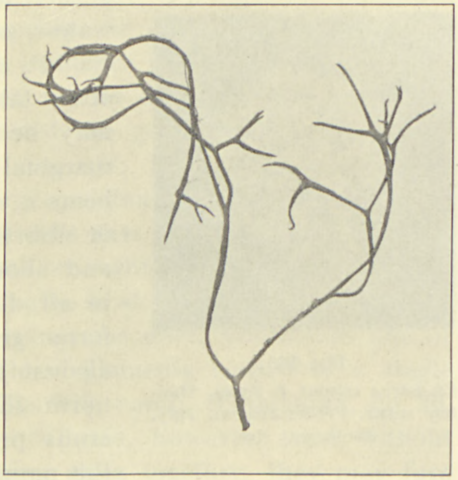


Fig. 470.
Chondrus crispus, f. *incurvata*. Off Vesterskovs Flak, north of Falster, 7,5 m. Photo, nat. size.

F. *incurvata* Lyngb., Tent. p. 16; *Chondrus incurvatus* Kützing, Sp. Alg. p. 735, Phyc. gener. p. 399, Taf. 73 II, Tab. phyc. Bd. 17, tab. 50 *c*, *d*.

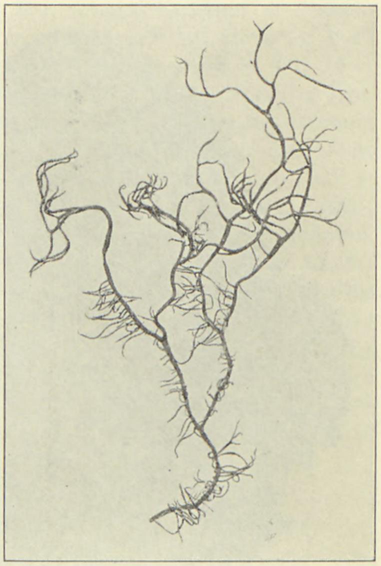


Fig. 471.
Chondrus crispus, f. *incurvata*. At Hofmansgave (Hofman Bang). Photo, $^2/_3$ n. s.

Frond long, up to 20 cm, narrow, subterete, sometimes with proliferations, variously curved, often to one side. This is the most common loose form met with repeatedly at Hofmansgave (North Fyn) and further in **Sb**, **Sf** and **Sm**. Fig. 470, 471.

F. *uncinata* Lyngb. Tent. p. 16. Frond small, cartilaginous, linear, cylindrical, complanated only at the bifurcations, at the ends recurved like the horns of a ram. This very characteristic form has only been found very rarely at Hofmansgave. It is so different from the typical form that an anatomical examination is needed for the identification (fig. 472).

F. *ægagropila*. A much branched specimen forming an irregularly rounded clump was found lying loose on the muddy bottom in shallow sheltered water at Frederikshavn in company with f. *densa*. The base was not visible, it was hidden in the interior of the clump the surface of which consisted on all sides of the irregularly outward directed ends of the shoots (fig. 473).

In the North Sea and Skagerak *Chondrus crispus* thrives only near land from a little over low-water mark to 2 metres' depth and only where the coast is stony, and the same can be said of its occurrence in the Limfjord. In the other waters within Skagen it occurs most frequently in similar localities (f. *typica* and *abbreviata*), but it also grows at greater depths among other Algæ on stones, down to 15 m, more rarely to 20 metres' depth. The boundary for its entrance into the Baltic is at Kriegers Flak and Saltholm, but in the most southerly part of its area it has only been met with at greater depths. At a higher level, near low-water mark, the southern boundary is more northerly, undoubtedly owing to the lower salinity of the surface water. In the Little Belt the southernmost locality known is at Sønderballe Hoved, at 2 metres' depth, but the specimens were very small, only 1—1,5 cm high. In the Great Belt it has not been met with near low-water mark south of Nyborg harbour, and in the Sound it has not been met with at this level south of Helsingborg.

Fig. 472.
Chondrus crispus f. *uncinata*. Hofmansgave, Car. Rosenberg. Photo, nat. size.

Chondrus crispus always grows on stones. Once only have I met with a small specimen growing on the stipe of *Laminaria hyperborea* in the Skagerak. It is often

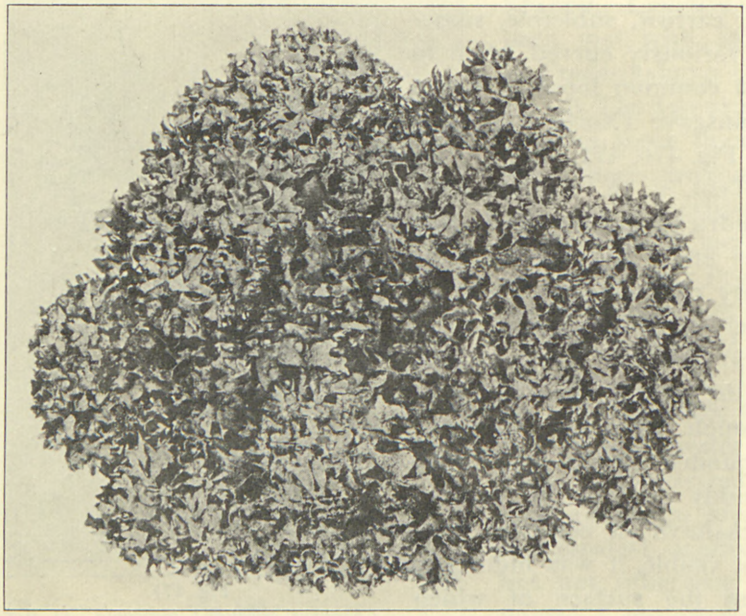


Fig. 473.
Chondrus crispus f. *ægagropila*. Shallow water, Frederikshavn. Photo. nat. size.

much overgrown by epiphytes, especially in Skagerak and Kattegat. The older parts of the frond may be totally covered by Bryozoans of the genus *Membranipora*, and incrusting Algæ as *Epilithon membranaceum* and *Melobesia limitata* may appear in the same way in the Kattegat, and further a number of other Algæ frequently occur as epiphytes, such as *Sphacelaria cirrosa*, *Ceramia*, *Polysiphoniæ*, *Brongniartella byssoides*, germlings of *Furcellaria fastigiata* a. o. At the coasts of the North Sea, Skagerak and the northern Kattegat the specimens of *Chondrus* growing in shallow water (1—2 metres', more rarely at 5,5 metres' depth) are often infested with the parasitic Pyrenomycete *Didymosphæria marina* (Rostr.) Lind, Danish Fungi as repr. in the herb. of E. Rostrup, 1913, p. 214 (*Leptosphæria marina* Rostr.), that gives to the sporangial sori and cystocarps a black colour and develops perithecia and pycnidia there. Another parasitic Fungus of the class Phycomycetes, *Pleotrachelus pollagaster* Henn. Petersen (Phycomycètes marins. Oversigt ov. d. K. D. Vid. Selsk. Forh. 1905), has repeatedly been found infesting the upper portion of fronds of *Chondrus crispus* growing at various depths in Kattegat and the inner waters.

Localities: **Ns:** Esbjerg harbour on muddy bottom with Zostera vegetation, f. *ciliata*; Blaavandshuk washed ashore, various forms, f. *æqualis*, f. *ciliata*, f. *incurvata*; Thyborøn, on a groin; Klitmøller, within Ørhage. — **Sk:** Hanstholm, Roshage 2 m, mole; Torup Strand, washed ashore (C. M. Poulsen); ZK^2 off Lønstrup, 8—9 m; Hirtshals, on the mole and on boulders, down to 2 m depth; Skagen, washed ashore on the North beach. — **Lf:** Common near low-water mark: Lemvig harbour; Mulle (J. P. Jacobsen); Thisted; Struer; Nykøbing, harbour and Ørodde; Ejerslev Røn; Knudshoved, Fur; off Lisehøj North side of Fur; Løgstør; Agersund (Th. Mortensen); Aalborg, large, very broad specimens with numerous proliferations (Th. Mort.); Hals (Børgesen). — **Kn:** Skagen harbour; Krageskov Rev; Hirsholmene; reefs and harbour at Frederikshavn; Bangsbostrand; Sæby; several places around Læsø Trindel, 8—19 m; several places North of Læsø; Vesterø. — **Ke:** IO, ZE, ZG, fH, Fladen, 11—17 m; Lille Middelgrund, 17—19 m; ES, S.W. of Lille Middelgr., 24.5 m; Store Middelgrund, 10—15 m; Gilleleje (Lyngbye); GJ, OO and Vesterlandsgrund north of Gilleleje. — **Km:** ZC, ZC^1 and XB, Kobbergrund; Asaa, mole; Anholt harbour; Gerrild bay (Lyngbye). — **Ks:** Grenaa harbour; at Hesselø (Lyngbye); RL near Ostindiefarer Grund; aU off Lumbsaas 13 m; Hastens Grund; GG Sjællands Rev; Holbæk harbour; on stones picked up near Roskilde. — **Sa:** Common on stony ground in 0 to 15 m depth, from KM, east of Øreflippen and the channel east of Sejrø to Endelave and DJ North of Fyn. Several specimens of f. *incurvata* from Hofmansgave (Hofm. Bang, Lyngbye). — **Lb:** Bogense harbour; Prins Frederiks Grund, Vejlefjord; FZ, Kasserodde; Fredericia harbour; Middelfart, harbour and 15 m; Assens harbour; at Sønderballe Hoved 2 m, 1—1.5 cm long specimens. — **Sf:** Faaborg harbour; UX at the North end of Ærø 9.5 m; CG, Skrams Flak, f. *incurvata*, loose. — **Sb:** Off Refsnæs (C. H. Ostenfeld); Kalundborg harbour; gU, east of Lille Grund 10—12 m; Elefantgrund 6—7 m; LP, Stavreshoved, 2—4 m; Kerteminde harbour; bay of Kerteminde; GY and fZ at Sprogø; AB off Teglgaardsskov; Knudshoved 5—6 m; Nyborg harbour; Palegrund 7,5 m; XS near Kløverhage; GZ North of Egholm 6,5 m; DN Vengeance Grund 12 m; gB, Vresens Puller; gE, Stokkebæks Flak 6 m, f. *incurvata*; fS, east of Kjelsnor ligthouse, 11.5 m. — **Sm:** Q, off Vesterskovs Flak, 7.5 m, f. *incurvata*. — **Sü:** Off Ellekilde and Hellebæk (Ørsted,!); washed ashore at Helsingør (Liebman a. o.); PX, off Tibberup, 8.5 m, with *Zostera*; TF[1], Staffans Flak, 12—13 m; QD, east of the North end of Saltholm. — **Bw:** bY, off Sønderborg Nordskov, 11 m, f. *incurvata*; Sønderborg (Frölich according to Reinke); UL, Øjet, 20 m, attached to the bottom. — **Bm:** bP, Kriegers Flak, 15 m (O. Paulsen).

Gigartina Stackh.

1. Gigartina mamillosa (Good. et Woodw.) J. Agardh.

J. Agardh, Alg. mar. mediterr. p. 104 (1842); Sp. g. ord. Alg. Vol. II, pars. 1, p. 273, 1851; Harvey, Phyc. Brit. Vol. II, 1849, pl. 199; Buffham 1896, p. 84, plate X, figs. 4—8; Oltmanns, Morph. u. Biol. I, 1904, p. 547. fig. 331.

Fucus stellatus Stackhouse in Withering, Bot. Arr. ed. 3, vol. IV, p. 99, excl. syn. omn. (1796), sec. Batters. (Not seen by the author).

Fucus mamillosus Good. et Woodw., Trans. Linn. Soc. Vol. III, 1797, p. 174.

Sphærococcus mamillosus Agardh, Synops. Alg. scand. 1817, p. 25; Lyngbye Tent. 1819, p. 14, tab. 5 C; Flora Danica tab. 2011, Hornemann 1830 (from the Færöes).

Mastocarpus mamillosus Kützing, Phycol. gener. 1843, p. 398, Tab. 76 III, Tab. phycol. XVII, pl. 39, 1867.

Gigartina stellata Batters Catal. of the Brit. Marine Algæ. Suppl. to the 'Journ. of Botany' 1902, p. 64.

This Alga reminds one in habit of *Chondrus crispus*, a tuft of upright fronds of a similar shape as in this species springing from a flat disc. The latter is composed of densely united vertical cell-rows and shows several transverse lines indicating a periodical growth. The upright fronds are placed closely together; they are more or less canaliculate and bear numerous papillæ on one or on both faces. The papillæ seem to arise in spring (comp. 476 *B*).

The upright fronds have a cortex built up of outward directed cell-rows consisting of small oblong cells becoming smaller towards the surface, the outermost being only 2 μ thick. The number of cells in these rows may be 7—10. Within this dense assimilating cortex a few layers of somewhat larger almost isodiametrical cells form an inner cortex. These cells are more distant from each other, being separated by a hyaline intercellular substance, and are connected with primary and secondary pits (fig. 474, 475 A). They pass into the inner medullar cells which in a transverse section show almost the same aspect being only somewhat larger and still more distant from each other, while in longitudinal section they appear as long cells having their long axis parallel to the longitudinal axis of the frond. The cells of the inner cortex and of the medullar tissue may produce long thin cell-filaments consisting of long cells, which grow out in a transverse direction downwards between the primary cell-rows and may sometimes be connected with these through secondary pits (fig. 475).

Fig. 474.
Gigartina mamillosa. Transverse section of frond. 560 : 1.

The sex organs have not been observed by me. The antheridia were described by BUFFHAM in 1896. The male plant, according to this author, differs much from the female one, "for it is thickly beset from near the base with flattened leaf-like branches arising just within the edges of the main portions of the frond, and with smaller ones from

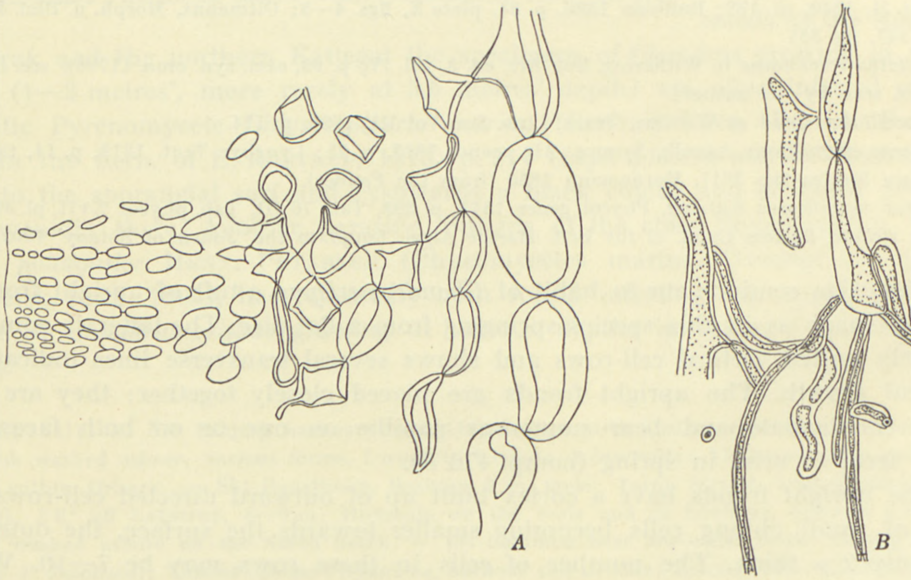


Fig. 475.
Gigartina mamillosa. A, longitudinal section of frond. 560 : 1. *B*, longitudinal section of medullar tissue. 350 : 1.

the other portions of the thallus". In some of these leaf-like branches the antheridia appear. The male plant was found in September; BØRGESEN found antheridia in June at the Faröes (M. A. Fær. 1902, p. 357). The cystocarps arise in the papillæ covering the flat frond. The procarps seem not to have been described; I have not observed them, perhaps owing to the fact that I have only examined specimens gathered in late summer (August, September). Ripe and partly emptied cystocarps were met with in August. According to the authors (J. AGARDH, SCHMITZ and HAUPTFLEISCH, SJÖSTEDT), the gonimoblast is surrounded in the genus *Gigartina* by an inner pericarp of medullary hyphæ. This pericarp, however, is not represented, or only feebly developed in KÜTZING's figures of this species (1843 and 1867) and I have not observed it on the outside of the gonimoblast. As shown by KÜTZING (1867), transverse secondary pits are very well developed in the inner part of the cystocarpial wall exactly corresponding to the inner cortical layer of the frond. Ripe and partly emptied cystocarps were met with at Thisted in August. Tetrasporangia are unknown. As they have been searched for by several phycologists, it seems most probable that they are really wanting. On the other hand one might imagine that they do occur in the papillæ, just like the cystocarps, and that the sori of tetrasporangia might have been confounded with the cystocarps, as has been the case repeatedly with *Chondrus crispus*.

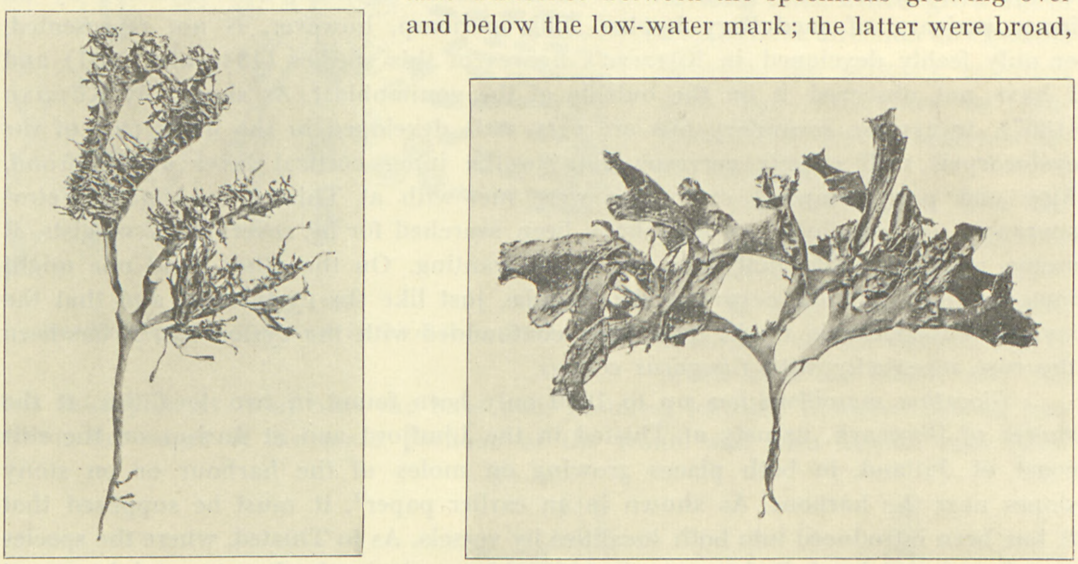
Gigartina mamillosa has up to 1929 only been found in two localities at the shores of Denmark, namely at Thisted in the Limfjord and at Aarhus on the east coast of Jutland, in both places growing on moles of the harbour or on stony slopes near the harbour. As shown in an earlier paper[1], it must be supposed that it has been introduced into both localities by vessels. As to Thisted, where the species was first found by J. P. JACOBSEN in 1869, this conclusion is almost certainly correct 1) since the salinity of the Limfjord before 1825, when the isthmus separating the fjord from the North Sea was broken through, was so slight that is was impossible for *G. mamillosa* to thrive here, 2) since the species has not been found elsewhere in the Limfjord and 3) since the part of the fjord (Thisted Bredning) where Thisted is situated is connected with the other parts of the fjord only by narrow channels with *Zostera* vegetation. The average salinity in the western part of the Limfjord is now 29 p. m. At Aarhus the species was found on a stony slope north of the harbour in 1911 or 1912. One might imagine that it might here be a relict from a time when the salinity was higher than now, when it varies probably about 20 p. m.; but that is quite improbable as the species has never been found elsewhere in similar localities in the Samsø waters or in Kattegat (except Skagen). It is therefore highly probable that the species has been introduced to this much frequented harbour by a vessel.

Gigartina mamillosa grows at low-water mark, at Thisted under the *Porphyra*-belt, over the *Fucus vesiculosus*-belt or partially in the upper part of this. It thrives well at Thisted, where it reaches a length of 5—8 cm, whereas at Aarhus it be-

[1] Om nogle i nyere Tid indvandr. Havalger i de danske Farvande. Botan. Tidsskr. Bd. 37, 1921, p. 126 and 133 (English abstract).

comes only 3—5 cm high, undoubtedly owing to the slighter salinity; here, however, it still produces ripe cystocarps.

In May 1929 I found *G. mamillosa* in the harbour of Skagen forming a continuous vegetation in the lover part of the tidal region and below the low-water mark. It was very well developed, reaching a length of 8,5 cm. There was a remarkable difference between the specimens growing over and below the low-water mark; the latter were broad,



A *B*

Fig. 476.

Gigartina mamillosa. Harbour of Skagen. *A* in the littoral zone, *B* at low-water mark. Photo, 4/5 nat. size.

of a proportionally bright colour, without or only with very feeble papillæ appearing as low warts, whereas the littoral specimens were much darker, nearly black, and bearing numerous long, partly branched papillæ, mostly near the border (fig. 476). The sublittoral specimens were perhaps a year younger than the littoral ones.

Localities. **Lf:** Thisted, first discovered by J. P. Jacobsen in August 1869, later found by me in Sept. 1890 and August 1893; it grew on the moles and on a stony slope east of the harbour. — **Kn:** Skagen, harbour, discovered May 1929. (The harbour was built in 1904—1907). — **Sa:** Aarhus, discovered in 1911 or 1912 by V. Petersson on a stony slope at the bathing-place "Kattegat" north of the harbour. I found it in 1917 and 1927 in the same place and on the outer side of the North mole, but it did not grow on the southern mole (at least 20 years old).

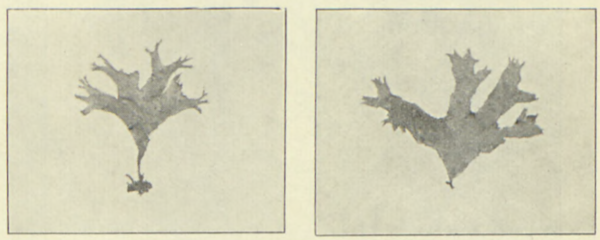
Phyllophora Greville.

1. **Phyllophora membranifolia** (G. & W.) J. Agardh.

J. Agardh, Alg. maris medit. (1842) p. 93; Harvey, Phyc. Brit. Vol. II (1849) pl. 163; J. Agardh, Sp. g. o. Vol. II, p. I (1851), p. 334; Wille, Bidrag (1885) p. 17, 32, 42, 65, 68, Tab. V, figs. 57, 58; Wille, Beiträge (1887), p. 79, Tab. VII, fig. 65; Buffham, Repr. Org. (1891), p. 248, Pl. 16 figs. 10—13 (antheridia);

B. Jönsson (1891, p. 19); Schmitz, Actinococcus (1893), p. 367; Darbishire (1895) pp. 5, 10, 20, 27, 31, 34; Kylin, Entwick. Florideenstud. (1928) p. 54, fig. 33.
Fucus membranifolius Good. et Woodw., Trans. Lin. Soc. III (1797), p. 120, pl. 16, fig. 1, 2.
Fucus crispatus Fl. Dan. tab. 826, fig. 1 (1778).
Fucus rubens Fl. Dan. tab. 827, fig. 1 (1778).
Sphærococcus membranifolius C. Agardh Synops. Alg. scand. (1817), p. 26; Lyngbye Tent., p. 10, tab. 3C.
Sphærococcus Palmetta Lyngbye 1819, p. 11 ex parte.
Phyllotylus membranifolius Kützing, Phyc. gener. (1843) p. 412, Taf. 62 I (cystoc.), Tab. phyc. XIX (1869) Taf. 75 (c. nemathec.).

The shoots arise in various number from an expanded basal disc, of a similar structure to that in *Ph. Brodiæi* (comp. Darbishire l. c.). It has a very thick outer wall and is built up of densely united vertical rows of cells that are square or higher or lower than broad; the uppermost cells are usually low. The cells contain numerous grains of floridean starch that are stained blue by iodine. The outermost cells, however, contain no starch grains but similar refractive bodies that do not stain with iodine. They give no reaction with osmic acid, and take a feeble red colour with hæmatoxylin (Hansen), while the starch grains remain quite colourless. By treatment with caustic potash they swell somewhat and become less refractive; by the following washing out in water and treatment with iodine they stain feebly yellow; they give no reaction with bichromate of potassium nor with nitric acid and with ammonia after treatment with nitric acid. Their chemical quality thus remains unknown.



A *B*

Fig. 477.
Phyllophora membranifolia. Small specimens with short stipe Sallingsund, Limfjorden. July. Photo, nat. size.

The young shoots that may be met with in summer on the vertical faces of boulders and which have arisen after the last winter, have often a very short terete stipe while the flat part of the frond is broad and repeatedly bifurcate, and this is especially so in the first erect shoot of young plants; a lateral shoot then often arises from the short stipe (fig. 477 *A*). In other cases the stipe is long, in particular in older plants, where it may be 4—5 cm or longer. At the end of the first period of vegetation the frond has thus the shape of a well developed fan

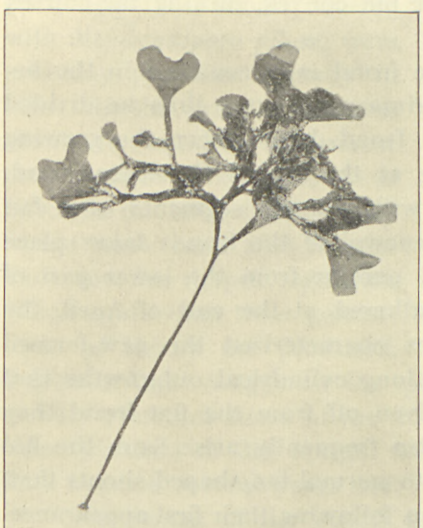


Fig. 478.
Phyllophora membranifolia. Groves Flak, eastern Kattegat, April. Photo, 4/5 n. s.

Fig. 479.
Phyllophora membranifolia. Fladen, eastern Kattegat. May. Photo, 4/5 n. s.

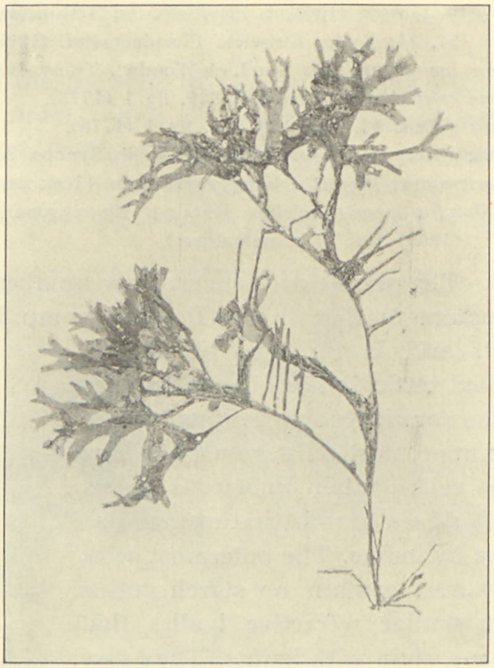


Fig. 480.
Phyllophora membranifolia. Limfjorden, at Jegindø. July. Photo, 4/5 n. s.

at the end of a cylindrical stipe. The fan is not plane but convex, turning the convex face upwards, towards the light.

The growth of the particular segments of the frond may continue in the beginning of the next season (fig. 478), and the primary fan may thus be divided into secondary ones. But all the segments of the frond do not keep the growing power; several of them definitively cease growing at the end of the season, and, at least in older fronds, this may be the case with all the segments of a fan (fig. 479, the lowermost fans). In such cases the renewal of the fronds takes place only by proliferations arising from the cylindrical part or from the lower part of the flat frond. In the plant shown in fig. 478, gathered at the end of April, the difference in colour, and the absence of epiphytes characterized the new-formed portions of the frond. The proliferations arise as long cylindrical outgrowths that later become flattened and forked above. When given off from the flat frond they are usually placed on the border, but they may also frequently arise from the flat surface of the frond. These proliferations give rise to normal fan-shaped shoots that, however, only reach their full fan-shape in the season following their first appearance. Cylindrical proliferations without a blade are frequently met with in summer and autumn (fig. 480, 481). The production of proliferations may be repeated in the new-formed shoots, and 3 (or 4) generations of shoots are therefore easily recognized in the ordinary plants. In full-grown plants collected in summer, the fan-shaped frond from the foregoing year is fully preserved even when its growth has quite ceased (fig. 479), while the flat portion of the foregoing generation is often decayed; only a narrow strip connecting the base of the new shoot with the cylindrical part of the foregoing is kept and strengthened by secondary cortical layers. The named 3 (or 4) generations of shoots undoubtedly represent an equal number of years, and it must therefore be supposed that the upright shoots normally reach an age of at least three years. In the plant represented in fig. 488, gathered in April 1906, the first generation is represented by the short stem having a nearly horizontal direction, the second reaches the middle of the picture. The next generation (of 1905) is represented by two long shoots bearing cystocarps on the margin; the lowermost portions of these shoots, covered with *Membranipora pilosa*, were probably produced already in 1904. On the margins of these shoots a number of narrow proliferations are seen; it is however doubtful whether they would have been able to produce new fan-shaped segments. When more than three generations of shoots are produced, a greater total length of the plant is scarcely obtained; the new shoots do not usually overreach those of the third generation. New shoots may, however, arise from older portions of the upright shoots and from the basal disc, and the plants may thus become several years old.

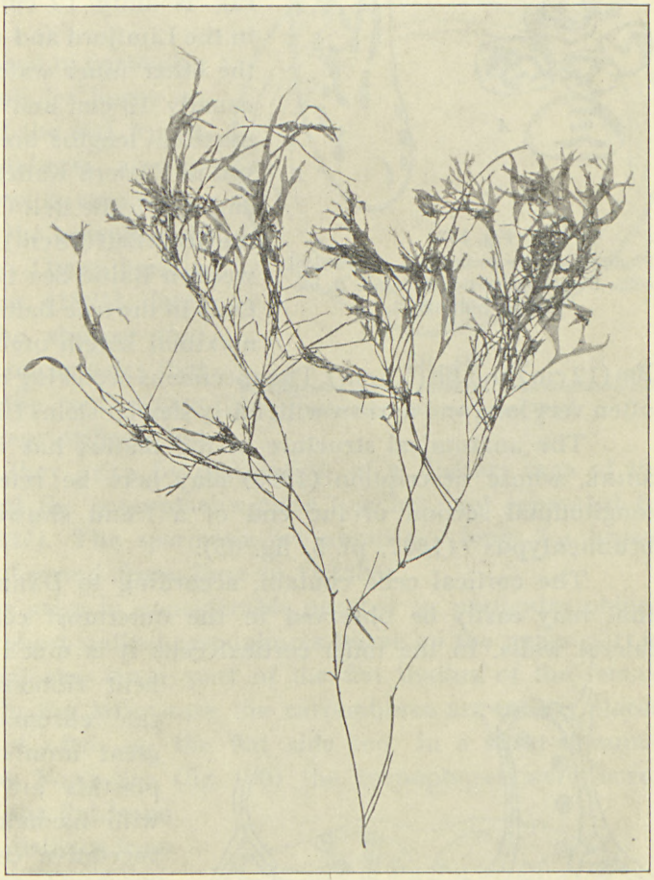


Fig. 481.
Phyllophora membranifolia. Store Belt, At Kløverhage south of Nyborg, October. Photo, $^4/_5$ n. s.

The length of the shoots produced in a year is rather variable, varying from a few to 10 cm, and there seem to be no great differences between plants from the different waters in this respect. Only in the true Baltic Sea is it less, scarcely exceeding 5 cm, and at Bornholm 3.5 cm. On the other hand, the total length of

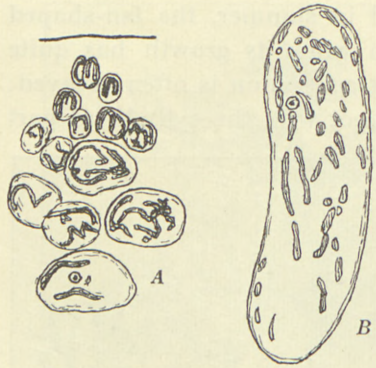


Fig. 482.
Phyllophora membranifolia. *A*, cortical cells, transverse section of frond. *B*, medullar cell. 840 : 1.

the plants exhibits considerable differences. The maximal total length observed in the North Sea and Skagerak is only 12 cm while in the Limfjord and most of the other inner waters it is usually 18 cm, and greater maximal lengths are observed in Eastern Kattegat (24 cm), the Little Belt (23 cm), the Great Belt (28 cm) and the western Baltic Sea (21 cm). Only in the true Baltic is the maximal length much less, **Bm** (12 cm) and **Bb** (5.5 cm). The specimens occurring in **Sb** are often very long and narrow with fairly slender stems (fig. 481).

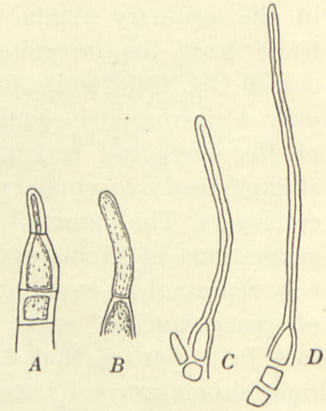


Fig. 483.
Phyllophora membranifolia. Hyaline hairs on carpophores. Prins Frederiks Grund, Vejle Fjord. 835 : 1.

The anatomical structure of the thallus has been treated at length by Darbishire, whose description (1895) may here be referred to. Wille has pictured a longitudinal section of the end of a frond showing the structure of the "Springbrunnentypus" (1887, pl. 5, fig. 65).

The cortical cells contain, according to Darbishire, each one chromatophore that may easily be observed in the outermost cells where it lines the outer and lateral walls. In the inner cortical cells it is much branched and appears as much bent ribbons that perhaps partly are separate chromatophores. In the inner cells a great number of rod-shaped or ribbon-like plastids are present which stain intensively with hæmatoxylin. A single nucleus in the vegetative cells may also be ascertained by this reagent (fig. 482). Hyaline hairs have only been observed in carpophores from a specimen gathered in Vejle Fjord in August (fig. 483).

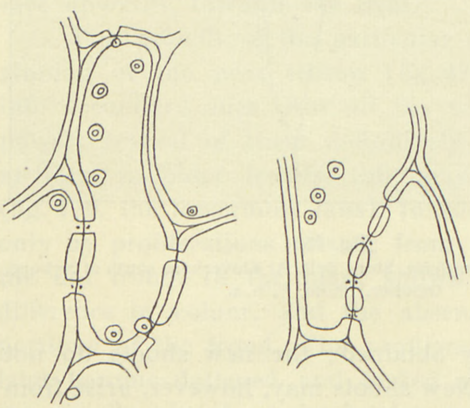


Fig. 484.
Phyllophora membranifolia. Longitudinal section of medullar cells showing numerous secondary pits. 520 : 1.

Secondary pits are produced in considerable number between the elongated cells of the medullary tissue with the effect that several pits are to be found in the same wall (fig. 484). A plug of callus is seen in the middle of each pit.

As shown by Jönsson (1891, p. 19) and Darbishire (1895), the lower portion of the stem has a thick cortex produced by secondary growth in thickness. The layers are, however, not regularly concentrical, the separate layers not usually continuing round the stem, for which reason the number of layers may be much greater on one side than on the other. The boundary of a layer may meet that of the foregoing layer or it may gradually disappear (fig. 485).

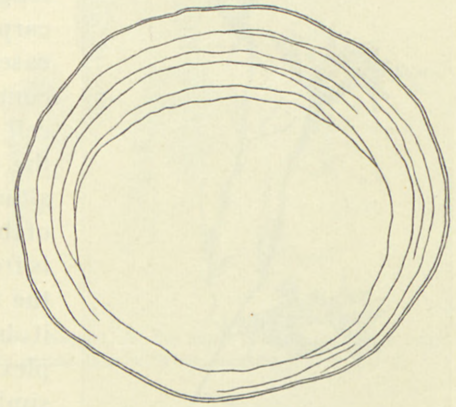


Fig. 485.
Phyllophora membranifolia. Transverse section of stem near the base. 86 : 1.

The antheridia are produced in particular yellowish or nearly colourless folioles borne on the border of the upper part of the flat fronds of the male plants. The androphores are up to 2 mm long, totally covered with spermatia-producing cells, sometimes with the exception of the outmost tip that remains sterile. The antheridia were first described by BUFFHAM (1891), later by DARBISHIRE (1895, p. 30) who showed that the spermatia are produced in conceptacles that are provided with an orifice in the roof. KYLIN (1928, p. 54) did not observe these orifices, but I can confirm their existence; they arise by dissolution of a distinct area of the outer wall. I found the conceptacles close together, not separated by sterile cells (fig. 487). The spermatia are about 6 μ long, 3 μ broad. Antheridia were observed from June to October.

Fig. 486.
Phyllophora membranifolia. Male plant with androphores. Nat. size.

The procarps arise in considerable number in particular oblong or nearly globular short-stalked carpophores borne on the upper part of the cylindrical and the lower part of the flat thallus of the female plants (fig. 488). In the latter case the carpophores are mostly placed on the border but often on the flat side too. In a short-stemmed specimen from the North-Sea (fig. 490) the carpophores were borne on the margin of the flat frond at a considerable distance from the cylindrical base. The carpophores arise in July. The carpogonial branch is three-celled (comp. SCHMITZ u. HAUPTFLEISCH p. 253, KYLIN 1928, p. 55, K. ROSENVINGE 1929, p. 12[1]). Fig. 491 shows carpogonial branches isolated by pressure and separated from the supporting cell which later functions as auxiliary cell. The carpogonium gives off downwards a prolongation that is connected with the second cell of the carpogonial branch through a lateral

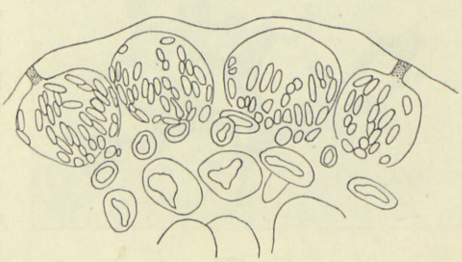


Fig. 487.
Phyllophora membranifolia. Transverse section of androphore showing four antheridial crypts. 625 : 1.

[1] According to DARBISHIRE 1895, p. 31 the carpogonial branch is four-celled; the first cell, however, does not belong to the carpogonial branch but is the supporting cell, the later auxiliary cell.

Fig. 488.
Phyllophora membranifolia. Specimen with ripe cystocarps. Hirtshals, April. $^4/_5$ n. s.

Fig. 489.
Phyllophora membranifolia. Specimen with nemathecia. Venø Bugt, Limfjord. September. $^4/_5$ n.s.

pit. The continuity of the protoplasm of the prolongation with that of the carpogonium was in all cases interrupted. The pit connection of the second cell with the first cell of the carpogonial branch is situated at the lower end of the second cell. A branch is frequently given off from the first cell; in fig. 491 *G* it has produced a complex of 7 cells. In fig. 492 similar stages are shown from sections through carpophores; the carpogonial branch is here seen borne on the auxiliary cell (*a*). In fig. 492 *B* a vegetative branch is given off from the auxiliary cell besides the carpogonial one, and this appears to be frequently the case (comp. KYLIN 1928, p. 55). In fig. 492 *D* the auxiliary cell has given off a prolongation apparently functioning by the transfer of the sporogenous nucleus. It appears that a great number of the procarps in a carpophore do not reach normal development (fig. 493 *A*, *B*); in many carpophores only few carpogonia are to be found, though there may be numerous supporting cells, but many of these bear only incompletely developed carpogonial branches or even no fertile branches at all.

Fig. 490.
Phyllophora membranifolia. Plant with short stem bearing carpophores on the border of the flat branched frond. North Sea, off Agger, 24 m, October. $^4/_5$ n.s.

To begin with the auxiliary cell contains one nucleus. In fig. 493 *C* is shown an auxiliary cell containing several small nuclei and four small protuberances at the lower face. It must be supposed that a sporogenous nucleus has entered into the cell, though a normal carpogonial branch could not be observed in this case. At all events the protuberances may be interpreted as the first stage of the gonimoblast. A similar stage is shown in fig. 494 *A* where a connection of the auxiliary cell with a normal carpogonial branch is not longer

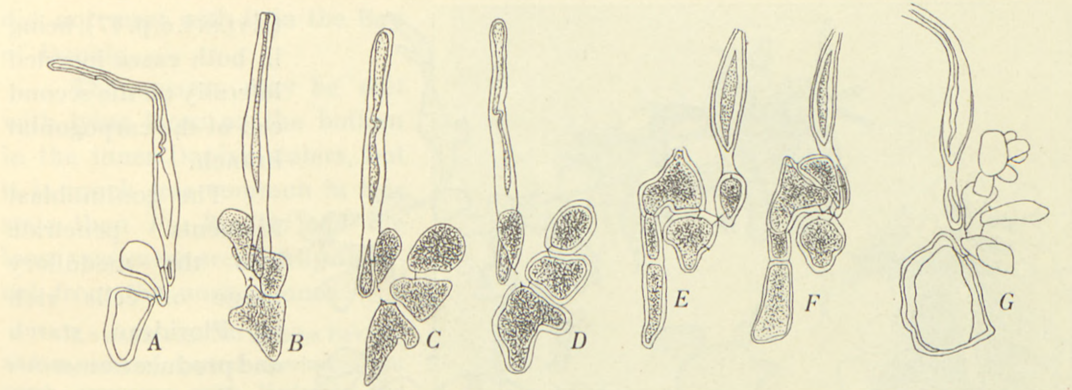


Fig. 491.
Phyllophora membranifolia. Carpogonial branches isolated by pressure, August. *D*, the same branch as *C* seen from another side. *F* the same branch as *E*. *G*, carpogonial branch in connection with the auxiliary cell. 390 : 1.

visible either. Later stages are shown in fig. 494 *B—D*, where the gonimoblast has arisen as several outgrowths from the lower and lateral sides of the auxiliary cell. The long cell or cell-complex at the upper face of the auxiliary cell probably derives from the carpogonial branch. It must be admitted that the fertilisation and the connection of the auxiliary cell with the carpogonium has not been ascertained. As to the first point reference may, however, be made to fig. 491 *A* where a pit in the wall of the trichogyne is undoubtedly the trace of a fusion with a spermatium. Kylin (1928, p. 54) has emphasized the accordance that exists in several respects between this species and *Stenogramme interrupta*; the development of the gonimoblast here pointed out is in good agreement with this conception. The carpogonium reminds one of that in *Iridæa cordata*

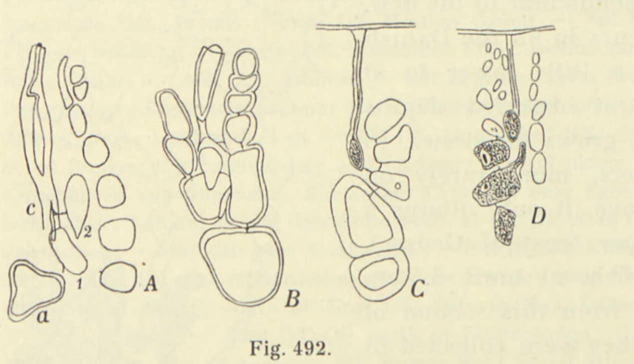


Fig. 492.
Phyllophora membranifolia Procarps from transverse sections of carpophores. In *B—D* the lower portion of the carpogonium is hidden behind the second cell of the carpogonial branch. In *D* the auxiliary cell has given off a prolongation towards the lower end of the carpogonium. *A*, *B*, Hanstholm, August. *C*, *D* Gilleleje, September. 390 : 1.

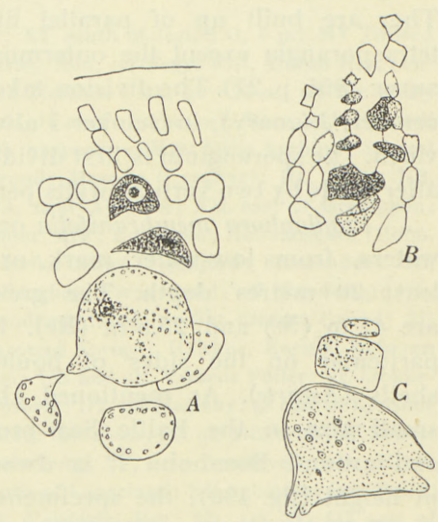


Fig. 493.
Phyllophora membranifolia. *A* and *B*, supporting cells with apparently not normally developed carpogonial branches. *C*, auxiliary cell containing several nuclei and producing four protuberances at the lower face. *A* 625 : 1. *B*, *C* 390 : 1.

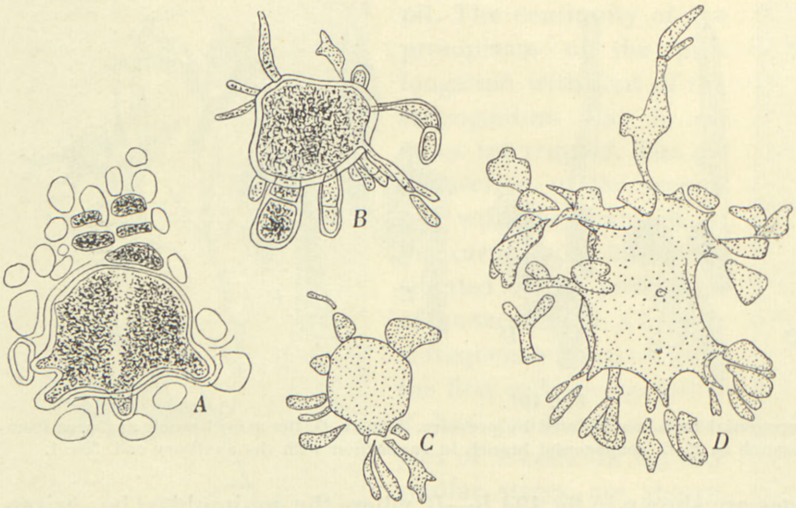


Fig. 494.
Phyllophora membranifolia. Auxiliary cells producing gonimoblast filaments in various stages of development. *B—D* isolated by squeezing. 390 : 1.

(Kylin l. c. p. 47), being in both cases inserted laterally on the second cell of the carpogonial branch.

The gonimoblast filaments penetrate into the medullary tissue of cells rich in Floridean starch and produce numerous small carpospores. In the ripe cystocarps cell filaments consisting of long narrow cells are seen traversing the mass of carpospores (fig. 495, comp. Kylin 1928, fig. 33 B). The cystocarps ripen in winter; they may still be met with in March to May, more or less empty.

The nemathecia arise in July, sometimes already in June (**Lf**, **Lb**) as deep-red wedge-shaped spots on both faces of the lower part of the flat frond (fig. 489). They are built up of parallel filaments, the cells of which develop slowly into tetrasporangia except the outermost cells (comp. Darbishire 1895, p. 27). The division takes place in winter (December, January); in October I always found them undivided. The sporangium is first divided by a transverse wall, afterwards by two vertical walls perpendicular to the first.

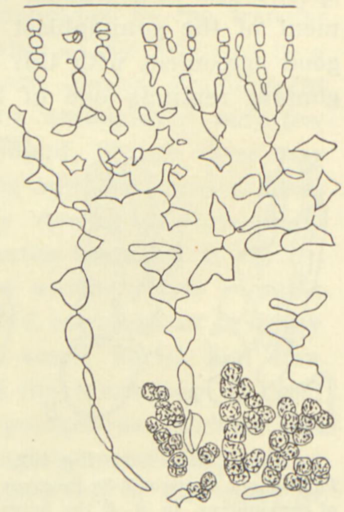


Fig. 495.
Phyllophora membranifolia. Portion of a transverse section of a ripe cystocarp. November. 390 : 1.

Phyllophora membranifolia occurs in all the Danish waters, from low-water mark or a little lower to at least 20 metres' depth. The greatest observed depths are 41 m (**Ns**) and 25.5 m (**Ke**). It grows on stones, in particular on the sides of boulders, more rarely on shells (*Astarte*). As mentioned above, it only attains a small size in the Baltic Sea proper (east of Gedser), and around Bornholm it is dwarfish, at most 5.5 cm in height (fig. 496); the specimens from this section of the Baltic were all sterile though they were collected in July, August (mostly) and November. The species has otherwise been recorded in the Batic Sea from Gotland (Krok, Svedelius) and from the east coasts of Småland and Skåne, but also here it was always sterile. Lakowitz did not meet with it in the Bay of Danzig.

The species may be met with lying loose on the bottom in the inner Danish waters, but it is much less common in this state than *Ph. Brodiæi* and the loose specimens are slightly different from the normal ones.

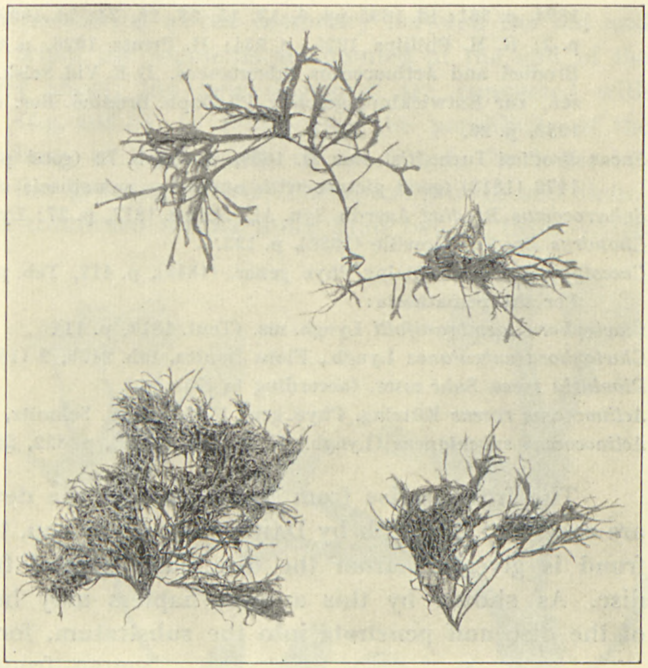


Fig. 496.
Phyllophora membranifolia. From the Baltic Sea. *A*, Gedser Rev 8.5m; *B* and *C* off Gudhjem, Bornholm. 5.5—11 m. August. Nat. size.

Localities. **Ns:** Jydske Rev ZQ, 24.5 m, several typical specimens but much overgrown with Hydroids and Bryozoa; eD, 41 m; aF, 31 m; eP, 24 m, (fig. 490); eQ, 27 m; eR, 27 m; eT, 34 m; XR, off Ørhage 5.5—13 m, small spec. In all localities except ZQ and aF only few and small specimens were met with. — **Sk:** Hanstholm, off Helshage, 5—13 m, on limestone, and off Roshage; eX north of Bragerne 16 m; eY, 15 m; YM, YN², Bragerne 2—10 m; Dana St. 2899, 14 m; SZ off Løkken 11 m; off Lønstrup, 7.3—13 m; Hirtshals, mole, Møllegrund 11—15 m and reef at Kjul, 5.5 m. — **Lf:** Nissum Bredning, XV Rønnen at Lemvig, ZY within Mullerne, 4.5 m; I, Venø Bugt; XT south of Jegind Ø, 6 m; MY Thisted Bredning; Sallingsund; Løgstør Bredning, Ejerslev Næse, Ejerslev Røn, off Fegge Klit, Amtoft Rev, Lendrup Røn. — **Kn:** Common everywhere on stony ground from Herthas Flak, 20—22 m, on the stony reefs from 1 m's depth. — **Ke:** Fladen, 16—18 m; Groves Flak, 19 m (F. Børgesen); Store Middelgrund, 25,5 m; Søborghoved Grund (OO); Vesterlands Grund; Gilleleje harbour. — **Km:** Sæby harbour; Several places south of Læsø; Gerrild Bay (Lyngbye). — **Ks:** Lysegrund; Hesselø (Lyngbye); RL, 15 m; NB, Havknude Flak; Briseis Grund; OS, Hastens Grund. — **Sa:** PA, near Albatros; KM, east of Øreflippen; PG near Hatterrev; Kyholm; PK, Norsminde Flak; Aarhus harbour. AH¹; Korshavn; Hofmansgave (Hofm. Bang, Lgb. a. o.); aY; AY, Ashoved. — **Lb:** Bogense; Prins Frederiks Grund, Vejlefjord; Kasserodde; OB, Stavrshoved; Fredericia harbour (C. M. Poulsen); Middelfart, Snoghøj; Fænø Sund; off Stenderup; DC, Aakrog Bugt; Linderum, 1 m. — **Sf:** CC, Hornenæs; UX; Svendborg Sund. — **Sb:** Elefant Grund; AG W. of Romsø; Kerteminde, bay and harbour; several places around Sprogø; Halskov, Korsør; between Knudshoved and Slipshavn; Kløverhage (XS); GZ near Egholm; UE and gB, Vresens Puller; gE Stokkebæks Flak; Lohals; fR off Hjortholm Skov, 21 m; DP N. of Onsevig; DT, off Magleby; fS east of Kjelsnor lighthouse. — **Sm:** CK near Staalgrund. — **Su:** BQ, CS, Ellekilde; Hellebæk; PX off Tibberup; off Skovshoved, 5 m; QC east of Saltholms Flak. — **Bw:** bY near Sønderborg; bV, near Sundeved; cD, cE, cF, dO south of Als; fT south of Ærø; UY, Vejsnæs Flak; DU south of Langeland; KU Schönheyders Pulle; KT, Gedser Rev. — **Bm:** QT, QG south of Flinterenden; QH, Falsterbo Rev; SD; QS, VG, QZ east of Møen. — **Bb:** Bay of Arnager; SQ, Broens Rev; SL off Allinge; off Gudhjem; Christiansø (C. Rosenberg).

2. Phyllophora Brodiæi (Turn.) J. Agardh.

J. Agardh, Alg. maris medit. 1842 p. 93, Sp. g. ord. Alg. Vol. II, 1. 1851, p. 330; Harvey, Phyc. Brit. Vol. I, 1846; pl. 20 (excl. var. β); Wille (1887) p. 79, figs. 66—69; Schmitz Actin. 1893; Darbishire

1894, p. 361; id. 1895 pp. 6, 13, 15, 23, 29, 34; id. 1899. Gomont Actinoc., Journ. de Bot. 1894, p. 2; R. H. Phillips 1925, p. 244; H. Printz 1926, p. 60; L. Kolderup Rosenvinge, Phyllophora Brodiæi and Actinococcus subcutaneus. D. K. Vid. Selsk. Biol. Meddel. VIII, 4. 1929; Hugo Claussen, zur Entwicklungsgesch. v. Phylloph. Brodiæi. Ber. deut. b. Ges., Bd. 47, 1929, p. 544; Kylin 1930, p. 26.

Fucus Brodiæi Turn. Hist. Fuc. II. 1809, p. 1, tab. 72 (good pictures), Hornemann, Flora Danica, tab. 1476 (1813) (good picture with numerous nemathecia on narrow sexual shoots).

Sphærococcus Brodiæi Agardh Syn. Alg. Scand. 1817, p. 27; Lyngbye Tent. 1819, p. 11, tab. 3.

Chondrus Brodiæi Greville (1830), p. 133.

Coccotylus Brodiæi Kützing Phyc. gener. (1843), p. 412, Tab. phyc. Bd. 19, Taf. 74. (1869).

For the nemathecia:

Chætophora membranifolii Lyngb. ms. (Tent. 1819, p. 11).

Chætophora subcutanea Lyngb., Flora Danica, tab. 2135, 2 (1834).

Rivularia rosea Suhr mscr. (according to Kützing).

Actinococcus roseus Kützing, Phyc. gen. 1843, p. 177, Schmitz, Flora 1889, Flora 1893.

Actinococcus subcutaneus (Lyngb.) K. Rosenv. (1893), p. 822, Schmitz Flora 1893.

The fronds arise from the basal disc the development and structure of which are described at length by Darbishire (1895, pp. 15—20). In young plants a single frond is given off from the disc, later several fronds may spring from the same disc. As shown by this author, hapters may be produced from the under face of the disc and penetrate into the substratum, for instance shells of bivalves. The young fronds are to begin with cylindrical but early become flattened above. The flattening may begin near the base or there may be a long cylindrical stem before the flattening begins. Some of the fronds represented in fig. 497 show narrowings, often occurring in the species but in this case probably not due to the influence of the winter. The ramification by dichotomy may begin in the first year, but often the first branching does not take place till the second year (fig. 498 *c*). Lateral ramification of the flat frond as in fig. 497 *c* only rarely occurs in the first year. Only one or two dichotomies are produced in one season. Adventitious shoots or proliferations are later often produced from the cylindrical stem or from the flat frond.

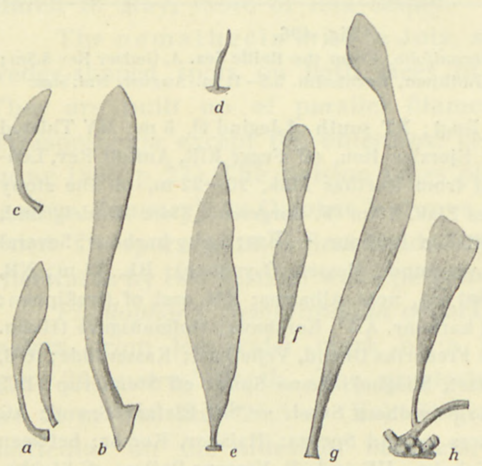


Fig. 497.
Phyllophora Brodiæi, young fronds, *a*—*c* from Holst's Banke north of Als, June; *d*—*h* from fR, Langelands Belt, August. 8 : 1.

The growth is arrested in winter (November to January). The young flat frond has then a growing zone in the upper margin of the frond or of each section of the frond. After the winter rest the growing zones resume their activity, and the difference between the old and the new frond is then very conspicuous, the first being darker, somewhat brownish, while the new segments are bright red. The growing margin may be long, and there is then only a feeble or no narrowing at the boundary between the old and the new frond (fig. 498 *b*, *c*); but when the segments are pointed at the end of the season, the growing zone is very short; the new segments are connected with the old ones by a narrow stalk (fig. 498 *a*). In both cases the periodicity of the growth is connected with a periodicity of the breadth of the frond, the latter becoming greatest in the middle of the growing period. The apical growth and dichotomy of the frond is usually not continued during more than two or three years. The growth then ceases and the upper portion of the flat frond is very often disorganised. This mode of growth occurs in particular in broad specimens reminding one of the arctic *f. interrupta* (fig. 488 *b*). In some cases new leaves arise as adventitious shoots from the cicatrized upper border of a flat frond (fig. 498 *b*, above in the middle, comp. HARVEY Phyc. Brit. pl. 20, fig. 3).

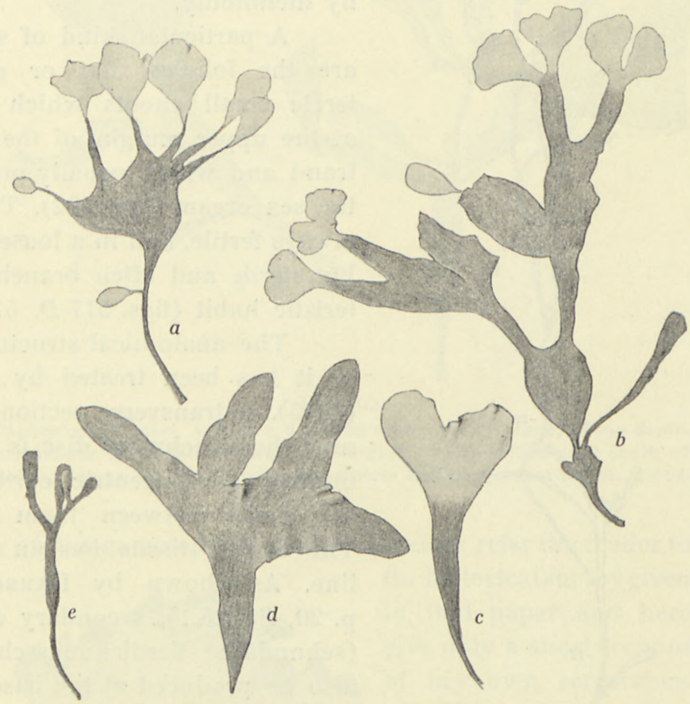


Fig. 498.
Phyllophora Brodiæi, fronds branched by dichotomy. *a* from Lille Belt, March. *b*, Fænø Sund, April. *c*, from UK, Langelands Belt, May. *d*, Store Belt, November. *e*, Busserev at Frederikshavn, December. *a*, *b*, *e* $^2/_3$ nat. size; *c* 2 : 1. *d* $^4/_3$ nat. size.

Besides the apical growth and dichotomy, a branching by adventitious shoots or proliferations arising at a lower level are very characteristic of the species. The proliferations become long shoots terete below, upwards gradually flattened and more or less divided by dichotomy; they arise from the margin or, not rarely, from the flat side of the frond (figs. 499, 502). Their number is less than in *Phyll. membranifolia*, sometimes only one, and they may be entirely wanting. When the branching by proliferations is much pronounced, the apical ramification is often feeble; the growth of the upper border ceases at an early period. The growth of the single proliferations sometimes endures only one year; the growth is then taken up again by the new proliferations that may cease to grow in the next year, and so on, and a series of generations of proliferations may thus be produced. This takes place particularly in specimens growing in the inner waters in deep localities where the water is agitated by the current but not by the waves. In the specimen pictured in fig. 499 at least

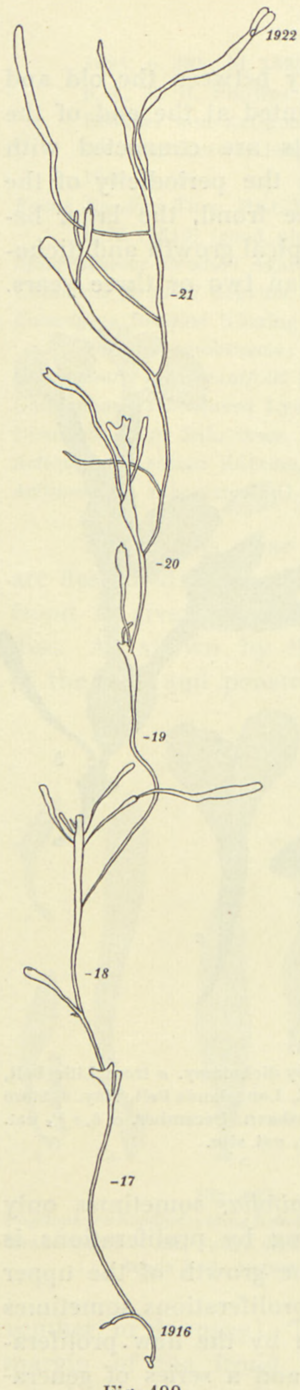


Fig. 499.
Phyllophora Brodiœi. Frond collected in June 1922 east of Hesteskoen NE of Als at 18—19 metres' depth. The oldest part of the frond has probably arisen in 1916. $^2/_3$ nat. size.

7 generations of shoots could be ascertained, undoubtedly representing an equal number of years. The specimens growing here attached to stones attained a length of 33 cm but had a very narrow frond, undivided or scarcely divided by dichotomy.

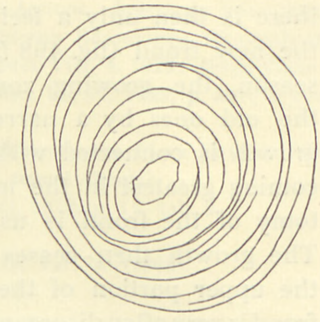


Fig. 500.
Phyllophora Brodiœi Transverse section of the stem near the holdfast.

A particular kind of shoots are the folioles, flat or nearly terete small shoots which arise at the upper margin of the leafy frond and which usually produce the sex organs (fig. 502). These shoots, however, are not always fertile, and in a loose form (*f. stellata*) similar shoots but sterile and often branched give to this form a characteristic habit (figs. 517 *D*, 518).

The anatomical structure will not be mentioned here, as it has been treated by Wille (1887) and Darbishire (1895). A transverse section of the stem of an older frond near the attachment disc is shown in fig. 500. There are a number of concentric cortical layers, partly incomplete, the limits between them often vanishing or merging. The central tissue has an elliptical outline. As shown by Darbishire (1895, p. 20, fig. 25,1), secondary cortical layers (sekundäre Verdickungsschichten) may also be produced at the base of branches, but they may further arise sometimes as local formations in the sexual shoots, as I, too, have observed. According to Darbishire, the young cells contain a single chromatophore. In the large cells in the interior of the frond several long ribbon-shaped chromatophores can be distinguished.

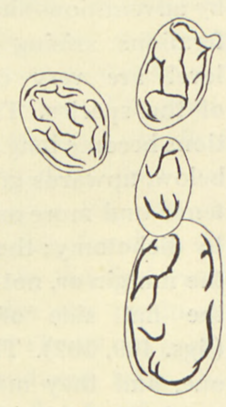


Fig. 501.
Phyllophora Brodiœi. Cells from the medullar tissue of leafy frond. 600 : 1.

According to H. Claussen the vegetative cells contain several small nuclei (1929, p. 546); the smaller cells of the cortex seem, however, to contain a single nucleus.

The reproduction of *Phyllophora Brodiœi* has been much disputed for more than a century. Turner, who described the species in 1809, interpreted the globular bodies situated on the upper border of the frond, or on particular small shoots, as the fructification of the species, but LYNGBYE as early as 1819 was in doubt whether this was really so. He suggested that they might possibly be some parasite, and since then these bodies, which were later named nemathecia, have been the subject of various interpretations and much discussion. I have recently published a special paper on this question (1929), in which I have shown that the nemathecium does not belong to a particular parasite (*Actinococcus*), but that it is the nemathecium of the much reduced sporophyte of *Phyllophora Brodiæi* growing on the gametophyte. I shall therefore refer the reader to the historical survey given in that paper and here give only a short account of my own researches.

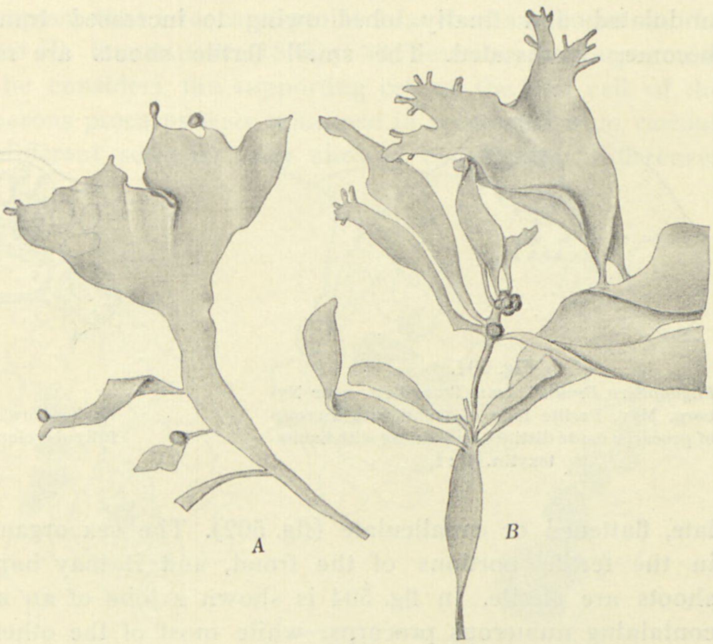


Fig. 502.
Phyllophora Brodiæi. *A*, from a dredging south of Als in June, 8.5 m's depth, nemathecia in leaflets, terminal or marginal. *B*, from 12 metres' depth off Ballen, Samsø in August; with nemathecia and new sexual leaflets. 1.8 : 1.

The sex organs occur in particular sexual leaflets situated on the upper border of the flat frond (fig. 502) or in a marginal zone of the upper segments of the frond (fig. 503 *A*). DARBISHIRE, who observed the sexual shoots, maintained that the species is diœcious, and it may perhaps sometimes be so, but the two sexes usually occur in the same plant and often in the same organ. When the upper border of the frond is fertile, it is much

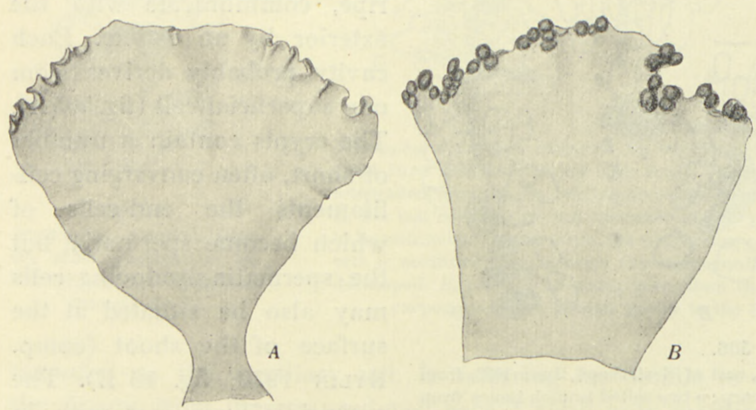


Fig. 503.
Phyllophora Brodiæi. Lille Belt, 18—19 metres' depth, June. *A*, upper end of frond with undulated fertile margin. *B*, similar with young nemathecia. c. 5 : 1.

undulated and finally lobed owing to increased transversal growth, and it also becomes incrassated. The small fertile shoots are narrow, nearly terete, angu-

Fig. 504.
Phyllophora Brodiæi, from Store Belt, near Nyborg, May. Fertile lobe of frond with a group of procarps made distinct by staining with hæmatoxylin. 47 : 1.

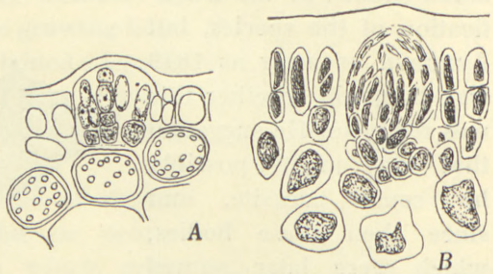


Fig. 505.
Phyllophora Brodiæi. Two antheridial crypts. *A*, not fully developed, June. *B*, ripe, partly emptied, August. 625 : 1.

late, flattened or canaliculate (fig. 502). The sex organs are irregularly distributed in the fertile portions of the frond, and it may happen that some of the small shoots are sterile. In fig. 504 is shown a lobe of an undulated margin of a frond containing numerous procarps, while most of the other lobes of the same margin were without procarps.

The antheridia are similar to those of *Phyll. membranifolia* (comp. Darbishire 1895, p. 29, 1899, p. 257, K. Rosenvinge 1929, p. 14). They are developed in small globular cavities in the sexual shoots and, when ripe, communicate with the exterior by an ostiole. Each cavity probably derives from one superficial cell (fig. 505 *A*). The crypts contain a number of short, often converging cell-filaments the end-cells of which become spermatia, but the spermatia-producing cells may also be situated at the surface of the shoot (comp. Kylin 1929, fig. 16 *E*). The antheridia were met with in the months of March and May to November.

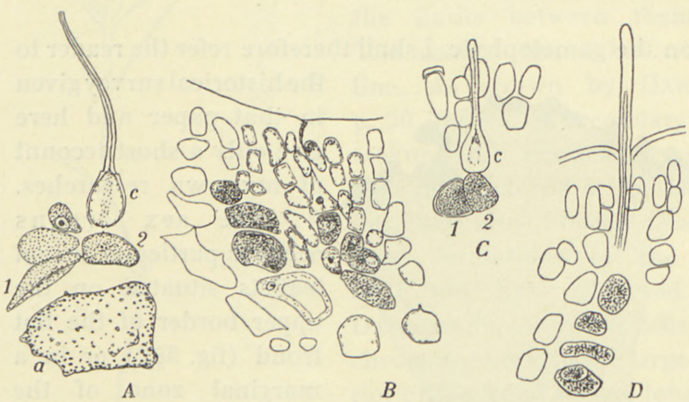


Fig. 506.
Phyllophora Brodiæi, from Lille Belt, east of Hesteskoen, June 1922, from frond with crenulated border. *A*, procarp; a two-celled branch issues from the first cell of the carpogonial branch; *a*, the auxiliary cell, *1*, *2*, *c*, the cells of the carpogonial branch. *B*, two procarps, that to the left without trichogyne. *C*, carpogonial branch isolated by pressure. *D*, protruding trichogyne, the base of which cannot be distinguished. 560 : 1.

The procarps are situated in the inner cortex. When fully developed they are composed of a tricellular carpogonial branch and a large supporting cell (Tragzelle Kylin) which becomes an auxiliary cell, but it may happen that two carpogonial branches are borne on the same supporting cell (fig. 508 *D*). Darbishire (1895, p. 33) describes the carpogonial branch as four-celled, but he considers the supporting cell as the first cell of the carpogonial branch. — Numerous procarps were examined in specimens from various localities and gathered at different seasons; they showed considerable differences and the great majority of the procarps were not completely developed. The procarps are easily recognizable by their abundant protoplasmic contents and their staining power with hæmatoxylin. The supporting cell is larger than the cells of the carpogonial branch; it must be regarded as the auxiliary cell. In referring for details to my paper of 1929 and to the figures from there reproduced here, I shall only mention the principal facts. The carpogonial branches are often only two-celled (fig. 507), and the last cell is most frequently not developed as a carpogonium but roundish like the other cells of the branch, also in the three-celled carpogonial branches. The best developed carpogonial branches were met with in May and June, when long, projecting trichogynes were often observed (fig. 506). But most of the carpogonia observed had an abortive

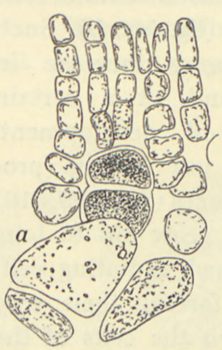


Fig. 507.
Phyllophora Brodiæi, from the same specimen as fig. 506. Tvo-celled carpogonial branch. 560 : 1.

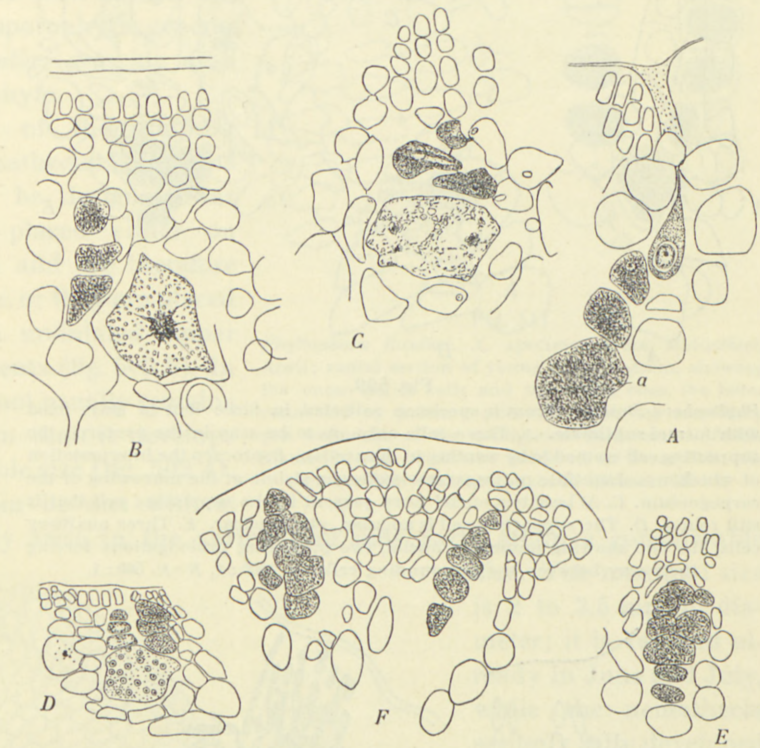


Fig. 508.
Phyllophora Brodiæi, collected by Dr. Henning Petersen at Ellekilde Hage, Øresund June 1910 and treated with Juel's solution. *A*, procarp; the carpogonium is attenuated towards the trichogyne channel but the trichogyne itself is wanting. *B*, the last cell has not the character of a carpogonium; the supporting cell seems to be uninuclear. *C*, the same, the supporting cell is plurinuclear. *D*, the supporting cell is multinuclear; it bears two carpogonial branches, but no carpogonium is developed. *E*, procarp showing more than the ordinary number of cells, without carpogonium. *F*, similar group to the left. *A*, *B*, 870 : 1. *C—F*, 480 : 1.

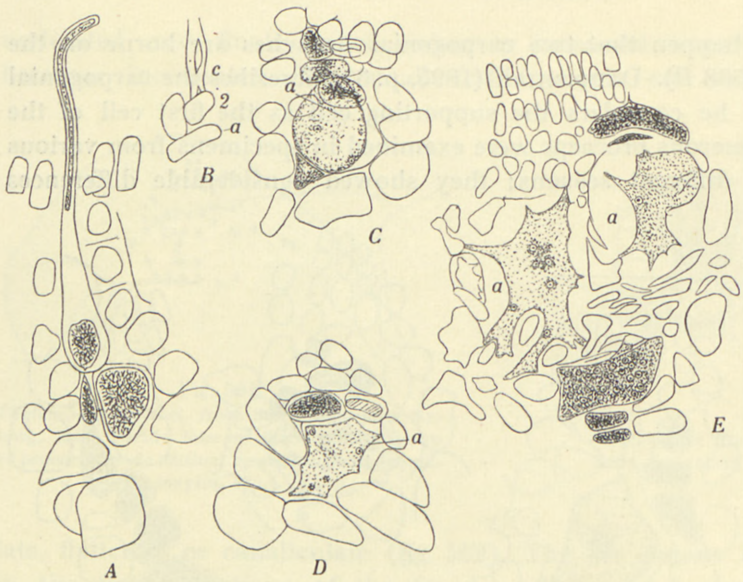


Fig. 509.
Phyllophora Brodiæi. From a specimen collected in Store Belt in May, fixed with formol-sublimate. *A.* Three cells only are to be seen in the procarp, the supporting cell seemed to be wanting in the section. *B*, procarp the interpretation of which was doubtful; no transverse wall was visible at the narrowing of the carpogonium. *C.* At least two nuclei were present in the supporting cell that is still round. *D.* The supporting cell is angular, plurinuclear. *E.* Three auxiliary cells, the two showing numerous nuclei, two producing prolongations forcing their way between the surrounding cells. *A*, 1000 : 1. *B—E*, 560 : 1.

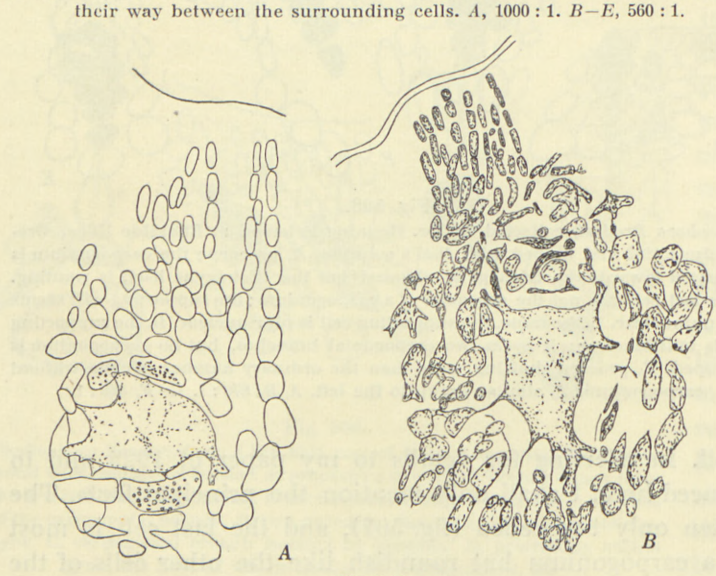


Fig 510.
Phyllophora Brodiæi. From Ellekilde Hage, Juel's solution. (Compare fig. 508). Auxiliary cells with protuberances. *A*, The protuberances penetrate between the surrounding cells. 625:1. *B*, more advanced stage. The protuberances have produced cells and cell-rows at their ends; some of these have begun to form a low tubercle, a young nemathecium. 390 : 1.

character (fig. 508). No spermatia were found adhering to the trichogynes and no other signs of a fertilization were observed. Furthermore, a transferring of a sporogenous, diploid nucleus from the carpogonium to the auxiliary cell could not be ascertained and I therefore concluded (1929) that it was uncertain whether or not a fertilization takes place in this species. The auxiliary cell, which originally seems to be uninucleate (comp. figs. 506 *B*, 508 *B*), later contains numerous nuclei (fig. 508 *D*). Such cells may increase in size and, at a certain stage of development, shoot out several protuberances (figs. 509, 510) which grow out to long branched radiating cell-rows forcing their way between the cells of the gametophyte and ending in nemathecial filaments. A globular body is then produced composed of radiating nemathecial filaments issuing from a system of more irregular cell-rows and containing in the middle a large central cell, the original auxiliary cell, from which they have all originated (Plate VIII figs. 1–3). These globular bodies have formerly by several authors (LYNGBYE, SUHR, KÜTZING, SCHMITZ, DARBISHIRE (1899)) been considered as a parasite (*Actinococcus subcutaneus* (LYNGB.) K. ROSENV., *Act. roseus* (SUHR) KÜTZ.), but have now turned out to be the much reduced sporophytic generation of *Phyllophora Brodiæi* growing as a parasite on the gametophyte.

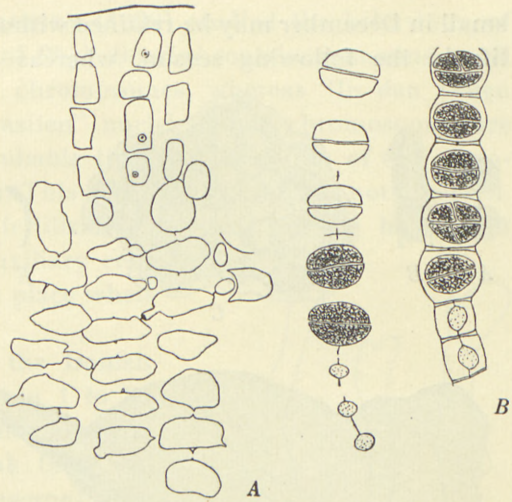


Fig. 511.
Phyllophora Brodiæi. *A*, specimen from Middelfart, April; radial section of young nemathecium, showing the outer sterile cells and the fertile ones, the latter connected by primary pits and partly by secondary pits with cells of the contiguous filaments. *B*, fertile filaments from specimen gathered in Store Belt. November 24th with sporangia in division 625 : 1.

The greater part of the globular bodies consists of nemathecial filaments and they can therefore be designated as nemathecia. They are placed either on particular sexual leaflets and are therefore often described as stipitate, or they are placed in great number in the undulated upper margin of flat frond segments (fig. 503 *B*). In the first case the fertile shoot usually remains short, but it may happen that it develops into a foliole of considerable size (fig. 502 *A*).

The nemathecia can be met with at all seasons; they usually arise in the spring and may early attain a considerable size. The maximal size is 2 to 3.5 mm in diameter; it is reached already in June and July, while the nemathecia are only fully developed in winter. The sporangia begin to ripen at the close of November, and ripe sporangia are met with in December to February. As the nemathecia occurring in winter are of different sizes and as nemathecia of considerable size are to be found in early spring, it is probable that some nemathecia (sporophytes) which are

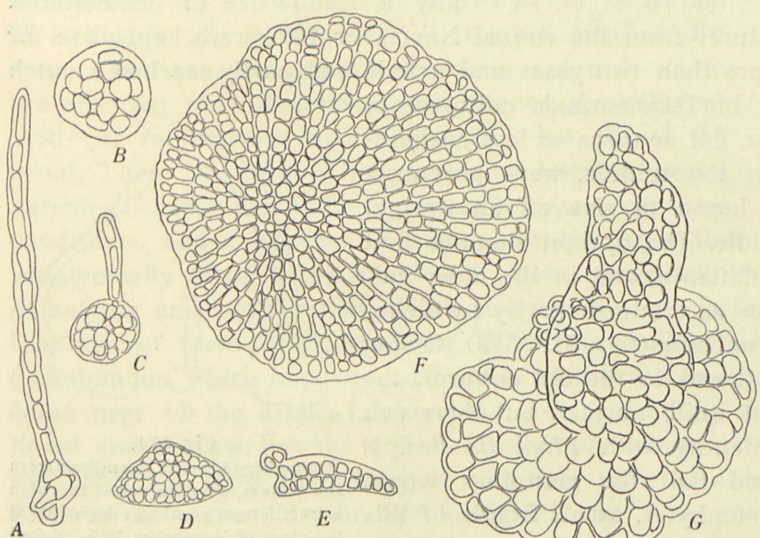


Fig. 512.
Germlings from tetraspores of *Phyllophora Brodiæi* sown in the beginning of December 1925. *A*—*B*, $3^1/_2$ months old, $^{22}/_3$ 1926. *C*—*F*, $6^1/_2$ months old, $^{29}/_6$ 1926. *G*, 7 months old, $^{8}/_7$ 1926. *E*, optical vertical section. *A*, *C*—*F*, 350:1. *B*, 410:1. *G*, 560:1.

small in December may be retained without producing tetrasporangia and continue their life in the following season, whereas most nemathecia perish in winter after the production of tetraspores. The 3 or 4 outermost cells in the nemathecial cell-rows are narrower than the other and remain sterile. It is remarkable that the young sporangial cells are sometimes connected with cells in the contiguous cell-rows by secondary pits (fig. 511 *A*). The fate of the nuclei transferred by the formation of these pits could not be followed. The sporangia are first divided by a transverse wall and later by two vertical or slightly inclined walls (fig. 511 *B*).

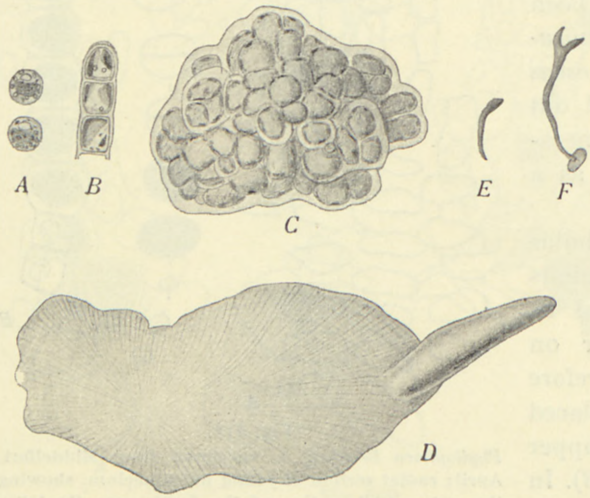


Fig. 513.

Phyllophora Brodiæi. Germlings from tetraspores sown in the beginning of December 1925. *A*, spores newly liberated. *B*, portion of filament from germling. *C*, eight months old germling, $^{14}/_{8}$ 1926. *D*, 14 months old germling with upright shoot springing near the border $^{10}/_{2}$ 1927, *E* and *F*, 20 months old germlings, $^{18}/_{8}$ 1927. *A—C*, 625 : 1. *D*, 70 : 1. *E—F*, 9 : 1.

The germination of the tetraspores was first observed by DARBISHIRE (1895); he found that the germlings were deep red bodies of various shape, filamentous, disc- or cushion-shaped, but they attained only a small size in his cultures. The germlings in my cultures from the end of November 1925 were kept alive for several months, up to more than two years and a half, and partly reached a much better development than in DARBISHIRE's cultures. In the best cultures orbicular, flat or more or less cushion-shaped discs, thickest in the middle, were produced, which after half a year began to give off an upright shoot, usually in the middle. The upright shoot is first terete but later becomes flattened, and in the older cultures ramification could be ascertained, partly by dichotomy, partly by lateral branching (figs. 513, 515). Owing to the unfavourable conditions in the old cultures, the germlings figured are not quite normal, but there can be no doubt of their identity with *Phyll. Brodiæi.* It must further be supposed that the germlings would have developed into gametophytes, as all fronds of this species are sexual plants, as far as we know.

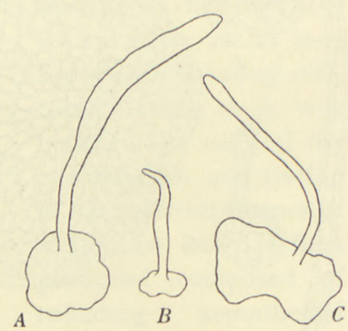


Fig. 514.

Phyllophora Brodiæi. Germlings from the bottom of a glass vessel in which a fructiferous plant was deposited at the close of November 1925, picked up $^{18}/_{6}$ 1927 (18 months old).

After the publication of my paper (1929) two authors have confirmed the general conclusions there advanced as to the relationship of *Actinococcus subcutaneus*, but they have both pointed out facts which suggest that a fertilization really takes place. HUGO CLAUSSEN (1929) studied the behaviour of the nuclei and found that the vegetative cells of *Phyll. Brodiæi* contain numerous small nuclei, about 2 μ in diameter, containing 4 chromosomes, whereas "In den Zellen des Karpogons [?] und im Gewebe des Parasiten" nuclei with 8 chromosomes are frequently to be found, which makes it probable that the formation of the sporophytic generation is preceded by a fertilization. This process however was not observed. Nor has KYLIN (1930, p. 26) observed the fertilization process, but he has found a carpogonium fusing together with an auxiliary cell, and he thinks that such a process only takes place when the carpogonium is fertilized.

Phyllophora Brodiæi is spread in all the Danish waters from the North Sea to Bornholm, from 1 to 36 metres' depth, attached to stones and sometimes to shells of bivalves. In the North Sea and Skagerak there are only few places where it thrives well (Bragerne); the frond is here fairly broad but only attains a height of 10 cm. It scarcely becomes higher in the northern Kattegat where it is much less common than *Ph. membranifolia.* In the inner waters it attains its best development and is often abundant. Its maximal height increases considerably, as will be seen from the following figures indicating the maximal heights observed in the respective waters: **Ke** 15 cm, **Ks** 17.5 cm, **Sa** 24 cm, **Lb** 34 cm, **Sb** 29 cm, **Su** 23. In the Baltic it is much smaller: **Bw** 11 cm, **Bb** 8 cm. Its appearance varies not only as to the size but also otherwise, according to the different mode of ramification and the varying breadth of the frond. There is, however, no reason to describe special varieties because the differences seem to depend on outer conditions, and I am not able to point out types that might be supposed to be genotypically distinct. As mentioned above, there are two modes of ramification: dichotomy and proliferation, which are usually both in function; but it may happen that one of them is predominant. When the ramification is chiefly or exclusively dichotomous, which happens particularly with broad fronds (fig. 498), the shape may come near to the arctic f. *interrupta*, characterized by the frond being alternately broad and narrow, but the typical f. *interrupta* hardly occurs in the Danish waters; the specimen most resembling it was met with in a bank south of Lyø, Lille Belt, in 22 metres' depth. Specimens of the type nearly exclusively branched by proliferations so extreme as that represented in fig. 499 are rare; they occur too in deep water; the great majority of individuals are intermediary between the two extremes. The specimens growing in exposed localities in shallow water have a firmer texture than those growing in deep water. In specimens growing in

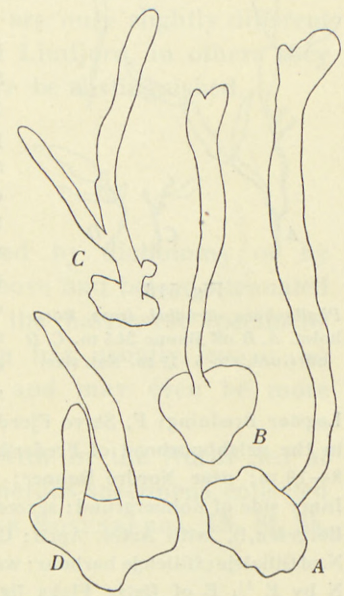


Fig. 515.
Phyllophora Brodiæi. 32 months old germlings from the walls and the bottom of the vessel mentioned in fig. 514. 64 : 1.

light localities the upper, exposed portions of the frond are green in summer. In the Baltic around Bornholm the dimensions are small, the individuals often dwarfish (fig. 516). They are usually sterile; specimens with small sexual shoots, however, sometimes occur. In a specimen from Rønne Banke imperfectly developed procarps were met with, and once I found, in a specimen collected in August, what seemed to me to be a young nemathecium.

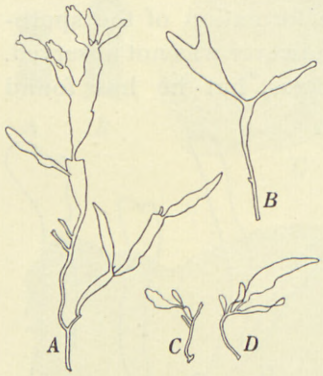


Fig. 516.
Phyllophora Brodiæi from Bornholm. *A*, *B* off Rønne 24.5 m. *C*, *D* off Gudhjem 5–11 m. Nat. size.

Localities: **Ns:** Not met with in a fixed state south of 56°48′ lat. N. aF, 31 m; dZ, 36 m; eS 25 m, scarce in all the localities. — **Sk:** Helshage and Roshage, Hanstholm 2—13 m; eX, north of Bragerne, 16 m; YN², S.E. of Bragerne 10.5 m, several broad specimens, 10 cm high, partly with nemathecia and new marginal leaflets; eY, 15 m; a small specimen; Hirtshals, near land c. 2 m, with Actinococcus 2 mm in diam.; August. — **Lf:** Found in several localities in the western Limfjord, but always without the basal part, so in most cases it must remain uncertain whether the species was growing on the locality in question. In most cases the specimens have certainly been lying loose on the bottom; they were usually found on soft bottom and bore no sexual leaflets. In two cases only did such leaflets occur and in one case Actinococcus. ZT, LX, LY and XV by Lemvig; LU, Thisted Bredning; XT; I; Sallingsund, several places, Th. Mortensen,!; MJ and LR, Løgstør Bredning; F, Skive Fjord. — **Kn:** Hirsholmene; Deget, Busserev, Frederikshavn, not abundant in the neighbourhood of Frederikshavn; Kummel Banke, (loose?) 38 m; several places near Læsø Trindel, 8—19 m; near Nordre Rønner; gL at Friis' Sten, south of Nordre Rønner, 2—3 m, abundant. — **Ke:** Inner side of Kobbergrund; several places 1—4½ miles of Fladens lightship, 15—30 m; Groves Flak (F. Børgesen,!), with Actin. April; GJ, Ostindiefarer Grund; OO, Søborghoved Grund and Vesterlandsgrund N. of Gilleleje; Gilleleje harbour; washed ashore by Gilleleje (Lyngbye). — **Km:** Usually loose; fixed on stones; N by E ¾ E of Østre Flaks light-ship 5½ miles (C. A. Jørgensen); ZC, XB and KF south of Læsø; Gjerrild Bay; Rygaard Strand (Lyngbye); KG near Anholt. — **Ks:** Grenaa harbour; FO, off Havknude; Jessens Grund; Hastens Grund; EJ, Lysegrund 4—5 m; D near Grønne Revle, 11 m; GF, Sjællands Rev; EH, Isefjord off Lynæs. — **Sa:** Common on stony ground at 1 to 15 m's depth from KM east of Øreflippen and PA, Albatros 7.5 m to Hofmansgave (ripe tetrasporangia in February (C. Rosenberg), aZ and OA, 7.5 m North of Fyn. — **Lb:** More than 20 localities, usually at depths from 6 to 15 m; off Stenderup and East of Hesteskoen (dH') at 19 m and at dQ south of Lyø at 22 m depth; at Linderum at 1 m depth. — **Sf:** Mostly loose; attached to stones at Hornenæs, 15 m; CV, Billes Grunde, 5.5 m; UV and UX North of Ærø; Svendborgsund, 7.5 m. — **Sb:** Numerous localities from Refsnæs to fS off the South end of Langeland at depths from 1 m (Kerteminde harbour) to 20 m. — **Sm:** CK, 9.5 m and HF West of Farø, 12 m. — **Su:** Common from BQ and CS near Ellekilde to QC and QD North of Saltholm, down to 13 m's depth, frequently with nemathecia. — **Bw:** Common from dL in Flensborg Fjord to KT, Gedser Rev and UM, Kadetrenden, at depths down to 25 m; deepest localities: UL, Øjet, 20 m; KX, more than 20 m, and UM, Kadetrenden, 25 m (small specimens). — **Bm:** Numerous localities. KS South of Falster, with nem.; VH South of Møen; several places East of Møen; VD, entrance to Bøgestrøm, with nem.; several places along the East coast of Sealand, partly with nem. — **Bb:** 14 miles SW ¾ S of Adler Grund light-ship, 30 m (C. A. Jørgensen); SF, Adler Grund c. 10 m (loose); SR, Rønne Banke, 15—16 m, on gravel and stones, with sexual shoots; YH, off Rønne 24.5 m; XZ, Davids Banke 10—29 m; off Gudhjem 5.5—11 m; off Svaneke; 3 miles SSE of Nexø, 21 m; Dueodde light-house in W 5¾ miles, 38 m; 5.5 miles NNE ½ W of Hammeren light-house, 35—40 m (C. A. J.); SV, North West Ground at Christiansø, 30—32 m.

Loose forms. *Phyllophora Brodiæi* very often occurs lying loose on the bottom in the inner Danish waters. It is able to keep living in this condition for a long time, growing continually in a sterile state, and it then usually takes a shape different from that of the typical species. Loose specimens occur in particular in the *Zostera*-associations and in other localities where the water is not too agitated by waves or by currents. They sometimes occur in great quantities in company with other loose Algæ. The loose forms are very variable, and distinct limits between the different forms cannot be drawn. In some cases they are only slightly different from the typical form, for instance those occurring in the Limfjord, in others they have a characteristic shape. The following types may here be distinguished.

f. *concatenata* LYNGB. (1819), p. 11.

Areschoug, Phyceae, 1850, p. 83, tab. III A.
β, elongata Hauck Meeresalg., p. 141.

Elongated often intricate frond repeatedly branched by dichotomy or by proliferations, the leafy portions lanceolate or bifurcate, above and below attenuated in cylindrical parts (fig. 517 *A*). The breadth is variable, the narrowest specimens merge imperceptibly into the following form. This form has usually few or no marginal shoots, but such shoots may sometimes occur, and may even be more numerous than in ARESCHOUG's figure.

Very common in the inner waters, but also met with in the North Sea at Blaavandshuk, in the inner waters in particular in **Sa** (numerous specimens collected at Hofmansgave by HOFMAN-BANG, LYNGBYE and CAROLINE ROSENBERG), **Lb**, **Sf**, **Sb**, **Sm** and **Su**.

f. *filiformis.*

Frond cylindrical or here and there a little flattened, mostly branched by proliferations. It occurs in a robuster form, the cylindrical part of which is about 0.5 mm in diameter while the flat expansions are usually only 1 mm broad (fig. 517 *B*), and in a thinner form with a threadlike frond. The finest specimens are sometimes so thin that they are only $^1/_6$ mm thick and almost without flat expansions, and one would therefore be inclined to doubt that they belong to the form-cyclus of *Phyllophora Brodiæi* if other specimens from the same gathering did not offer intermediate forms connecting them with less aberrant forms. Moreover, even the finest specimens may be infested by *Ceratocolax Hartzii*, which is a specific parasite of *Phyllophora Brodiæi* (fig. 517 *C*). In its typical form it is only found in **Sf** and **Bw**.

Localities: **Sf:** Højen at Faaborg, between broad-leaved Zostera, very thin; DZ, Egholms Flak at Mørke Dyb, with Zostera. — **Bw:** cF south of Kegnæs lighthouse.

f. *stellata.*

Phyllophora parvula Darbishire ex p. (1895) fig. 10, 6—8.

The proportionally small flat frond bears at the top a bunch of radiating small, narrow, undivided or forked shoots. These shoots are similar to the sexual shoots in the normal plants but are sterile. They remain for the most part short, but some of the shoots in a bundle may grow out and develop into a long shoot like the mother shoot and bear a similar bunch of short shoots at the top (figs.

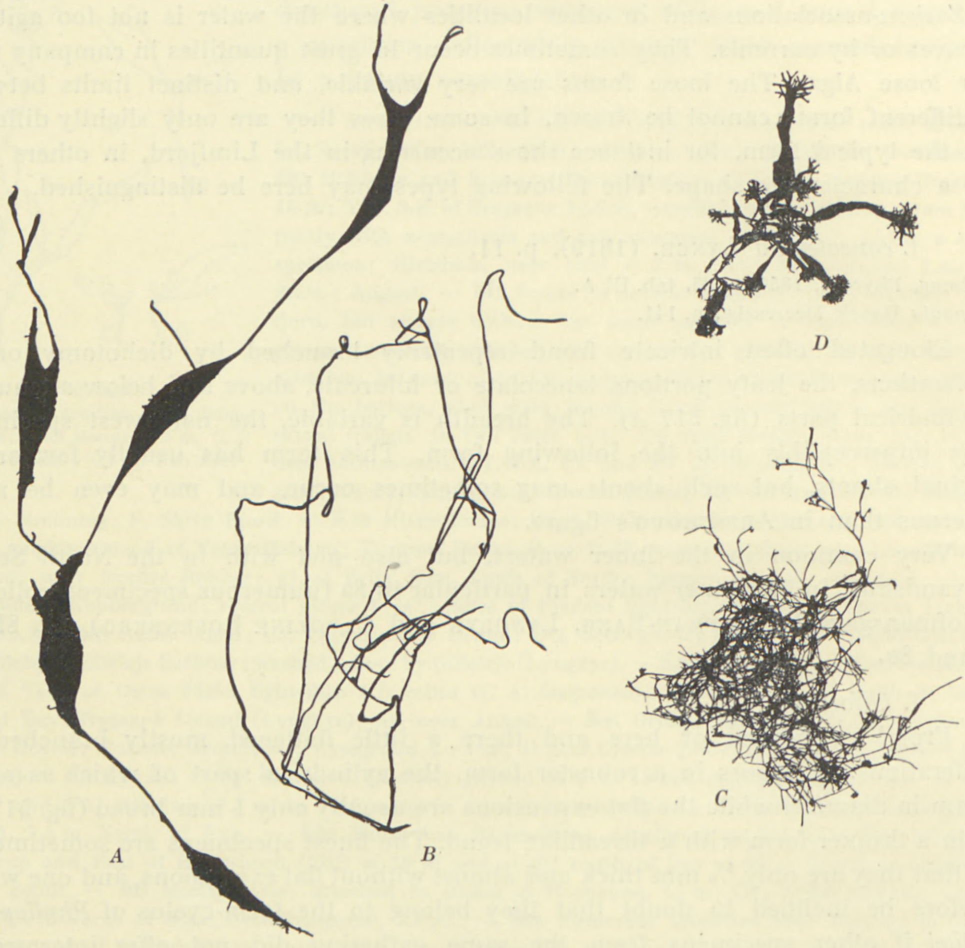


Fig. 517.
Phyllophora Brodiæi loose forms. *A*, f. *concatenata*, Store Belt. 3/4 nat. size. *B*, f. *filiformis*, at Kegnæs south side of Als, 3/4 nat. size. *C*, f. *filiformis* very thin, infested by *Ceratocolax Hartzii*, dredged near Faaborg. Nat. size. *D*, f. *stellata*, from ZC south of Læsø. Nat. size.

517 *D*, 518). This form is analogous to the f. *stellata* of *Chondrus crispus*, (comp. p. 505). The radiating shoots are sometimes repeatedly forked, and when, as will sometimes happen, they are partly reflexed, the plants may remind one of f. *uncinata* of the said species. Some of the specimens referred by Darbishire to *Phyllophora parvula* (see above), belong to this form, while the other figured specimens probably represent other reduced loose forms of *Phyllophora Brodiæi*.

Localities: **Kn:** Kummel Banke 38 m. — **Km:** ZC and EZ south of Læsø; 6 miles SSW ½ W of Læsø Rendes lightship 8 m (C. A. J.); BK, Tangen. — **Sa:** East side of Wulff's Flak; AO; Endelaves SE Flak, 7.5 m; Fyns Hoved in E ¾ N 5½ miles. — **Sf:** fV, south side of Svelmø, 4 m; — **Sb:** fP, E of Hov light-house, 5.5 m. — **Bw:** fU, south side of Ærø, 7 m.

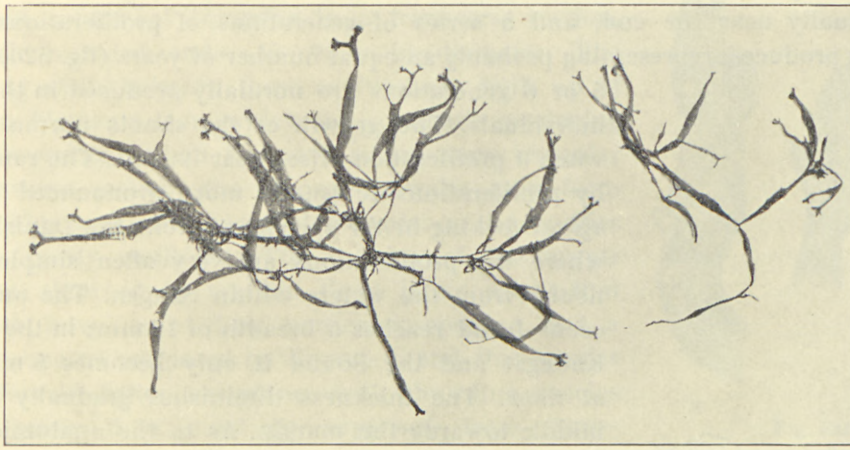


Fig. 518.
Phyllophora Brodiæi f. *stellata*. South of Ærø. 2 : 1.

3. Phyllophora epiphylla (Fl. Dan.) Batters.

Batters, A Catalogue of the British Marine Algæ, 1902, p. 65.
Fucus epiphyllus O. F. Müller, Flora Danica, Tab. 705. 1777. (from Norway).
Fucus prolifer Lightfoot, Fl. Scot. II, p. 949, tab. 30. 1777.
Fucus rubens Good. et Woodw. Trans. Lin. Soc. III, 1797, p. 165.
Chondrus rubens Lyngb. Tent. p. 18.
Phyllophora rubens (G. & W.) Greville Algæ Brit. p. 135, pl. 15; Harvey Phyc. Brit. II, Pl. 131, (1849); J. Agardh, Sp. g. o. II, I p. 331, (1851); Kützing Tab. phyc. IX, tab. 76, (1869); Buffham, Antherid. (1893), p. 292, pl. XIII, fig. 5; Schmitz, Actinoc. 1893, p. 399 ff.; Darbishire (1894), p. 369, id. (1895), pp. 4, 7, 12, 21, 28, 30, 33, 34, 36).

The fronds arise from a basal disc that, according to Darbishire, may be 5—15 mm in diameter and up to 1.5 mm thick. The lowermost portion of the frond is cylindrical, but this stemlike portion may be extremely short; when it is more developed it may give rise to a considerable number of branches that take a similar appearance as the primary frond (fig. 519 *B*). The shoots gradually expand in a membranaceous linear frond which grows by the activity of an apical meristeme

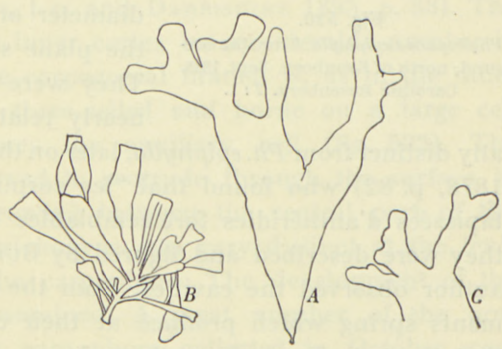


Fig. 519.
Phyllophora epiphylla. *A*, frond dredged off Lønstrup, Skagerak. *B*, lower portion of frond from the same locality. *C*, upper portion of frond dredged in the North Sea 15 miles off Hanstholm lighthouse. *A*, *C* ½ natural size. *B* natural size.

and may remain simple or branch by dichotomy. Sometimes the ramification is lateral as in fig. 519 *A*, C, which may perhaps be due to the checking of one of the products of the dichotomy. Besides this apical ramification a branching by proliferations regularly takes place. The latter, one or more, arise from the plane surface of the frond, usually near the end, and a series of generations of proliferations is consequently produced, representing probably an equal number of years (fig. 520). At least 5 or 6 generations are normally produced in the Danish individuals. The growth of the shoots normally ceases when a proliferation arises near its end. The ramification by proliferations is usually more pronounced than the apical forking in the specimens from the Danish waters, where the proliferations are very often simple, in particular from the waters within Skagen. The membranaceous frond reaches a breadth of 10 mm; in the southern Kattegat and the Sound it only becomes 5 mm broad at most. The thickness diminishes gradually from the middle towards the margin. As to the anatomical structure of the frond reference may be made to Darbishire's paper (1895, p. 12). As shown by this author, small interstitial cells are wanting between the medullary cells. The shoots are often furnished with a midrib in their lower part. It is formed by local thickening of the cortex, produced by activity of the outer cortical layer on both sides (comp. Darbishire l. c. p. 12).

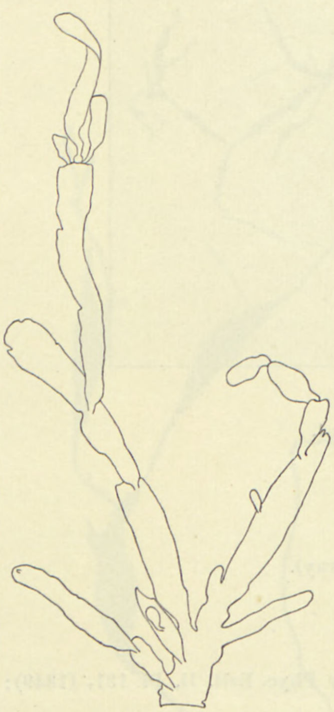


Fig. 520.
Phyllophora epiphylla. From the Øresund; north of Kronborg. Sept. 1848. Caroline Rosenberg. 2 : 1.

The antheridia are produced in small androphores on particular male specimens. The androphores are spherical or subspherical bodies, about 0.5 mm in diameter or a little more, borne on a short pedicel on the plane surface of the frond near the border (fig. 521). They were first pictured by Derbès et Solier[1] in the nearly related *Ph. nervosa* which is probably not specifically distinct from *Ph. epiphylla*, later on they were briefly mentioned by Thuret (Et. phyc. 1878, p. 82) who found that "les corpuscules males sont contenus dans des cryptes tapissées d'anthéridies fort semblables à celles du *Gracilaria confervoides*". In 1883 they were described and figured by Buffham (1883, p. 292, pl. XIII, figs. 5—7). This author observed the cavities, from the walls of which numerous tufts of thin filaments spring which produce at their extremities the spermatia, and he presumed that these bodies escape through one common issue at the top of the androphore (comp. l. c. fig. 7). My observations on the structure of the androphores however, are, not in accordance with those of Buffham. A vertical section of an androphore shows a layer of cavities or crypts covering the whole surface of the globular body

[1] Ann. sc. nat. III. S. tome 14 p. 278, pl. 37 figs. 10—11, 1850.

and surrounding a globular parenchymatous medullary tissue (fig. 521). This parenchymatous columella seems not to have been observed by BUFFHAM, but it has been distinctly represented by DERBÈS et SOLIER (l. c. fig. 10—11). The crypts are deep, 120—150 μ, nearly prismatic but somewhat irregular in a transverse section, and with rounded ends, 45—63 μ in diameter. The separating walls between these cavities are built up of very thin filaments from which the spermatia producing filaments spring. When the cavities are more irregular in transverse section, the separating walls may form folds in the cavity like incomplete septa, or the cavities may be partly confluent. The ostioles of the crypts were not observed by me but there is no doubt that the latter have each their particular opening, not a common one as supposed by BUFFHAM, and this species is therefore in better accordance with the other species of the genus than must be supposed from BUFFHAM's representation. The spermatia are very small, about 4 μ long, 2 μ broad; one nucleus was easily recognisable in the dried material. The antheridia were met with in September (Kn and Su). According to KYLIN (1907, p. 125) antheridia-bearing specimens collected in May are present in the Riksmuseum at Stockholm.

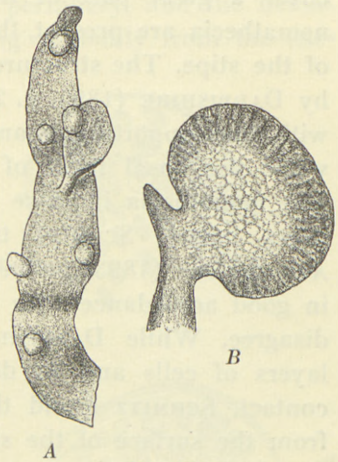


Fig. 521.
Phyllophora epiphylla. A, male specimen, September 5 : 1. *B*, vertical section of androphore. 30 : 1.

The procarps are developed in particular globular carpophores which have a similar position to that of the androphores. To begin with they are like these globular, sessile or furnished with a very short stalk but early become beset with anastomosing crests (comp. HARVEY, l. c. and DARBISHIRE 1895, p. 33). The procarps arise in the inner cortex in considerable number in each carpophore. The carpogonial branch is, as in the other species of the genus, three-celled and borne on a large cell that probably becomes the auxiliary cell (fig. 522). The trichogyne was observed to protrude through the surface in some cases; the narrowing between the ventral part of the carpogone and the trichogyne was very distinct at the level of the surface of the carpophore. The development of the cystocarp was not examined. A great number of the procarps observed in a carpophore collected in October were not fully developed and many of them would probably never have reached maturity. Carpophores with procarps were observed in September and October, cystocarps in winter (November to March); as late as May cystocarps may be met with but more or less empty.

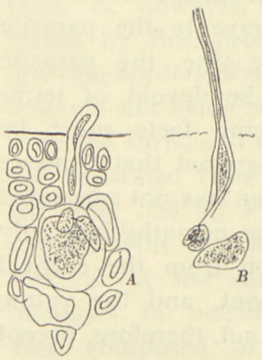


Fig. 522.
Phyllophora epiphylla. Procarps. *A*, with a young, *B*, with a fully developed carpogonium. 390 : 1.

The nemathecia are borne on the short stipe of peltate leaflets dispersed on the surface of the frond of separate asexual plants. They are flat broad bodies that cover a great part of the stipe, in a number of two or more. When several nemathecia are present, they may meet and jointly cover a great part of the surface of the stipe. The structure of the nemathecia has been well described and pictured by DARBISHIRE (1895, p. 28) who ascertained that the nemathecium is only connected with the supporting organ in the middle where it has arisen from the cortical tissue, while the basal layer of the nemathecium is for the rest appressed to the frond. The nemathecia increase at the margin by the formation of tangential walls. Two years before, SCHMITZ treated the nemathecia of this Alga in his paper on *Actinococcus* (1893, p. 399 et sequ.). DARBISHIRE's statements are in many respects in good accordance with those of SCHMITZ but as to the basal layer the two authors disagree. While DARBISHIRE describes this layer as consisting of one or two layers of cells and as distinct from the surface of the frond with which it is in contact, SCHMITZ found that the growing border of the nemathecium is separated from the surface of the supporting frond by a slit. At a certain distance from the margin, the basal layer appears in contact with the surface of the frond with which it becomes closely united, the cells of the basal layer giving off prolongations toward the superficial cells of the frond with which they are said to fuse, with the result that the slit entirely disappears, and finally almost all the superficial frond-cells are united with one or more cells of the basal layer, and the arrangement of the cells of the latter becomes very irregular. This fusing process takes place, according to SCHMITZ, even at the insertion of very young nemathecia and the author concludes from this that the nemathecia of this and some related species are particular parasitical algæ growing on the surface of the fronds of *Phyllophora* and fusing with the presumed host-plant through cell-fusions. SCHMITZ gave to the parasite the name of *Calacolepis incrustans.* If this interpretation were true, the parasite would only attack the asexual plants and these would then be devoid of tetrasporangia. As this is very improbable, particularly convincing facts must be demanded for supporting such an interpretation. It must be regretted that SCHMITZ has given no drawings illustrating the fusing process. DARBISHIRE has not succeeded in observing it (1894, p. 369); he declares (1895, p. 28) that the nemathecium only is in connection with the stipe in the place where it has arisen from the cortical cells. In this place the cortical cells first divide and grow out, and the young nemathecium thus formed breaks forth from the cortex; he can not, therefore, accept the view of SCHMITZ.

I, too, have not succeeded in observing the fusions recorded by SCHMITZ. In specimens collected in September the formation of the nemathecia is easily observed. In the youngest stages a small group of cells situated just within the surface are seen dividing and extending outwards, causing a vaulting and distending of the cuticle. This distending early involves a bursting of the cuticle, and the active cells protrude, surrounded by their thin special membranes (fig. 523 *B, C*). The bursting of the cuticle usually takes place in the middle, and the borders of the old cuticle are then later found surrounding the base of the young nemathecium (fig. 523 *D*). In other cases the bursting seems to take place at the periphery, and the nemathecium is then covered by a calotte of cuticle originating probably from the surface of the stipe (fig. 523 *E*). In the young stages the arrangement of the cells may be rather irregular; sometimes a single cell is seen to be more active and rich in cell-contents than the others, and producing a great part of the cells of the excrescence (fig. 523 *A*). The diameter of the quite young nemathecia is small, corresponding only to the diameter of a very small number of cortical cell-rows, but the diameter early begins to increase, the marginal growth taking place by vertical division of the marginal cells. The insertion of the nemathecium is, however, not enlarged by this process, the growing borders of the nemathecium not being connected with the surface of the frond but separated from it by a slit (fig. 523 *E*, *F*) or in contact with it. The nemathecium at the same time increases in height and is then composed of parallel or radiating filaments which later, in winter, produce tetrasporangia. As mentioned above, I have never seen a fusing process like that described by SCHMITZ; at all events it did not take place in the younger stages such as those represented in fig. 523. From the above it must be concluded that the nemathecia are the true organs of *Phyllophora epiphylla* and do not belong to a parasite. The name of *Colacolepis incrustans* must therefore be abandoned.

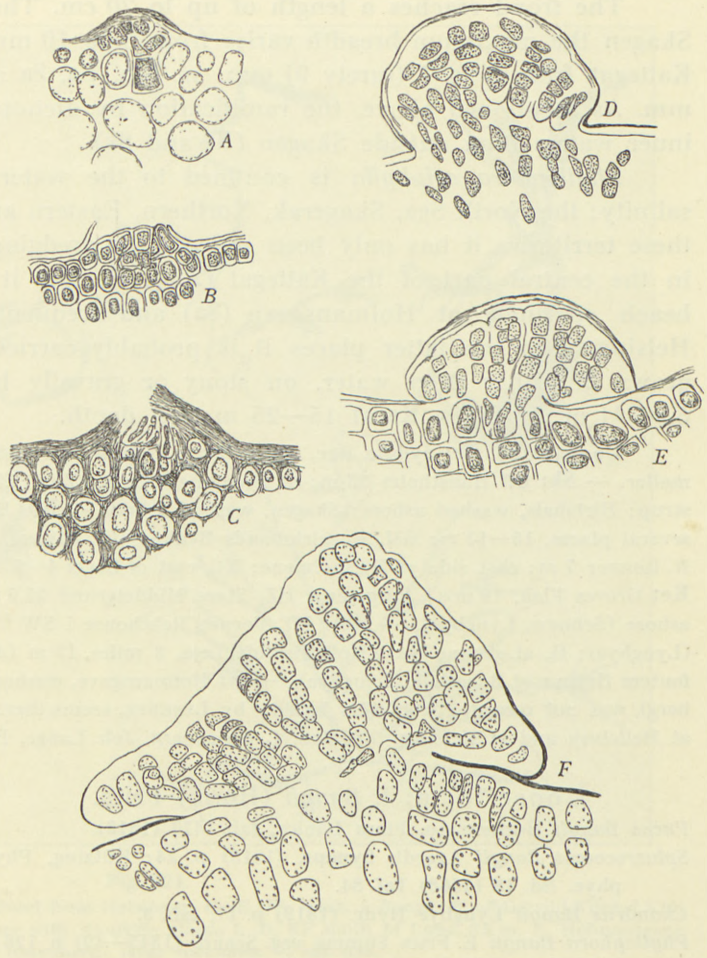


Fig. 523.
Phyllophora epiphylla. Young stages of nemathecia in September. 625 : 1.

The sporangia form long chains in the nemathecial filaments; only the ultimate cell is sterile, as shown by Darbishire (1895, p. 28, fig. 36). As late as April I found sporangia partly divided into four cells, partly only divided by a transverse wall; they measured 9—14 × 6—7 μ (9 × 7 to 14 × 6 μ).

The frond reaches a length of up to 20 cm. The breadth is variable; outside Skagen the maximum breadth varies from 5 to 10 mm, in the northern and eastern Kattegat from 4 to 7 (rarely 9) mm, in **Km**, **Ks**, **Sa** and **Su** from 2 to 4 (rarely 5) mm. As mentioned above, the ramification by dichotomy is less pronounced in the inner waters than outside Skagen (**Ns** and **Sk**).

Phyllophora epiphylla is confined to the waters with a comparatively high salinity: the North Sea, Skagerak, Northern, Eastern and Southern Kattegat. Outside these territories it has only been collected by dredging in one place (one specimen) in the central part of the Kattegat (**Km**). Further it has been found loose on the beach sparingly at Hofmansgave (**Sa**) and frequently in the Øresund north of Helsingør; to the latter places it is probably carried from the Swedish coast. It grows in rather deep water, on stony or gravelly bottom, in **Ns**, **Sk** and **Kn** in 5.5—41 m depth, in **Ke** at 15—25 metres' depth.

Localities. **Ns:** Jydske Rev, eD, 41 m; eC, 26 m; eO and eP off Agger; eR; eT; XR off Klitmøller. — **Sk:** Off Hanstholm 13 m; at Bragerne, 10.5 m; ZK^1, 7.5—9.5 m and ZK^6 11.3—13 m off Lønstrup; Hirtshals, washed ashore; Skagen, washed ashore. — **Kn:** Herthas Flak, 19—22 m; Læsø Trindel, several places, 15—13 m; GM, Engelskmands Banke; UB, east of Nordre Rønner, 9—11.5 m; north of N. Rønner 7 m; east side of Hirsholmene; XG, east of Deget 4—5.5 m; Frederikshavn (Schmidt 1863). — **Ke:** Groves Flak, 19 m (!, Børgesen); HZ, Store Middelgrund 25.5 m; Gilleleje and Nakkehoved, washed ashore (Schouw, Lyngbye). — **Km:** HT, Fornæs lighthouse i SW 5/8 W 7 miles, 16 m. — **Ks:** At Hesselø (Lyngbye); D, at grønne Revle; off Tisvilde Leje, 3 miles, 15 m (A. Otterstrøm); ad littus Vejbye prope fontem Helenæ et Raageleje (Lyngbye). — **Sa:** Hofmansgave, washed ashore (Hofm. Bang, Caroline Rosenberg), was not recorded from this locality by Lyngbye, seems therefore to be rare. — **Su:** Washed ashore at Hellebæk and at Helsingør (Ørsted, C. Rosenberg, Joh. Lange, Børgesen, !).

Loose form: f. *Bangii* (Horn.) Fries.

Fucus Bangii Hornemann, Flora Danica, tab. 1477 (1813).
Sphærococcus Bangii Agardh Synops. (1813) p. 24; Kützing, Phyc. gen. (1843) p. 410, Taf. 59 II, Tab. phyc. Bd. 18 (1868) Taf. 84.
Chondrus Bangii Lyngbye Hydr. (1819) p. 17, tab. 3.
Phyllophora Bangii E. Fries Summa veg. Scand. (1845—49) p. 126; Darbishire (1895).
Rhizophyllis ? *Bangii* J. Agardh. Sp. g. o. II.1 p. 223. (1851).

This pretty little alga, characterised by its much incised frond, was discovered by Hofman Bang at Hofmansgave at the North coast of Fyn, where it is frequently found washed ashore and from which locality innumerable specimens have been distributed, in particular by Hofman Bang and by his foster-daughter Miss Caroline Rosenberg. Lyngbye referred it to the genus *Chondrus* and described a fructification consisting in "tubercula subglobosa 4-granulata in substantia frondis remote et inordinate sparsa". This supposed fructification, however, does not belong to this Alga but is due to some alien organism, probably germinating spores of *Furcellaria* *fastigiata*, which frequently occur on this substratum (comp. KÜTZING, Phyc. gen. Taf. 59 II). The only later author who has considered them as tetrasporangia is J. AGARDH who on this basis, though with doubt, referred the Alga to the genus *Rhizophyllis*. E. FRIES transferred it to the genus *Phyllophora*[1], where it has since had its place, and with which genus it agrees well in the anatomical structure.

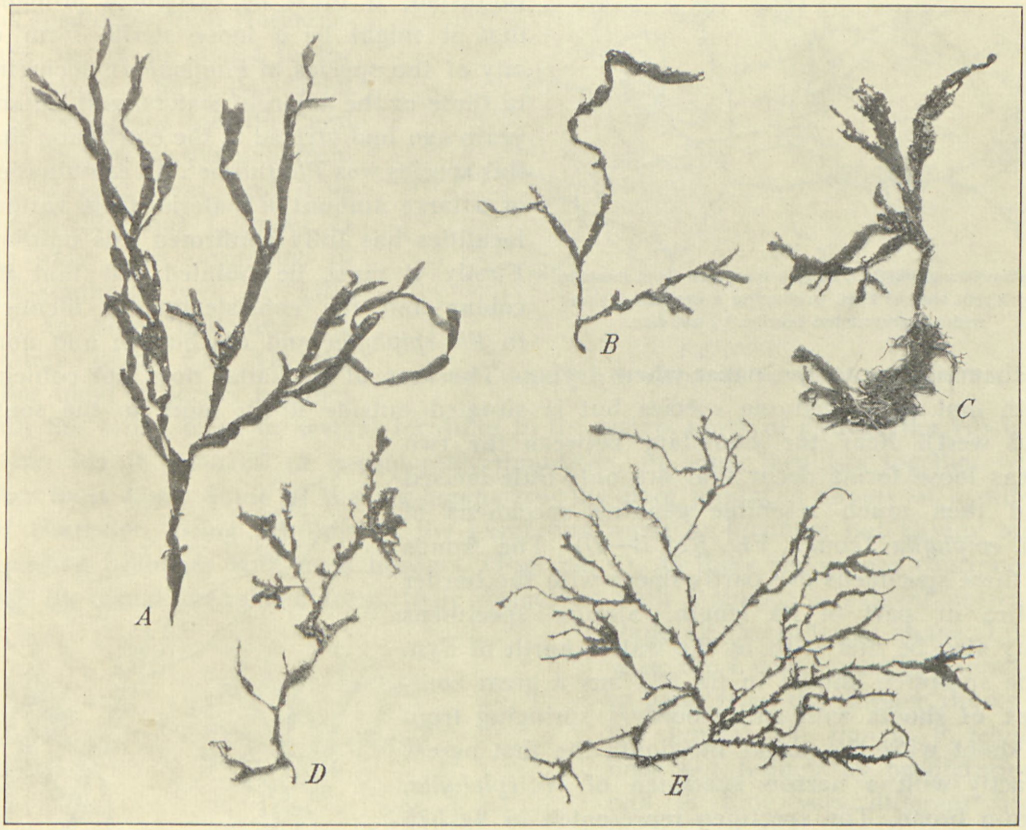


Fig. 524.
A, *Phyllophora epiphylla*, typical narrow frond from Helsingør. *B—E*, *Ph. epiph.* f. *Bangii*. *B*, off Gerrild Klint, 7.5 m. *C*, Silderøn south of Læsø, 2—4 m, together with *Ahnfeltia plicata* f. *D*, KF south of Læsø, 6.5 m. *E*, Hofmansgave (Caroline Rosenberg), large specimen. 6/7 nat. size.

The plant has always been found loose, and reproductive organs have never been found.

During my dredgings in the Danish waters I have met with this Alga in numerous localities in the inner waters where the water is comparatively little agitated, on sandy bottom, very often in company with *Zostera marina*, entangled between its

[1] HAUCK, Meeresalg. p. 144 cites JENSEN as author of the combination *Phyllophora Bangii*, owing to the fact that he has only known it from Rabenhorst's Alg. Europ. exsicc. No 1299 where TH. JENSEN has communicated it with FRIES' name.

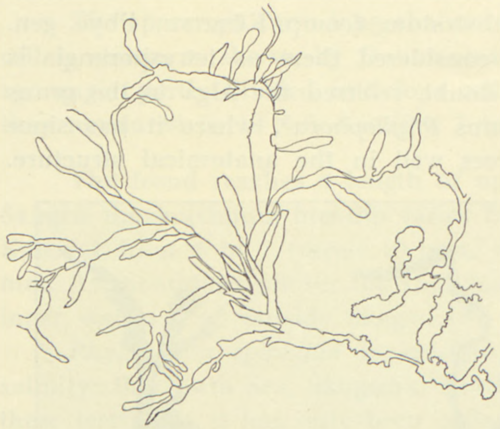


Fig. 525.
Phyllophora epiphylla f. *Bangii*, specimen from Baaring Vig, North side of Fyn, producing a branched shoot without crenulated border. 1/2 nat size.

rhizomes and together with various other loose Algæ. As it has been found only in the inner Danish waters and the adjacent part of the western Baltic Sea and, according to J. Agardh, at the coast of Bohuslän, it must be extremely probable that it might be a loose sterile form of any of the species of *Phyllophora* occurring in these or the adjacent waters, and I many years ago had arrived at the conviction that this species was *Ph. rubens*[1]. An examination of a large amount of material from various localities has fully confirmed this opinion. Firstly it must be pointed out that the colour and the consistency are identical in *Ph. epiphylla* and *Ph. Bangii*; and none of them adhere to the paper when drying. The area of the latter does not coincide with that of the genuine species but is situated outside it (ɔ: more to the south and west). Near the boundary between the two areas loose forms occur that are only little incised and then much resemble genuine specimens of *Ph. epiphylla* (comp. Fig. 524 *B—D*). The fronds of these specimens are partly linear with the border entire in part of its length. Similar specimens may also be met with in the waters north of Fyn. The specimen shown in fig. 525 has a great complex of shoots with entire borders springing from a shoot with the usual incisions; the first agrees exactly with a narrow specimen of *Ph. epiphylla*, 1 mm broad. The specimen represented in fig. 526 is also very instructive; it shows the proliferation characteristic of the species and a feeble mid-rib, and further the linear segments of the frond with border partly entire partly more or less incised. In the specimens agreeing with the typical *Chondrus Bangii* Lyngb. the broader parts of the frond are always present but are usually shorter and provided with feebler or deeper incisions, and a midrib is never present. Fig. 524 *E* shows a well developed specimen of this form; some of the lateral shoots are narrow without broader parts.

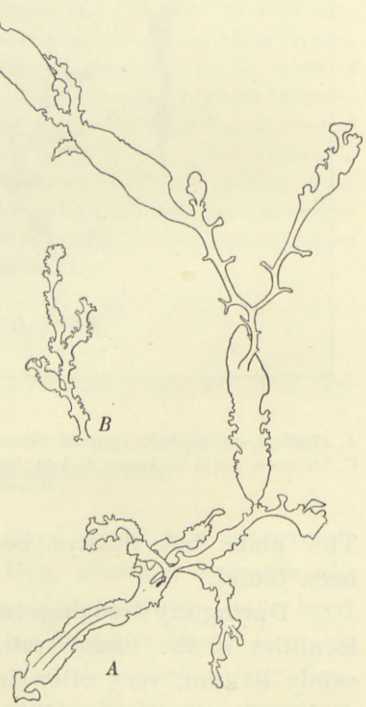


Fig. 526.
Phyllophora epiphylla f. *Bangii*. Hofmansgave, Caroline Rosenberg. 2 : 1.

[1] Comp. Warming, Oecology of plants. Oxford 1909, p. 178.

In other specimens the frond is much narrower than in the just named ones; the breadth of the frond is, indeed, variable, but 1—2 mm broad parts of the frond with feeble incisions as in the typical *Ph. Bangii* do not occur. LYNGBYE named this form f. *tenuior* and numerous specimens from Hofmansgave are to be found in the herbarium. I have also found it in numerous localities and it is easy to distinguish from the broader form, and it is remarkable that f. *tenuior* is the only form occurring in the southern part of Lille Belt, in Store Belt and the western Baltic Sea. On the other hand it occurs together with the broad form in several localities in the waters north of Fyn. In the Western Baltic Sea it occurred in considerable quantities, in some localities together with other loose Algæ. Some of the specimens growing here produced shoots of a different character, being destitute of the numerous warts or lacinulæ but having long diverging branches with even borders. (Fig. 528 *C*). As these shoots are continuous with the usual crenulated form, their connexion with f. *tenuior* is evident notwithstanding the different shape. Likewise, the f. *tenuis* must be supposed to arise from the thinner shoots of the typical *Ph. Bangii*. F. *tenuior* does not branch by proliferations and is thus very different from the typical *Ph. epiphylla*.

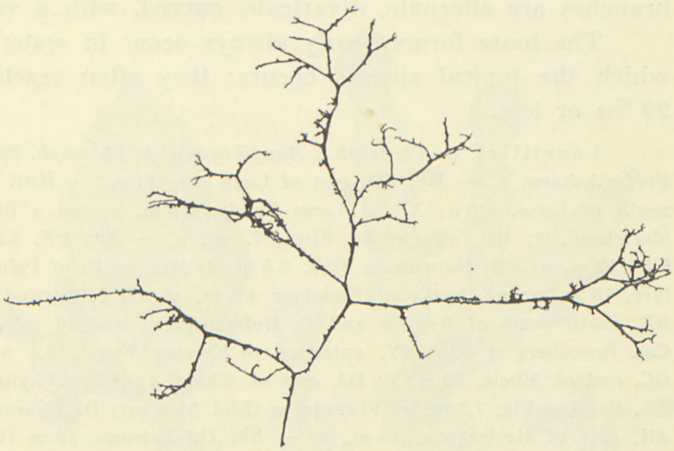


Fig. 527.
Phyllophora epiphylla f. *Bangii*, *tenuior*. Dredged south of Ærø, 7 m. 2 : 1.

This species has thus the power of keeping alive in a loose condition, the shape of the frond being gradually much altered. In localities situated near the boundary of the genuine species specimens occur that are only different by the frond being partly more or less incised. In the typical *Ph. Bangii* the border is incised in its whole length, some parts of the frond being, however, broader, 1—2 mm broad, and only minutely crenulated; branching by proliferations

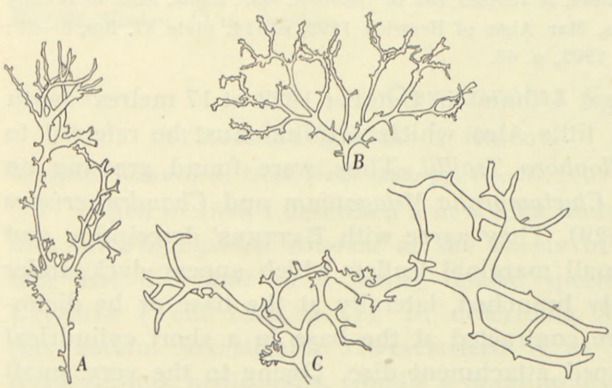


Fig. 528.
Phyllophora epiphylla f. *Bangii*, thinner form (f. *tenuior* Lyngb.). *A* with an expansion, *C* producing shoots without lacinulæ. *A* and *B* Hofmansgave; *C*, south of Ærø. *A* and *C* 3 : 1, *B* 2 : 1.

may be met with. In the inner localities only a finer form, usually only 0.2—0.5 mm broad or less, is met with, f. *tenuior* Lyngb., without proliferations. The branches are alternate, divaricate, curved, with a varying number of branchlets.

The loose forms nearly always occur in water of lower salinity than that in which the typical species occurs; they often vegetate in water with a salinity of 20 ‰ or less.

Localities. *α*: *Ph. epiph.* f. *Bangii typica*. *β*: *Ph. epiph. Bangii* f. *tenuior*. — **Kn:** Frydenstrand by Frederikshavn, *α*. — **Ke:** FD, east of Læsø 9.5—11 m. — **Km:** ZC, 4—5 m, XE 2—4 m and KF, 6.5 m south of Læsø, all *α*; XF at Læsø Rende, 8.5 m, *α* and a little *β*; entrance to Mariager Fjord, Th. Mortensen, *β*; BH, off Gerrild Klint, 7.5 m, *α*. — **Sa:** PN, Kalø Vig, 5.5—11 m, *β*; PL, Wulffs Flak, 9.5—13 m, *α*; PK, Norsminde Flak, 5.5 m, *β*; MQ, south of Paludans Flak, 11.3 m, *β*; aV, east of Endelave, 10 m, *α*; aX south of Endelave 4.5 m, *α*; aH Lillegrund at Fyns Hoved, 7,5 m, *α*; aY, aZ and NZ, north coast of Fyn, *α* and *β*; Hofmansgave, washed ashore, *α* and *β*. (Hofman Bang, Lyngbye, Car. Rosenberg a. o.); NY, entrance to Odense Fjord, 6.5 m, *α*; Einsidelsborg (Car. Rosenberg); GC, east of Æbelø, 13 m, *α*; DJ, east of Æbelø, *α*; Æbelø (Lyngbye). — **Lb:** Off Bjørnsknude, 9.5 m, *α*; AL, Baaring Vig, 7.5 m, *α*; Flækøjet *α* (Biol. Station); DE, Thorø Rev. 5.5 m. *β*; DB, Lille Grund, 7.5 m; dH, east of Hesteskoen, 15 m, *β*. — **Sb:** Off Refsnæs, 19 m (C. H. Ostenfeld) *β*; Lerchenborg Strand, washed ashore, *β* (O. Smith); GS, Lysegrunde, *β*; LN, Stavreshoved, *β*; GQ, Slettings Grund, 7,5 m, *β*; NU, off Strandskov at Bovense, 13 m, *β*; AB, off Teglværkskov by Nyborg, 7.5 m, *β*; cL, NE of Sprogø, 25—27 m, *β*; BS, Palegrund, 7.5 m, *β*; VB Omø Tofte, 5.5 m, *β*; fP, east of Hov lighthouse, 5.5 m, *β*; DP and UJ at Onse Vig, 7 m, *β*; DQ, west of Nakskov Fjord, 5.5 m, *β*. — **Bw:** cF, south of Kegnæs, 8.5 m, *β*; dO, north side of Bredgrund, 5 m, *β*; dP, east side of the same, 7.5 m, *β*; fT, south side of Ærø, 7 m; off Drejet, 7 m, *β*; UQ, off Tillitse, 12 m, *β*.

4. **Phyllophora Traillii** Holmes et Batters.

Traill, Monograph of the Algæ of Firth of Forth. Proceedings of the Roy. Phys. Soc. of Edinburgh 1882, p. 13, sine descr., Holmes et Batters, A revised list of the Brit. Mar. Algae, Ann. of Botany Vol. V, 1890, p. 89, sine descr.; Batters, Mar. Algæ of Berwick 1899, p. 114, plate XI, figs, 6—11; id., A Catalogue of the Brit. Mar. Alg. 1902, p. 66.

At Fladen in the Eastern Kattegat I found in October 1922 at 17 metres' depth a small number of specimens of a little Alga which I think must be referred to the imperfectly known species *Phyllophora Traillii*. They were found growing on stones together with young plants of *Chætomorpha Melagonium* and *Chondrus crispus* and were only 3—6 mm high (fig. 529). They agree with Batters' description and drawings, and some of them bear small marginal leaflets which appear dark under the microscope. The fronds are feebly branched, laterally at the base or by dichotomy or they are still entire. They are contracted at the base in a short cylindrical stipe and issue from a well developed attachment disc. Owing to the very small number of specimens I cannot ascertain whether the leaflets contain procarps. According to Batters the cystocarps, which are entirely immersed in the leaflets, ripen in January and February at the British coasts. I have had for comparison original specimens from E. M. Holmes collected at Cumbrae, Scotland in March and April; they were small and sterile, without marginal leaflets.

In the harbour of Østerby on the north coast of Læsø in the Northern Kattegat three specimens were met with (July 1924) which must probably be referred to the same species. They are up to 1.5 cm high with a linear frond, partly bearing numerous marginal leaflets which are often longer and narrower than in the above mentioned specimens; the leaflets are all flat and sterile. These specimens are all without base; they were perhaps loose.

A specimen dredged in the North Sea NW of Thyborøn in 31 metres' depth was finally referred to this species, though with some doubt. It is 1.8 cm high, branched, with marginal leaflets, and sterile in August.

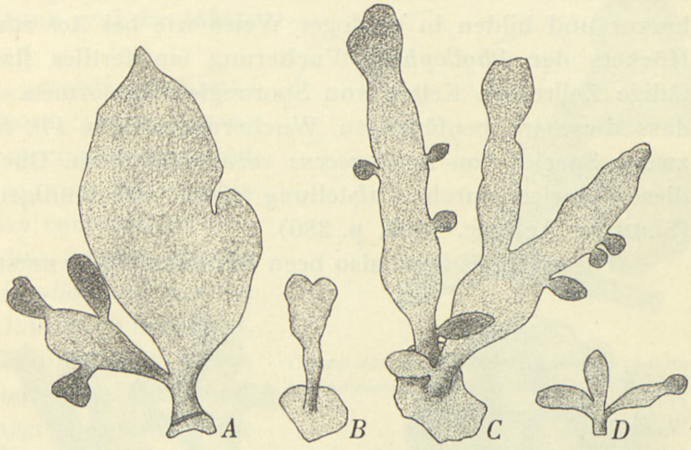


Fig. 529.
Phyllophora Traillii. Fladen, 17 metres' depth. 10 : 1.

The species has been met with at several places on the coasts of the British Isles (comp. BATTERS 1902), and it has also been recorded from the East coast of the United States by COLLINS. Tetraspores are unknown, and the structure and development of the cystocarps have not been examined.

Localities. **Ns:** aT Thyborøn beacon SE $^1/_2$ E 14 miles, 31 m. — **Kn:** Østerø harbour, Læsö. — **Ke:** fH, Fladen, 17 m, October.

Ceratocolax K. Rosenv.

1. **Ceratocolax Hartzii** K. Rosenv.

Kolderup Rosenvinge, Deux. Mém. 1898, pp. 34—39.

When in 1898 I described a new Alga under the above name, growing parasitically on *Phyllophora Brodiæi* at the coasts of Greenland, I was not aware of the fact that the same or a nearly related species had long before been observed by LYNGBYE (Tent. 1819, p. 11). In describing *Sphærococcus Brodiæi β, concatenatus,* this careful investigator characterized it as being set with "verrucis aggregatis, uvæformibus, pedicellatis, frondis e margine ortis". He did not take these bodies for fructifications, as they contained no "semina". REINKE directed the attention of SCHMITZ to these bodies and repeatedly sent him specimens of them from the Baltic Sea. SCHMITZ took much pains in examining them and finally arrived at the conclusion that they must be interpreted as "Produkte parasitischer Florideen". "Unter der Einwirkung eines ziemlich kleinen intramatrikalen Parasiten-Geflechts entwickeln sich traubenförmige Wucherungen des *Phyllophora*-Thallus; in diesen Wucherungen verbreiten sich intramatrical und langsam fortsprossend die intercellular kriechenden verzweigten Zellfäden des Parasiten; dann aber wachsen zu gegebener Zeit reichlich Zweigbüschel des Parasiten von den central gelagerten Parasiten-Geflechte auswärts hervor und bilden in analoger Weise wie bei *Act. roseus* an der Oberfläche je eines Höckers der *Phyllophora*-Wucherung ein fertiles flaches Polster, dessen antiklinfädige Zellreihen Ketten von Sporangien ausformen. Ich bin geneigt anzunehmen, dass diese traubenförmigen Wucherungen von *Ph. Brodiæi* durch eine eigenartige zweite Species von *Actinococcus* verursacht seien. Doch unterlasse ich es, schon jetzt diese Species durch Aufstellung eines selbständigen Namens zu unterscheiden" (SCHMITZ, Actinoc. 1893, p. 380).

These bodies have also been examined by DARBISHIRE who found them at Helgoland as well as in the Baltic (Botan. Centralblatt, 1894, p. 369). He met with tetrasporangia which were usually quite colourless (white) and procarps with long, protruding trichogynes. On the other hand he did not observe the "intramatrical" filaments described by SCHMITZ. He concludes as follows: "Ich halte die ganze Erscheinung für eine pathologische Wucherung von *Ph. Brodiæi.* Hierfür spricht u. A. die weisse Farbe der Tetrasporen und ferner der Umstand, dass von den sehr zahlreichen Prokarpen aus nie ein Cystocarp gebildet wurde, obgleich ich öfters an den Trichogynen wohl erhaltene Spermatien haften sah".

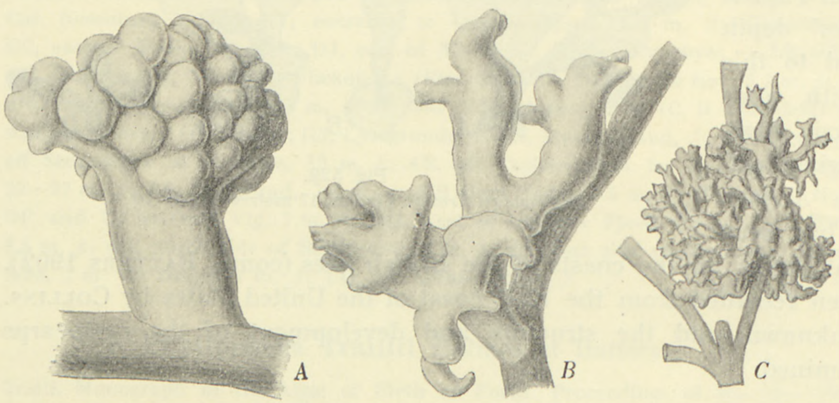


Fig. 530.
Ceratocolax Hartzii. A, from Hesteskoen east of Als, June. 11 : 1. *B*, from Højen near Faaborg. September. 11 : 1. *C*, from fN off Ballen, east of Samsø. August. 6 : 1.

The Greenland plant which I described in 1898[1] grows on the arctic form *interrupta* of *Phyll. Brodiæi*, on the flat side or on the border of the frond. It formed much branched bushes, 4—5 mm in diameter. At the base it penetrates a little way into the host plant, growing intercellularly. The cylindric branches bear globular nemathecia, while sex organs were not observed. The nemathecia remind one of those in *Phyll. Brodiæi.* The plants were not holoparasitic as they were red when living. The same species has later been met with at the coasts of Iceland (JÓNSSON) and in the Arctic American archipelago[2], on the same host-plant.

[1] On page 35 in my paper (Deux. Mém. 1898) l. 5 *fig.4* should be corrected into *fig. 7 A*.
[2] K. ROSENVINGE, Mar. Alg. coll. by Simmons dur. the 2nd Norw. Arct. Exped. Oslo 1926.

The specimens from the Danish waters to be described below agree so well with the Greenland specimens that I think they must be referred to the same species. In describing them the differing views of SCHMITZ and DARBISHIRE will be taken into consideration.

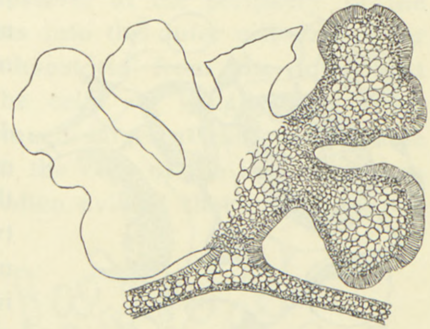


Fig. 531.
Ceratocolax Hartzii, Vertical section of tetra-spore-bearing plant. From Lille Belt, April. 30 : 1.

The organism in question, according to LYNGBYE, always grows on the loose, sterile f. *concatenata* of *Ph. Brodiæi*, and the specimens examined by SCHMITZ were probably also growing on this host-plant. It is, in reality, very common on this form in the Danish waters, but it also attacks the typical, fructiferous *Phyll. Brodiæi* and has the same appearance in both cases. It is much branched, the branches pointing in all directions. When the branches issue near the base, the outer outline of the plant becomes nearly globular, the ends of the branches reaching about the same distance from the centre (fig. 531). In other cases there is a cylindric stipe under the branched frond (fig. 530 *A*, *B*). The branches are repeatedly branched and often so crowded that the whole complex of branches is head-like. The branches are cylindric or a little complanated but never flat, often irregularly curved; in spring they usually end in a globular swelling, while later in the year the tips of the branches are not swollen but often much branched (fig. 530 *B*, *C*).

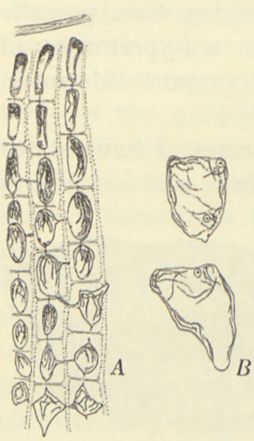


Fig. 532.
Ceratocolax Hartzii. *A*, section of cortex of the lower portion of the frond. *B*, medullar cells showing nuclei and chromatophores. 625 : 1.

The colour of the plant is pink, in particular in spring, or somewhat varying from yellowish to greenish according to the season and other external conditions, like that of the host-plant, but usually brighter, and brighter toward the tips of the branches.

The structure of the frond is somewhat similar to that of *Phyllophora Brodiæi*, but the consistency is softer. The cortex consists of outward directed cell-rows the innermost cells of which gradually pass into the medullary tissue. In the lower, sterile parts of the branches, the cortex is comparatively thick, consisting of regular parallel cell-rows, up to 6—8 cells long (fig. 532). In the upper, fertile regions, the cell-rows are shorter and not so densely crowded; the intercellular substance is here especially soft, and the arrangement of the cells is therefore often disturbed by microtomizing owing to the swelling of this substance (comp. figs. 537—539). The cortical cells are connected by primary pits in the transverse walls, but secondary pits may also occur in the longitudinal walls (fig. 532 *A*). The cells seemed often to contain a single calotte-shaped chromatophore, but in well-fixed material the cortical cells showed in some cases a system of narrow, thread-like bodies of which it was not easy to decide whether they were distinct chromatophores or branches of a much divided single chromatophore. In several cases a single nucleus was met with.

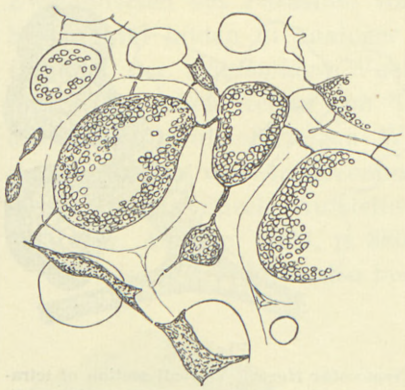


Fig. 533.
Ceratocolax Hartzii. Section of medullar tissue with smaller cells of secondary origin.

The inner tissue consists principally of isodiametric cells, increasing in diameter inwardly. The outer medullary cells have a structure similar to that of the inner cortical cells but they usually show two or three nuclei, and the inner cells a greater number. The medullary cells, in particular the larger inner ones, usually contain numerous small starch-grains and can be said to constitute a storage tissue (fig. 533). These cells are connected by numerous pits, primary and secondary ones, and it may happen that a wall separating two cells is traversed by two pits.

A system of smaller cells situated between the large storage cells and produced by budding from them is present in the interior of the frond; they are usually long and narrow and must if anything be regarded as representing a conducting tissue. Its cells are connected with the surrounding cells by secondary pits (fig. 533). It seems probable that these cell-rows have been interpreted by Schmitz as belonging to a parasite while the surrounding larger cells were supposed to belong to a hypertrophy of the host plant; nothing has, however, been found by me to support this interpretation.

In the paper (1898) where I have first described the species, I have stated that *Ceratocolax* penetrates into the medullar tissue of *Phyllophora* and sometimes even reaches the opposite face of the frond. In the Danish specimens I have never found the parasite penetrating so far into the host; usually the boundary line between the two organisms is situated nearly at the level of the surface of the host or is a little elevated towards the middle (Plate VIII, fig. 5). The limit is usually fairly distinct, though it is not always possible to say with certainty whether a cell belongs to the one or the other of the two organisms. This is in particular so in the central part of the limiting zone. The parasite has a softer consistence than the host, and its walls swell much more when treated with distilled water and various reagents; I also in some cases succeeded in obtaining a sharp boundary line when staining with hæmatoxylin after Heidenhain and then with

Fig. 534.
Ceratocolax Hartzii. Vertical section of the marginal zone growing in the outer wall of Phyllophora. The walls of the parasite are hyaline. The undermost cells of the parasite penetrate into the cell-walls of the host. 670:1.

orange or safranine, the walls of *Phyllophora* staining intensely while those of *Ceratocolax* remain unstained or much feebler stained (fig. 534). In thin vertical sections it is then in some cases possible to observe, at the periphery of the insertion of the parasite, that the latter penetrates into the outer cell-wall under the cuticle, lifting the latter and sending thin haustoria from the lowermost cells into the cell-walls of the host (fig. 534). The cells are usually very small at the periphery of the insertion while they are much larger at the centre where it may sometimes be rather difficult to distinguish the cells of the two organisms from each other (Plate VIII, fig. 5, 6). But it is often evident that medullar cells of the host are separated from their neighbouring cells and incorporated in the tissue of the host as described already in 1898 (fig. 8 *A*).

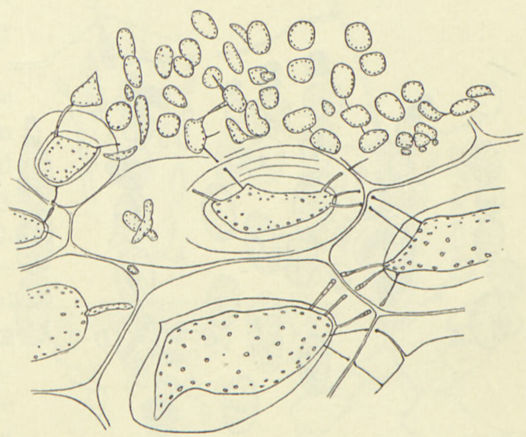


Fig. 535.
Ceratocolax Hartzii. Section through the limiting zone between the parasite and the host. 550 : 1.

In the plant represented in fig. 531 the lowermost part has the character of an attachment disc growing under the cuticle of the host plant (comp. Plate VIII, fig. 5), and such a disc may sometimes have a considerable extension. An unusually strong development of the attachment disc is shown in Plate VIII, fig. 8, where it is very thick and encompasses the marginal part of a frond of *Phyllophora*. More frequently, however, the limit between the parasite and the host is in the angle where the short cylindric stem meets with the surface of the host (fig. 530 *A*, Plate VIII, 4). It seems further to happen sometimes that the lowermost portion of the parasite is encompassed by a funnel-shaped outgrowth from the host consisting of a continuation of the cortical tissue of the latter, as shown in Plate VIII, fig. 7, where the medullar tissue of the host, too, extends considerably upwards in the centre of the stem. It is owing to the firm consistency and the high staining power of the cell-walls of the funnel-shaped cortex that it is assumed to belong to the host-plant. On the other hand the parasite may penetrate into the host-plant (Plate VIII, 4). When the small cells of the parasite meet with the large medullar cells of the host, they penetrate partly between, partly into the cells. The formation of secondary pits is very lively on both sides of the boundary line, and pits between the host and the parasite may be observed (fig. 535); but in other cases the medullar cells are invaded and often filled with the small cells of the parasite and then evidently killed (comp. fig. 535 to the right and Plate VIII, 4), and a number of the cortical cells must also have perished as a consequence of the attack of the parasite.

As mentioned above, nemathecia were observed by SCHMITZ (1893), DARBISHIRE

(1894) and myself (1898). They are very common in the Danish waters in spring. The branches of the nemathecia-bearing plants usually terminate in a globular swelling, and the nemathecia arise on the surface of these swellings. Nothing has been found to support the supposition of a genetical relation between the intercellular conducting tissue and the nemathecia, for the said tissue is only to be found at a certain distance below the young nemathecia. These arise by simultaneous division of the peripheral cells on a long stretch by periclinal walls, with the result that the surface on the stretch in question is covered with close anticlinal cell-rows (fig. 531, Plate VIII, fig. 9). The cells of these rows are rounded oblong or ellipsoidic and have an abundant plasmatic content; the thin plasmatic threads connecting the cells of the filaments are often easily visible in the young stages (fig. 536 *D*), later they could not be observed, and the regular arrangement of the cells is usually disturbed in the microtomized sections owing to the swelling of the intercellular substance.

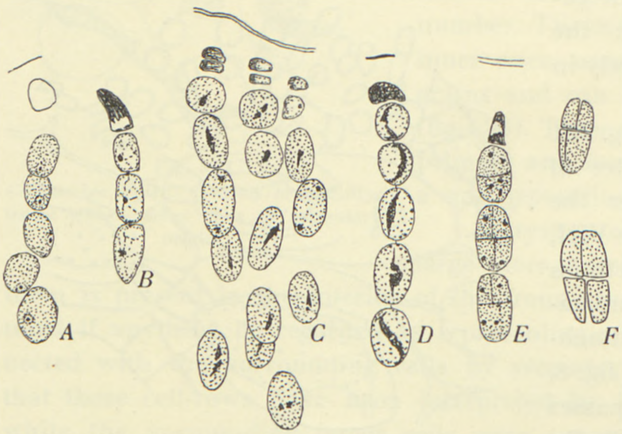


Fig. 536.
Ceratocolax Hartzii. Upper ends of nemathecial filaments. *A*, nuclei in the resting stage, February. *B—F*, April and May. *C—D*, nuclei in the first division. *E*, sporangia two- or four-parted. *F*, sporangia four-parted. 625 : 1.

The nemathecia have often a limited extent, but two or more young nemathecia may fuse together; the best developed ones form globular bodies at the end of the branches about 1/2 mm in diameter (fig. 530 *A*, 531). In such cases the nemathecium occupies only the outer portion of the globular body while the central part is a parenchymatous tissue identical with the medullary tissue of the branches.

The last one or two cells of the nemathecial cell-rows are sterile, the others develop into sporangia. The number of the fertile cells in the cell-rows is usually only 6 or 7. Fig. 536 *A* shows young sporangia with nuclei in the resting stage, but without distinct chromatophores. Nor could the latter organs be distinguished in the later stages, perhaps with the exception of fig. 536 *B* where some of the seriate small bodies may possibly be reduced chromatophores. The dividing nucleus is lengthened with pointed ends, often curved and eccentric, sometimes of the same length as the cell. I regret that I was not able to observe the chromosomes in material treated with Flemming's weaker solution or with formalin-sublimate. The spindle-shaped bodies were often found divided in the middle, but the following divisions were not observed, so that it was not decided whether the next nuclear divisions take place before the first cell-division. At any rate, the sporangial cell is first divided by a transverse wall and afterwards by two longitudinal walls (fig. 536 *E*, *F*). The ripe sporangia are colourless; they contain a dense mass of protoplasm and numerous very small starch-grains. Chromatophores could not be detected, but colourless plastids are probably present. Young nemathecia with cells in the resting stage were met with in February, but as early as March four-parted sporangia were found, though most of them were still undivided, and in April and in particular in May numerous ripe sporangia were observed. Sporangia were rarely met with in June and never after that month. The ripe sporangia are 9—19 μ long, 8—11 μ broad, most frequently 14—15 μ long, 8,5—10 μ broad. — Single long sterile cells may occur between the sporangia; they are most easily observed in partly emptied nemathecia.

The sexual plants differ from the sporangia-bearing ones by having no swollen globular ends. They are often much branched at the tips, but these branches have only the character of small warts (fig. 530 *C*). In sections of such irregular tips of the frond procarps may be found, often several together. A great number of procarps were observed in several plants, but only incompletely developed. The fertile character of these groups of cells is disclosed by their size and their abundance in plasmatic contents. When treated with hæmatoxylin after HEIDENHAIN they remained nearly black even after differentiation for a long time, so that the structure of the cells, in particular the presence of nuclei, could not be distinguished. Only in a specimen gathered in November and treated with formalin-alcohol it was observed that most of the cells of the procarps contained several small nuclei (fig. 539). The best developed procarps were found in specimens gathered near Samsø in August. Fig. 537 *C* shows such a procarp with long, protruding trichogyne; the carpogonial branch is here three-celled and borne on a large cell which is probably an auxiliary cell, much as in *Phyllophora Brodiæi*. Spermatia adhering to the trichogyne like those observed by DARBISHIRE, I have never observed. The other procarps from the same plant (fig. 537 *A-B*) can probably be interpreted in a similar manner, a trichogyne, however, being only developed in fig. *A*. In both procarps a lateral cell is borne on the first cell of the carpogonial branch. Feebly developed trichogynes are shown in fig. 538 but at any rate in some of the procarps here represented a three-celled carpogonial branch cannot be pointed out, and the procarps shown in fig. 538 *C*, too, can scarcely be reconciled with the type of a three-celled carpogonial branch. If the

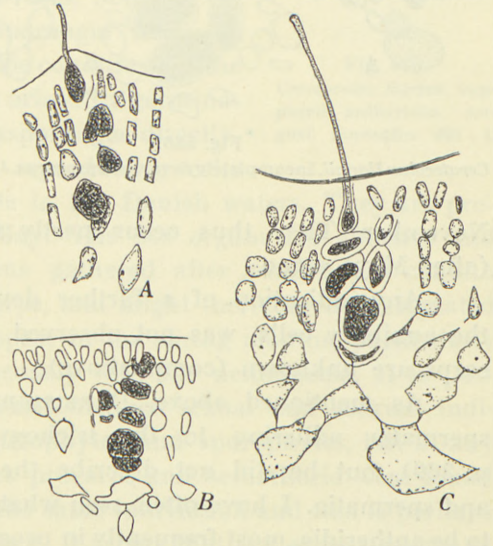


Fig. 537.
Ceratocolax Hartzii. Procarps, two with protruding trichogynes. August. 625 : 1.

three-celled row of dark cells in fig. *A* is a carpogonial branch, a lateral cell is borne on its second cell. Fig. *B* apparently shows a supporting cell with two two-celled carpogonial branches. The interpretation of fig. *C* is difficult; to the left is shown what seems to be a three-celled carpogonial branch, but to the right of it two trichogynes are seen, the connection of which with carpogonial branches is doubtful. Nearly all the procarps observed had no well developed carpogonium and no trace of a trichogyne. Procarps were observed in nearly all the months of March to November, in particular from May to November. They thus occur partly at the same time as the nemathecia, partly (after May) alone.

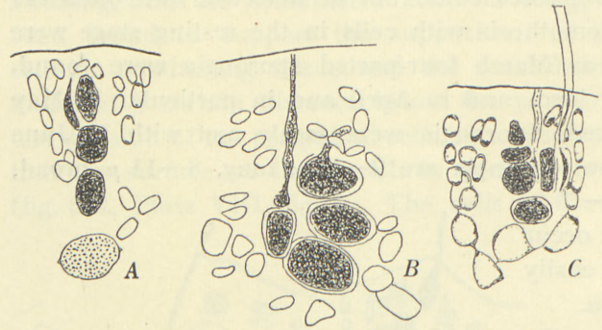


Fig. 538.
Ceratocolax Hartzii. Incompletely developed procarps. June. 625:1.

Any indication of a further development of the procarps, in particular from the auxiliary cells, was not observed, and cystocarps are unknown (comp. above).

As mentioned above, Darbishire observed spermatia adhering to the trichogynes (1894, p. 369), but he did not describe the antheridia and spermatia. I have often seen what I supposed to be antheridia, most frequently in procarp-bearing specimens but I am not fully convinced of their sexual character. In sexual individuals the outer cortical cells are often disunited to a greater or less extent, in particular in specimens treated with Flemming's solution, and the outer cortex then consists of oblong or short cells imbedded in a hyaline gelatinous substance. The cells are not very different from the ordinary cortical cells but often contain a very distinct nucleus, situated near the lower end of the cell and stained intensely by treatment after Heidenhain; the subjacent cells may then be the antheridia-producing cells (spermatangial mother-cells, Svedelius). Comp. fig. 540 (Plate VIII, fig. 10). If the here described cells are really antheridia, the species is usually monoecious.

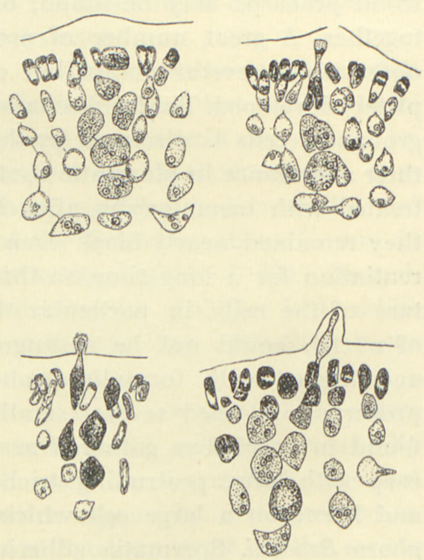


Fig. 539.
Ceratocolax Hartzii. Procarps with short trichogynes or without trichogynes. Nuclei visible in most of the cells. November. Sublimate-alcohol. 625 : 1.

Evacuated tetraspores have not been observed, nor their germination, but young plants raised in a culture were met with. On the 25th of May 1929 specimens of *Phyllophora Brodiæi* partly beset with *Ceratocolax Hartzii* bearing ripe tetrasporangia were placed in a glass vessel with sea-water and kept there for a long time. Three months later a number of young plants of *Ceratocolax* had arisen on other fronds or other shoots of *Phyllophora*, undoubtedly from tetraspores set free from the nemathecia, comp. fig. 541. In the middle of September these specimens contained no organs of reproduction. In April 1930 the tips of the branches of one of them were globular and turned out to be nemathecia, being composed of radiating cell-rows. Some of the cells of the latter were 4-parted, but the sporangia were not quite normal, probably owing to the unfavourable conditions of the culture. It must then be concluded that plants arisen by germination of tetraspores are able to produce tetrasporangia directly.

Fig. 540. *Ceratocolax Hartzii*. Supposed antheridia. August. Formalin. 625 : 1.

The tetraspores seem to be the only reproductive cells which reach normal development, at any rate in the Danish waters. They are produced in spring, particularly in March to May. The sex organs are abortive and cystocarps are never produced. The specimens gathered after June never contain nemathecia but only sex organs, at least procarps, and might therefore be designated as gametophytes, but sex organs may also appear in the spring months, particularly in May, simultaneously with the nemathecia. It is possible that there exist distinct sexual and asexual individuals, resp. gametophytes and sporophytes, but at any rate in some cases procarps and nemathecia were found with certainty in the same individual, and this is perhaps a normal occurrence. It seems that sex organs normally arise in specimens first producing tetrasporangia, but this point deserves further investigation.

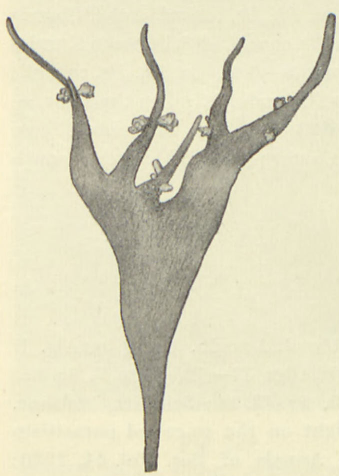


Fig. 541. *Ceratocolax Hartzii*. Nearly 4 months old plants produced in culture in a glass vessel in which had been deposited in May specimens of *Phyllophora Brodiæi*, one of which bore a nemathecium-bearing *Ceratocolax*. Drawn in September. 2 : 1.

The Danish specimens have here been referred to the same species as the Greenland ones though there are or seem to be some differences. In specimens from East Greenland the parasite was found penetrating deeply into the frond of *Phyllophora*, deeper than in the Danish specimens, but I have later found Greenland specimens where the connection between the two organisms was much as in the Danish specimens. Another difference is that sex organs have not been observed in the Greenland specimens, but that may perhaps be due to insufficient investigation. Finally the sporangia seem to be larger in the Greenland specimens than in the Danish ones; in the former I found them 22—26 μ long, 12—16 μ broad, while in the latter they were only 9—19 μ long, 8—11 μ broad; but the dimensions of the sporangia seem to be variable.

In the Arctic Sea *Ceratocolax Hartzii* has been found with ripe tetrasporangia in spring (March, May), just as in the Danish waters. But it is remarkable that unripe nemathecia have been met with repeatedly in summer, June (West Greenland), August (East Greenland), July and September (Arctic America, K. ROSENVINGE, 1926). It seems probable that nemathecia occur all the year round in the Arctic Sea.

The systematic position of the genus *Ceratocolax* remains uncertain so long as cystocarps are unknown, and the sex organs are only known as imperfectly developed and abortive. An affinity to the genus *Phyllophora* on which it is parasitic is highly probable.

The species is spread in nearly all the Danish waters, in particular the inner, more protected waters where it occurs at depths from 2 to 18 metres, perhaps most frequently on *Ph. Brodiæi* f. *concatenata*. It is met with in all seasons and reaches a diameter of from 2.5 to 5 mm. The greatest diameter, 5 mm, was met with in specimens gathered in May and September.

Localities. **Ns:** On *Ph. Brod.* f. *concatenata* at Blaavandshuk (C. M. Poulsen). — **Lf:** LY, on *Ph. Br. concat.*, between Gellerodde and Inderrön at Lemvig. — **Kn:** At Friis' Sten between Vesterø and N. Rønner, on *Ph. Br. typ.* 3 m. — **Ke:** HY, Store Middelgrund, 15 m, on *Ph. Br. typ.*; ad Nakkehoved (Lyngbye), on *Ph. Br. typ.*, washed ashore. — **Sa:** fN^3, off Ballen, Samsø, 11.3 m, on *Ph. Br. typ.*; Hofmansgave, on *Ph. Br. concat.*, numerous specimens gathered by Hofman Bang, Lyngbye, Car. Rosenberg. — **Lb:** Off Snoghøj; Fænø Sund; dE, Holst's Banke 8—13 m, on *Ph. Br. typ.*; dH and dH^1, east of Hesteskoen, 15—19 m, on *Ph. Br. typ.* — **Sf:** CA, Højen near Faaborg, on *Ph. Br. concat.* and *filiformis* (fig. 517 *C*). — **Sb:** Off Stavreshoved at Kerteminde; Bay of Kerteminde, on *Ph. Br. concat.*; NS, between Knudshoved and Slipshavn, on *Ph. Br. concat.*; XS, Kløverhage south of Nyborg, 5—6 m, on *Ph. Br. concat.*; fP, $^1/_2$ mile east of Hov lighthouse, 10 m, on the same; UJ, near the broom at Onsevig, 7.5 m, on the same. — **Su:** OH, north of Lous' Flak, 10 m; at Dragør, on *Ph. Br. concat.* — **Bw:** bV, N. E. of Kobbel Skov, 7—13 m, on *Ph. Br. conc.*; bY, off Sønderskov, Sønderborg 11 m, on the same; cD, Middelgrund south of Als., 8—12 m, on *Ph. Br. typ.*

Ahnfeltia E. Fries.

1. Ahnfeltia plicata (Huds.) Fries.

El. Fries, Corpus florar. provincial. Sueciæ. I. Flora Scanica 1835, p. 310; J. Agardh, Sp. g. o. Alg. II pars I, 1851, p. 311; N. Wille, Bidr. (1885) pp. 13, 15, 50, plate II, figs. 11—12, plate V, fig. 52; B. Jönsson, Dickenwachst. 1891; Buffham, Anther. (1893), p. 302, fig. 43, 44; Schmitz, Actinoc. 1893, p. 397; Printz, Trondhjemsfj., (1926), p. 63; Gregory, New light on the so-called parasitism of Actinococcus aggregatus K. and Sterrocolax decipiens Schm., Annals of Bot. Vol. 44, 1930; Chemin, Ahnfeltia plicata Fries et son mode de reproduction. Bull. soc. bot. de France, t. 77, 1930, p. 342; Kolderup Rosenvinge, The reproduction of Ahnfeltia plicata. K. D. Vid. Selsk. Biol. Meddelelser, X, 2, 1930.

Fucus plicatus Hudson Fl. anglica, ed. alt. 1778, p. 589. English Botany, Vol. 16, 1803, plate 1089.

Fucus albus ? Oeder, Flora Danica, tab. 408, 1768.

Gigartina plicata Lamouroux, Thalass. 1813, p. 48; Lyngbye, Hydr. 1819, p. 42.

Gigartina Griffithsiæ Lyngbye Hydr. 1819, p. 43, tab. 11 C, (non Turner)[1].

[1] An examination of the specimens from Funen referred by LYNGBYE to *Gigartina Griffithsiæ* has shown me that the "tubercula" interpreted by LYNGBYE as "fructus" are not nemathecia but attachment discs of *Cystoclonium purpurascens* growing on *Ahnfeltia plicata*.

Gymnogongrus plicatus Kützing, Spec. Algar. 1849, p. 789; Tab. phyc. 19, 1869, pl. 66; Harvey, Phyc. Brit. Vol. III, 1851, plate 288.
Sterrocolax decipiens Schmitz, Actinoc. 1893, p. 397.

The upright fronds spring from an expanded, thin firm disc intimately attached to the substratum, always stones, of a characteristic violet blue colour. By the colour it is usually easily distinguishable from other incrusting Florideæ, as for instance *Hildenbrandia prototypus*, which has a similar consistence but is either blood-red or yellow. The crust may reach a considerable extension before the first upright frond arises. Young fronds 1—5 mm high are often met with singly on the sides of stones picked up in summer at 1 to 2 metres' depth (fig. 542). But young fronds in greater number placed close together may also occur; then it is not always easy to decide whether they spring from one particular disc or from several fused together. Old specimens form light bushes composed of numerous fronds springing from an area of small extent. Such a case is shown in fig. 543 where about 100 fronds spring from an area with a maximal diameter of 1 cm whereas the basal crust from which they have arisen has a maximal diameter of more than 2 cm. In this case the crust has the appearance of being of single origin.

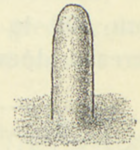


Fig. 542. *Ahnfeltia plicata*. Young frond springing from an expanded disc. 10 : 1 (?).

Fig. 543. *Ahnfeltia plicata*. Cluster of fronds springing from a thin disc appearing light in the photograph, extending as far as to the dark area to the right. Slettings Grund, Store Belt. November. 3 : 1.

The crust is built up of small almost squarish cells, about 3 μ in diameter, arranged in vertical rows, with firm, not gelatinous cell-walls. The superficial cells are rounded outwards, but the outer cell-wall is scarcely thicker than the others (fig. 544). In older crusts this structure is sometimes interrupted by tissue with larger, more irregular cells.

The upright frond arises as a wart from the disc, a great number of the vertical filaments participating in it and showing divergence of the filaments, of which it is composed, and thus early showing conformity with the upper end of the cylindrical fronds.

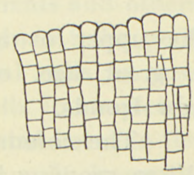


Fig. 544. *Ahnfeltia plicata*. Vertical section of crust. 625 : 1.

The fronds are cylindrical, rigid, horny, branched by dichotomy and by lateral ramification. They are usually forked at the top and later produce lateral branches, which have usually the character of adventitious shoots, but the lateral branches may also arise near the top. They appear in great number on the older fronds when the apical growth has been arrested by decay. A lateral branch often arises early near the dichotomy, and may then later suggest a trichotomy (fig. 545 *A*, *C*). HARVEY's figure (1851, pl. 288) shows a specimen branched throughout by dichotomy, whereas KÜTZING's picture 1869, pl. 66 represents a specimen almost exclusively branched by lateral ramification.

The thickness of the frond is nearly the same in its whole length, varying from 500 to 900 μ. It increases a little from the growing apex downwards, but the increase does not continue gradually from the growing apex to the base of the frond. From a short distance downwards the diameter varies irregularly between 400—500 μ and 900 μ. The branches are often thinner at the base than at a higher level. The cross section of the frond is circular or a little oblong.

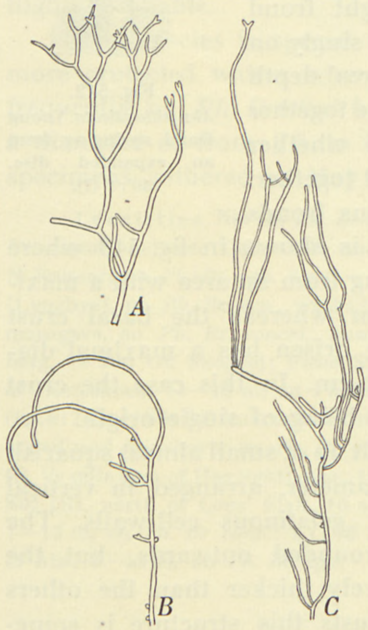


Fig. 545.
Ahnfeltia plicata. *A*, frond branched by dichotomy. *B*, frond with dichotomous and lateral ramification. *C*, frond mainly with lateral ramification. $^4/_3$ n.s.

The frond may often reach a height of 16 cm but scarcely exceeds this size. It is unknown how long it takes before this size is reached. The growth of the perennial frond ceases in winter and begins again in early spring. In a specimen collected in the middle of May, the new portions of the frond were 1 to 1.5 cm, long, but I have not ascertained the annual increase in length of the frond. In a vigorous specimen from Frederikshavn (Deget) gathered in the middle of July I judged the increase of the year to be up to 3 cm, and I think that the annual increase in length will not generally exceed this figure. If this is correct, the tallest specimens should be at least 5 years old. But the specimens may certainly become much older, for many shoots die entirely or in part and are replaced by new lateral shoots. In autumn specimens may be met with in which a great number of the shoots have white tips, a sure sign of death and decay. The species often forms large carpets covering the upper or lateral faces of larger stones. Such carpets may certainly attain a great age, owing to the power of the expanded basal layer to produce new fronds.

The colour of the frond depends on the amount of light to which it is exposed. When growing in shady places it is lurid, showing a characteristic violet tint when observed against the light, and the same is the case with the lower parts of older fronds in the shadow of the younger ones, but the upper part of the fronds which are exposed to the full day-light in summer are prettily green, in autumn yellowish green. In winter the young portions of the fronds are much darker, not very different in colour from the older ones. JÖNSSON thinks that the darker colour of the older fronds is caused by the new cortical layers becoming darker than the foregoing ones, and that the lowermost parts of the fronds are the darkest because they contain the greatest number of cortical layers. In my opinion the dark colour of these portions of the frond is due to the fact that they are best protected against the destructive action of the light upon the phycoërythrine. I have once, at Frederikshavn (Borrebjergs Reef), met with a frond having the ordinary lurid-violaceous colour, but bearing a branched shoot, 6.5 cm long, having a pronounced blue-green colour contrasting with the colour of the rest of the frond. This shoot was at least 2 or 3 years old. It evidently contained much phycocyanin but not phycoërythrine.

The apical meristeme of the frond is built up of numerous thin, closely united filaments directed vertically towards the periphery and thus diverging. The outer cell-rows are gradually, by the growth of the frond, directed vertically to the longitudinal axis of the frond. The diameter of the outer cells is about 3.5 μ, and the superficial cells are scarcely thicker in the older parts of the frond. These rows of cells branch frequently in the meristematic portion of the frond, the apical cell dividing by an oblique cell-wall by which a new apical cell is cut off, while a branch is produced from the segment cell, the upper portion of which is cut off by a cross wall (fig. 546 *B*).

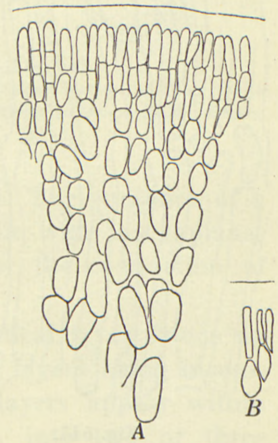


Fig. 546.
Ahnfeltia plicata. *A*, vertical section of apical meristeme. *B*, from a similar section showing ramification of the cortical cell-rows. 625 : 1.

The central part of the frond is built up of long cylindrical cells with very rigid refractive cell-walls, giving the central cylinder the character of a mechanical tissue (comp. Wille, 1885, p. 13, 50, Plate II, fig. 12, V, fig. 52). The cells are terminated by transverse walls which are about as thick as the longitudinal ones; they do not, therefore, seem much adapted to the function of conducting substances, so much the more as the central pits are very thin and not easy to observe (fig. 547). The length of the cells is, however, great, though very variable; some cells were very long, up to 780 μ long, others much shorter, and it seems that a distinction can be made between very long-celled filaments and others consisting of short cells; the latter are perhaps of secondary origin. At the periphery the cells are shorter and gradually approach the inner cortical cells in size. Wille (1885, p. 50) attributed *Ahnfeltia plicata* to the Florideæ with incompletely developed conducting tissue; he considered the last-named tissue, situated between the mechanical and the assimilatory systems, as such a conducting tissue. It, however, seems more adapted to a conduction between the assimilatory tissue and the central cylinder than for conduction in a longitudinal direction. The central cylinder has not only a mechanical function but also serves as storage tissue; I found the cells filled with starch-grains in summer and autumn (July to October) whereas in fructiferous plants they were without starch in spring (March to May). The intermediary

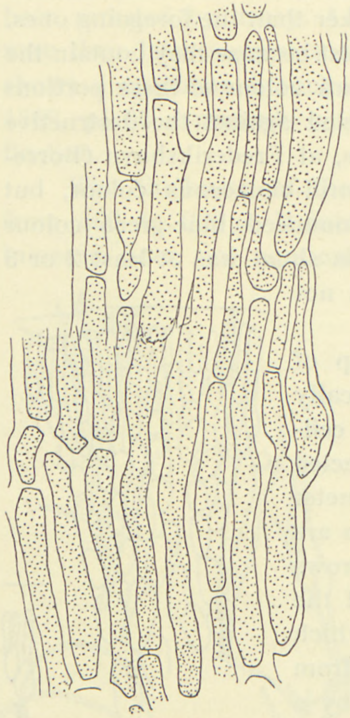


Fig. 547.
Ahnfeltia plicata. Longitudinal section of central tissue. 350 : 1.

tissue thus serves to convey the products of the assimilation to the central cylinder, and later to transport the dissolved nutrient media from the central tissue to the periphery.

The cortex has about the same structure as the basal disc; it is composed of small, nearly squarish cells with slightly rounded angles, arranged in radial rows having the same diameter in their whole length (comp. Kützing, 1869, pl. 66, fig. *e*, Wille, 1885, fig. 11). The cell-walls are moderately thick, the outer wall thicker, firm, not gelatinous. The whole cortex has a firm structure owing to the small diameter of the cells, and certainly contributes to the rigidity of the frond. The cortical cells contain one small nucleus. The chromatophores are not easy to distinguish owing to the small dimensions of the cortical cells. There often seemed to be one parietal plate at the upper end of the cells; but in a specimen treated with Flemming's weaker solution and stained after Heidenhain with erythrosin and examined under high power several disc-shaped chromatophores were observed in each cell, as shown in fig. 548 *B*, where also the primary pits are to be seen. Secondary fusions between cells of different cell-rows now and then appear (fig. 548 *A*). The cortex of the older fronds shows a stratification which is the effect of a periodical increase in thickness, which has been the subject of a thorough investigation of B. Jönsson (1891). The growth in thickness takes place in the outermost layer of cells which keep their dividing power. This, however, is not always in activity but is interrupted by resting periods leaving their trace in boundary lines characterized by thicker and more refractive membranes. Jönsson thinks these boundary lines arise because the walls of the outermost cells become thicker and more refractive than the inner walls during the resting period, whereas the new cells formed at the beginning of the growing period have comparatively thin walls. This explanation is certainly true but the figure (l. c. plate I, fig. 4) illustrating it does not give a true idea of the real structure. The boundary line is shown by Jönsson as a continuous thick wall corresponding to the outer wall of the frond,

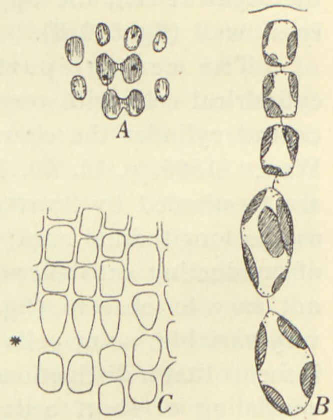


Fig. 548.
Ahnfeltia plicata. Transverse section of cortex. *A*, showing transverse fusion of cells. *B*, cell-row showing pit-connections and chromatophores 2100 : 1. *C*, section through the limit between two layers (*) 1200 : 1.

whereas the radial walls show no thickenings. This is undoubtedly due to the fact that the drawing has been made from a section which was not sufficiently thin. In examining a section only one cell thick it is evident that the thickenings in particular concern the radial walls. In the cells situated at the limit between two cortical layers the radial walls are much thickened at the base but the thickening diminishes upwards, with the consequence that the lumen of the cell is conical downwards and the area of the basal wall is very small. Thus no continuous thick transverse wall arises by the thickening of the transverse wall, but the thickened lower parts of the radial walls of the limiting layer of cells appear in thick sections as a thick refractive wall traversing the cortical tissue. The presence of a continuous thick transverse wall would not be easy to reconcile with the explanation given by JÖNSSON, and it would be very unfavourable for the conduction of matter in a radial direction.

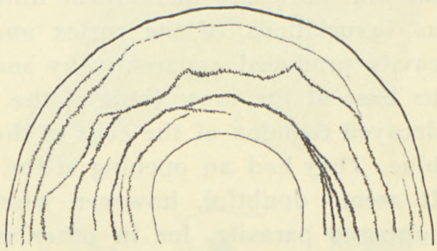


Fig. 549.
Ahnfeltia plicata. Cross section of older frond showing several irregular layers in the cortex. 83 : 1.

In older fronds, JÖNSSON usually found from 4 to 6 cortical layers, once up to 12. The layers may be regular, but irregularities occur, the layers being incomplete, encompassing only a part of the stem, or secondary layers appear within the primary ones, dividing them, over part of their extent, into two or three subdivisions. PRINTZ (1926, p. 63), who often found 6—8 layers, thinks that they indicate the number of years, while JÖNSSON speaks with reservation of this question. I found the stratification so irregular in some cases that it was impossible to state the number of the layers. On one side of the frond the number of layers was high, e. g. 9, while on the other side it was much smaller owing to the fact that some boundary lines were vanishing, others confluent (fig. 549). Moreover, it was not always possible to distinguish the secondary layers from the primary ones. If the layers were regular annual productions like those of the ligneous Dicotyledons, one might expect to find the number of layers increasing from the top downwards; but that is, at any rate, not always the case. For in a large specimen I found about 3 layers near the base, at a higher level about 7. The diameter of the stem and the thickness of the cortex was also smaller than at a level one cm higher up, namely 530 μ and 130 μ against 670 μ and 248 μ. In the same frond the thickness of the cortex increased from the top to nearly one cm above the base (100; 125; 158; 178; 200; 248 μ). In this case the cortex has thus continued growing except in the lowermost part of the stem. A regular increase of the number of cortical layers could not however be ascertained in this case.

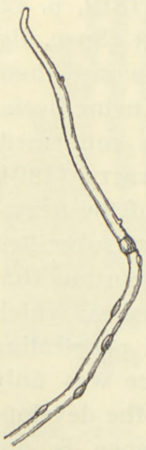


Fig. 550.
Ahnfeltia plicata. End of frond with nemathecia. December. $2^1/_2$: 1.

The older fronds are often beset with warts which have nothing to do with the fructification, nor do they seem to be undeveloped young branches, for they do not show the anatomical differentiation of the latter and must be considered as luxuriations of the cortex and may show stratification like this. Sometimes a cavity produced apparently by some parasite was found at the bottom of it, having its base at the inner limit of the cortex, and partly filled with what seemed to be decayed remains of the cells of the host which took a deep blue stain by methylen blue. They had an opening at the top of the wart and had been left by the parasite. It seems doubtful, however, whether the warts had really been caused by the supposed parasite, for in other warts no cavity seemed to be present, and similar cavities were found without causing such warts. In other warts the cavity was found filled with a granular matter which seemed to be small bacteria. The first described cavities have perhaps also been inhabited by bacteria which have left them later. The bacteria observed were very small; there seemed to be cocci and short rods. SCHMITZ has described tubercles containing bacteria in several other Florideæ (Botan. Zeit. 1892).

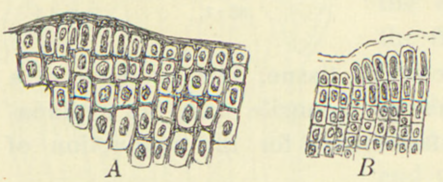


Fig. 551.
Ahnfeltia plicata. First origin of nemathecia. September. 670 : 1.

Reproduction. The reproduction of *Ahnfeltia* has been imperfectly known and disputed until quite lately. From the beginning of the ninetienth century, at least, cushions on the frond have been described and usually considered as the fructification of the species. LYNGBYE (Tent. 1819, p. 42) observed them in spring but did not meet with any spores. C. AGARDH (Spec. alg. 1822, p. 313) stated that they were composed of articulate filaments and named them nemathecia. KÜTZING (Tab. phyc. **19**, tab. 66, 1869) thought that the nemathecial filaments were transformed into seriate spores, but that has not been confirmed. The spores were first described by BUFFHAM (1893, p. 302) and SCHMITZ (1894, p. 397) who found that the spores are only produced in the end-cells of the nemathecial cell-rows, these cells each giving rise to one monospore. SCHMITZ submitted the nemathecia to an anatomical investigation and arrived at the conclusion that these bodies were not organs of the *Ahnfeltia* but that they were parasites, which he called *Sterrocolax decipiens,* growing on the surface of *Ahnfeltia* and penetrating into the cortex of the latter by numerous "Senker". But this inference was only founded on the presence of the said processes and not on the study of the development of the nemathecia or of the "Senker". Hence SCHMITZ's inference is not conclusive, and it would lead to the absurd conclusion that no kind of reproductive organs had ever been observed in *Ahnfeltia plicata.* To elucidate the question of the nature of the nemathecia I have examined their development and the germination of the spores. The results of my investigations have been published in a particular paper (1931) where I have also mentioned two smaller papers of GREGORY and CHEMIN treating the same question and published shortly before the publication of mine. Referring the reader for details to the latter, I shall here shortly give its substance, using again most of its illustrations.

The nemathecia form small cushions on the surface of the frond, orbicular or usually elliptical or oblong in outline (fig. 550). They arise in September from a group of superficial cells growing out simultaneously and dividing by cross walls (fig. 551). In September the cushions were only 1—2 cells high; in the middle of October the nemathecial cell-rows had grown longer, and the nemathecia had attained a larger extension by continued production of new nemathecial filaments at the margin (fig. 552). The continuity of the nemathecial filaments with the cortical cell-rows was stated in 1930 by GREGORY and CHEMIN. The first-named author maintained that the development of the cushion begins with a localized hypertrophy of the cortical tissue of *Ahnfeltia*. The nemathecial filaments are very thin, often only 2—3 μ broad. At this period (October) two kinds of cells different from the others appear. 1) flask-shaped cells, attenuated upwards, often appear in great number at the bottom of the nemathecium, arresting the growth of the filaments on which they are terminal (fig. 553). They have some resemblance to carpogonia but are not borne on particular cells comparable to carpogonial filaments and have only a small and feebly developed nucleus, and they cannot, therefore, be considered as true carpogonia but might probably better be interpreted as reduced hair-cells (comp. K. ROSENVINGE 1931, p. 8). 2) generative cells, thicker and richer in contents than the other cells, terminal or lateral, arise at the upper end of the nemathecial cell-rows, singly or in small groups which seem to arise by division of a single cell. The generative cells or some of them grow out, at first in particular in a horizontal direction, forming more or less irregular cell-rows, the cells of which are larger than the sterile cells. Some of them may be rather hyaline

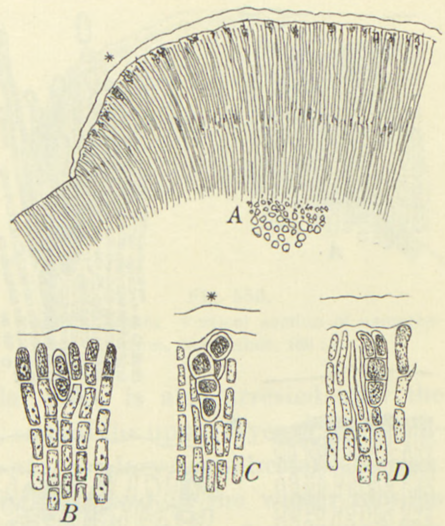


Fig. 552.
Ahnfeltia plicata. Nemathecium, October. *A*, vertical section, 244 : 1. *B—D*, upper ends of nemathecial filaments with generative cells. 670 : 1.

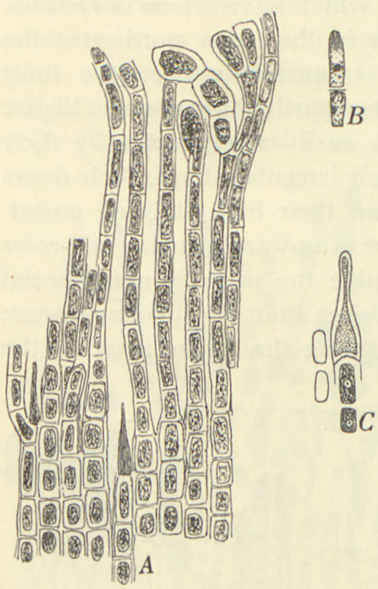


Fig. 553.
Ahnfeltia plicata. From a nemathecium, October. *A*, nemathecial filaments showing flask-shaped cells below and generative cells above. *B*, upper end of primary nemathecial filament. *C*, flask-shaped end-cell. 1080 : 1.

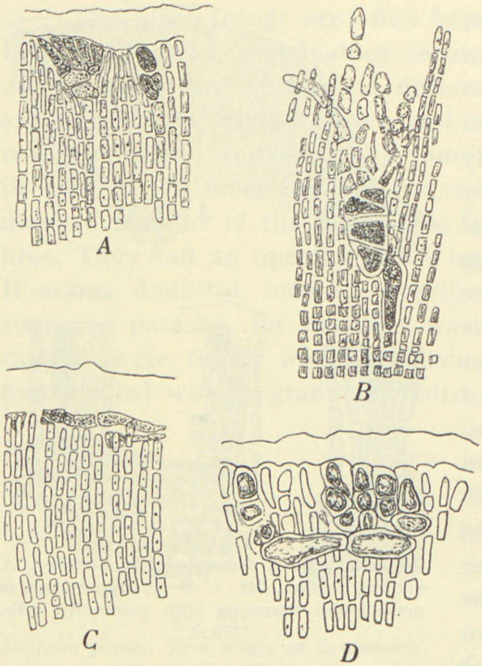


Fig. 554.
Ahnfeltia plicata. Vertical sections of nemathecia, October, showing groups of generative cells and horizontal or obliquely upward growing cell-rows springing from them. 625 : 1.

and poor in contents, while others have a rich plasmatic content (figs. 554, 555). Fig. 555 *A* shows the border of a nemathecium the outer portion of which is built up entirely of generative cells and their derivates. In fig. 554 *B* is shown a group of generative cells, situated at a low level in a nemathecium, from the upper cells of which new branched cell-rows growing obliquely upwards are produced. The lower part of this group is reminiscent of the "Senker" described by Schmitz.

In specimens collected in the middle of November the nemathecia had grown thicker and had also increased in circumference (fig. 556, Plate VIII, fig. 11). The generative cells which have arisen in October are found again in the lower portion of the cushion, partly immediately over the limit towards the cortex, partly at a somewhat higher level. They are easily recognisable by their greater size, their irregular shape, their dense cell-contents and their high staining power. A great number of upward growing cell-rows issue from them (figs. 557, 558). These cell-rows resemble the primary nemathecial filaments, but are, at any rate at first, somewhat thicker than the primary ones; they form new, secondary nemathecial filaments constituting the upper layer of the nemathecium. The irregular shape of the generative cells depends partly on the fact that fusions often take place between cells from different cell-rows (fig. 557). It is probably these fusions to which Gregory refers (1930, p. 768), when he thinks it possible that they may represent a very much reduced sexuality. The nuclei of these cells were usually not very

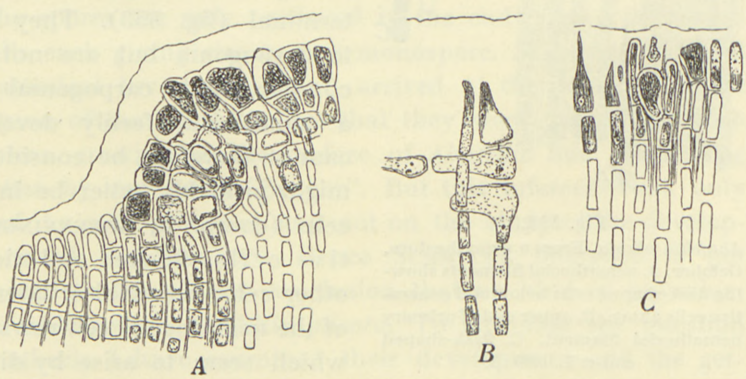


Fig. 555.
Ahnfeltia plicata. From a nemathecium, October. *A*, vertical section of the border. *B*, generative cells giving rise to horizontal cell-rows. *C*, generative cells and flask-shaped cells. *A* 960 : 1. *B* and *C* 1080 : 1.

distinct; at all events nothing has been found to support such an assumption, and it must be remembered that fusions occur between ordinary cortical cells too (comp. p. 558).

The development of the primary nemathecial filaments is to a great extent stopped by the formation of the flask-shaped cells and the generative cells; these filaments are replaced by new, secondary nemathecial filaments, and it seems probable that the development of the other primary nemathecial filaments, which have not produced any of the aforementioned particular cells, is also arrested after the formation of the generative cells and their derivates, so that the upper layer of the nemathecium is exclusively or for the most part built up of secondary nemathecial cell-rows.

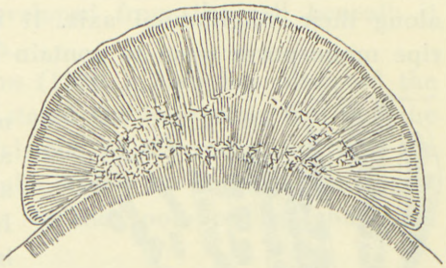


Fig. 556.
Ahnfeltia plicata. Vertical section of nemathecium, November. 160 : 1.

The marginal portion of the nemathecium is composed in the winter months of horizontal cell-rows which have probably taken their origin from generative cell-rows or their derivates like those shown in fig, 555 *A*, and must therefore be considered as secondary nemathecial filaments. The under side of the peripheral part of the nemathecium is appressed to the surface of the frond, but the undermost nemathecial cell-rows are not connected with the cells of the cortex (fig. 556).

The narrow cells of the secondary nemathecial filaments contain a small nucleus and one or more chromatophores. The apical cell has more plasmatic contents and a larger nucleus. It is at first scarcely thicker than the other cells but, when the cell-divisions are finished, it takes an oblong or obovate shape and develops into a monosporangium. This organ contains 2 to 4 or more very distinct chromatophores, most frequently rod-shaped or ribbon-shaped, and it is remarkable that these bodies not seldom were found lying in pairs close together (figs. 560, 561). My assumption is that they were on the point of fusing together

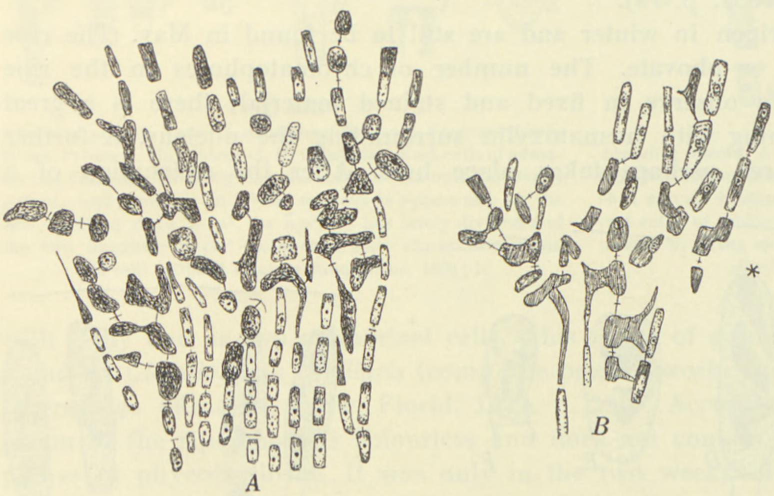


Fig. 557.
Ahnfeltia plicata. Vertical section of lowermost part of nemathecium, November. The irregular cells rich in plasmatic contents are situated at the level of the surface of the frond*. 1080 : 1.

along their longitudinal axis. It is in accordance with this interpretation that the ripe monospores seem to contain one single chromatophore (fig. 562 *G*).

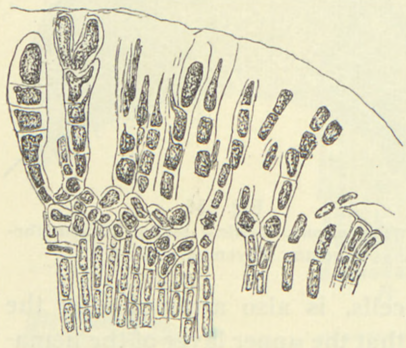


Fig. 558.
Ahnfeltia plicata. Vertical section of nemathecium near the border, December. 670 : 1.

The nucleus of the monosporangium is most frequently found in the resting stage, showing a large nucleolus or central body surrounded by a well marked hyaline halo but no chromosomes. In other cases the central body was differentiated into small grains staining intensely with hæmatoxylin. When they were most distinct, the number of the latter was seen to be four (fig. 561). In a dividing nucleus (fig. 561 *A*2) two groups of such 4 grains were to be seen. There can be no doubt that these grains were chromosomes. When Gregory (l. c. p. 768) states that "There is some evidence that there are eight chromosomes in the apical cells and in the monospores of *Sterrocolax decipiens*", it seems probable that this remark alludes to such dividing stages. The nuclear divisions observed were evidently all mitotic, and no indication of a synapsis stage or a heterotypic division was ever met with. It must be concluded from my investigations that the chromosome number of the (secondary) nemathecial filaments and the monospores is 4, and the nuclei of the frond seem to have the same number (comp. K. Rosenvinge 1931, p. 19).

The monospores ripen in winter and are still to be found in May. The ripe sporangia are ellipsoid or obovate. The number of chromatophores in the ripe sporangia is not easy to observe in fixed and stained material; there is a great amount of matter staining with hæmatoxylin surrounding the nucleus. A further fusion of chromatophores perhaps takes place here. After the evacuation of a

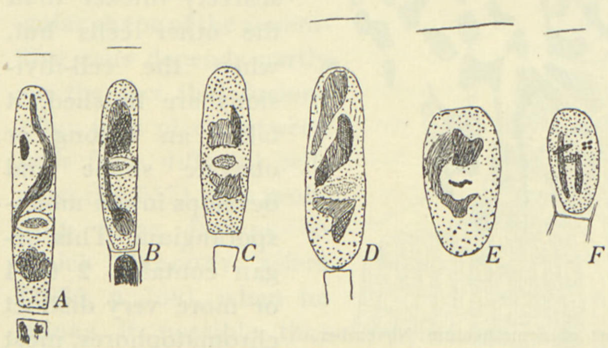


Fig. 559.
Ahnfeltia plicata, November (Flemming, Heidenhain). End-cells of (secondary) nemathecial filaments showing nucleus and chromatophores. In *F* the limitation of the nucleus is indistinct, a group of 4 chromosomes is situated to the right of the central body. 1800 : 1.

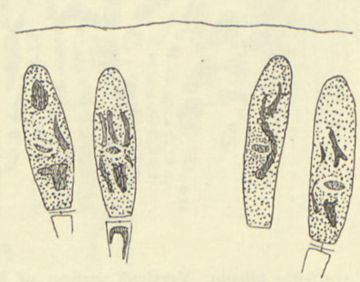


Fig. 560.
Same material as fig. 559. Four end-cells from the same section showing nucleus and chromatophores, the latter apparently partly fusing together. 1800 : 1.

monosporangium, a new sporangium can be developed from the cell beneath it (fig. 562 *D*, *E*). The ripe nemathecia are yellowish.

Germination of the monospores. Chemin (1930, p. 350) has observed the first stages of the germination of the spores and stated the interesting fact that the attachment disc does not arise directly by cell-divisions of the spore, but that the germinating spore first gives off a short germ tube which by segmentation forms a small orbicular disc. This may be contiguous to the spore cell or connected

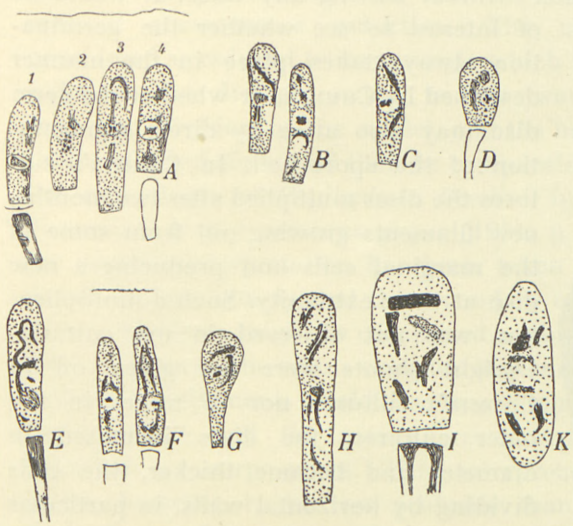


Fig. 561.
Ahnfeltia plicata. From a nemathecium from Frederikshavn, Henn. Petersen, May (Alcohol, Heidenhain). End-cells of nemathecial filaments showing very distinct chromatophores partly paired, and nucleus. In A^4 the nucleus is apparently in the first dividing stage, in A^2, the nucleus has lately divided and the two daughter nuclei show each four chromosomes but are still without nuclear membrane. 1800 : 1.

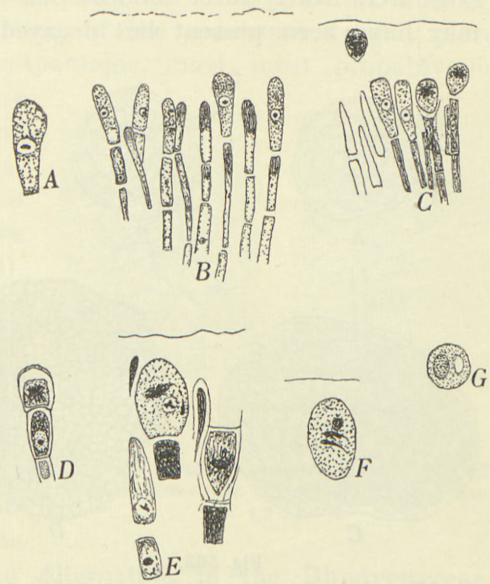


Fig. 562.
Ahnfeltia plicata. *A*—*F* from the same material as in fig. 561. Ripe monospores are present in *C*. The narrow, clavate intensely stained cells in *E* are perhaps end-cells of obliterate primary nemathecial filaments. *G*, living spore set free in May. *A*—*D* 670 : 1. *E*—*F* 1080 : 1. *G* 670 : 1.

with it by one or two cylindrical cells. This mode of germination agrees with that found in *Gloiosiphonia capillaris* (comp. the present work, part II, p. 277; comp. also *Dudresnaya* (Killian, Entw. Florid. 1914, p. 238). According to Chemin the protoplasm of the ripe spore is colourless and does not contain any trace of chromatophores or phycoërythrine. It was only in the two weeks old discs that "des chromatophores pariétaux s'organisent dans les cellules les plus âgées et chaque germination apparaît sous forme d'une petite tache rose". I did not find the spores just set free from the nemathecium colourless, but containing a yellow-brown chromatophore and numerous refractive bodies (starch). It is probable that the single chromatophore has arisen by repeated fusions of the originally multiple chromatophores, as described above. In the cultures established in May 1927 the first stages of the germination were unfortunately not observed. Only about three months after the sowing the young germlings were detected as small violet (not rosy) orbicular discs recalling those described and figured by Chemin. They were merely somewhat larger, the smallest ones consisting of about 30 cells, and no germ-tube was to be seen. In several cases the discs bore single hyaline hairs. Nor was I able to observe any germ tube on recently re-examining a slide containing numerous germlings from my culture in 1927, conserved in glycerin. As the germlings were nearly three months old, it is, however, quite possible that a germ-tube may have been present but decayed later without leaving any trace. It would be of interest to see whether the germination always takes place in the manner described by Chemin, or whether the germ disc may also arise by direct segmentation of the spore cell. In Chemin's cultures the discs multiplied after two months, new filaments growing out from some of the marginal cells and producing a new disc at their extremity. Such a multiplication was not observed in my cultures. Upright shoots were not given off in Chemin's cultures nor in mine. In my older cultures, the discs increased in diameter and became thicker, the cells dividing by horizontal walls, in particular in the middlemost part. An old disc measured 90 μ in diameter. These discs agreed exactly in colour and structure with the more expanded discs found in Nature from which the upright fronds of *Ahnfeltia* spring (comp. figs. 542 to 544). The discs met with in Nature often reach a considerable size before the formation of the first upright frond takes place.

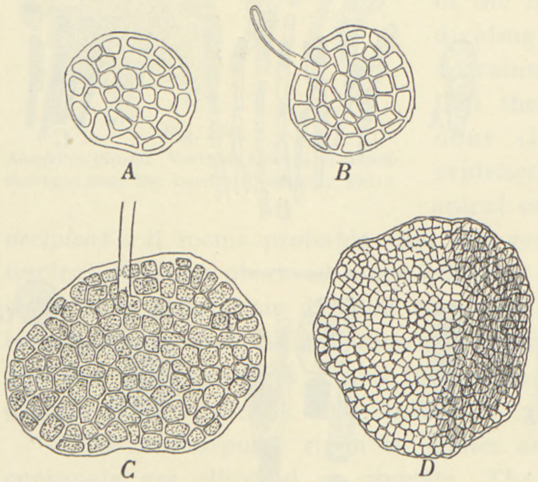
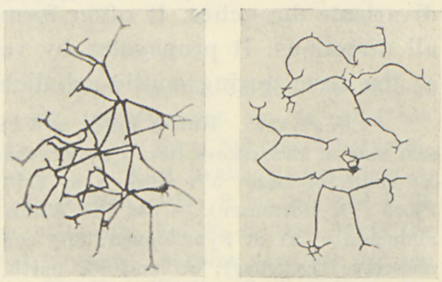


Fig. 563.
Ahnfeltia plicata. Germlings obtained by sowing monospores in May 1927. *A—C* about three months old, in *B* a young hair-cell, in *C* a long hair springs from the disc. *D* a two years old germling. *A—C* 625 : 1. *D* 350 : 1.

The principal conclusion from what has been set forth above is that Schmitz's view that the nemathecia are of a parasitic nature cannot be upheld. The nemathecia are outgrowths from the frond of *Ahnfeltia*, as maintained also by Gregory and Chemin. They are the only organs of reproduction and finally produce monospores. Sex organs and tetrasporangia do not exist. As to the interpretation of the very peculiar mode of reproduction of *Ahnfeltia* reference may be made to the discussion in my previous paper (1931, conclusions, p. 21—25). Here I shall merely emphasize that the generative cells appearing in the young nemathecia are considered as reduced procarps, and that the cell-filaments growing out from them are considered as corresponding to the sporophytic phase of the typical diplobiontic Florideæ. The frond and the primary nemathecial filaments make the first generation, corresponding to the gametophytic generation of the diplobiontic Florideæ, though sex organs are not produced, whereas the cell-filaments springing from the generative cells, the secondary nemathecial filaments and the monosporangia, belong to the second, sporophytic generation arising from the first without any process of fertilization. As no fertilization takes place and no other nuclear fusion has been observed, it must be supposed that no diploid nuclei occur, and it is in good accordance herewith that the number of chromosomes seems to be the same (4) in the two generations, and that the formation of the monospores takes place without chromosome reduction. The monosporangia must most probably be considered as reduced tetrasporangia which have failed to be divided owing to the wanting reduction division of the nuclei, and the nemathecia of *Ahnfeltia* would then be comparable to the nemathecia of *Phyllophora Brodiæi.* In the discussion in my previous paper (1931, p. 24), yet another interpretation has been taken into consideration, namely that the secondary nemathecial filaments might be considered as gonimoblast cell-rows. The whole complex of secondary nemathecial filaments would then be a compound cystocarpium and the monospores must be regarded as carpospores. This interpretation seems, however, to be less probable than the first. Comp. SVEDELIUS, Nuclear Phases and Alternation in the Rhodyphyceae. Beih. z. Botan. Centralbl. Bd. 48 (1931) Abt. I, p. 57.



A *B*

Fig 563 bis

Ahnfeltia plicata, f. *tenuior. A,* from NU, off Bovense, Store Belt. *B,* from aV, east of Samsø. 1.2 : 1.

The systematic position of the genus *Ahnfeltia* remains doubtful, as sex organs and cystocarps are wanting. The presence of nemathecia perhaps warrants its classification among the *Gigartinaceæ.*

Ahnfeltia plicata occurs in all the Danish waters except the Baltic Sea around Bornholm (**Bb**), from a little below low-water mark to 10 metres' depth, always growing on stones.

Localities **Ns:** Thyborøn, on a groin. — **Sk:** Hanstholm, washed ashore; 13 miles SW by W $^{1}/_{2}$W of Rubjerg Knude light-house, 14 m, sand, a small specimen (C. A. J.); Hirtshals, the mole, stones west of the mole, Emstenen. — **Lf:** Common on stony ground from Kobberød, 2—4 m, to Hals mole (F. Børgesen). — **Kn:** Krageskovs Rev; Hirsholmene; Strandby; stony reefs around Frederikshavn; several localities north of Læsø; Nordre Rønner; TL. — **Ke:** Søborg Hoved Grund and Vesterlands Grund at Gilleleje; Gilleleje harbour. — **Km:** Vesterø harbour Læsø; XF South of Læsø; BO off Stensnæs; Gerrild Bay (Lyngbye); KG off Nordstrands Klint, Anholt. — **Ks:** Grenaa harbour; NB, Havknude Flak; Jessens Grund; EJ and HQ, Lysegrund; Hesselø (Lyngbye); Lynæs harbour; GG, Sjællands Rev. — **Sa:** Common on stony ground. — **Lb:** Common from Bogense harbour to Brandsø, Linderum, at Sønderballe Hoved and dG, Hesteskoen. — **Sf:** CC, Hornenæs; CA near Faaborg; Ærø (Kjærbølling); Skaarupør (E. Rostrup). — **Sb:** Numerous localities along the coasts from 1 to 7 metres' depth, abundantly e. g.

off Stavreshoved near Kerteminde at 2—4 metres' depth. — **Sm:** Orehoved. — **Su:** Off Ellekilde and Hellebæk; Sletten harbour; Middelgrunds Fort. — **Bw:** Off Kobbel Skov, 1—2 m; dO, Bredegrund; fT south of Marstal, c. 10 m. — **Bm:** Præstebjergs Rev, 7 m.

Loose form: f. *tenuior* Lyngbye Tent. Hydr. 1819, p. 42.

In the inner Danish waters, in sheltered localities a loose form frequently occurs, in particular in the *Zostera*-formation, entangled among the rhizomes together with other loose Alga. It is well described by LYNGBYE under the above name, and authentic specimens collected at Hofmansgave by LYNGBYE are to be found in the herbarium of the Botanical Museum at Copenhagen. It is characterized by small dimensions (about 1—2 cm in diameter) and by the thin dichotomous frond with divaricate branches. It often forms irregular clumps with the branches pointing in all directions. It propagates by vegetative division, the frond by degrees dying away at the base during continued dichotomizing at the top (fig. 563 bis).

Localities. **Kn:** 6 miles SSW $^{1}/_{2}$ W of Læsø Trindel's light-ship, 8 m (C. A. Jørgensen); fE, east side of Krageskovs Rev, 7 m; Frydenstrand near Frederikshavn. — **Km:** XC, XE (Silderøn), KT and XF south of Læsø; 5$^{1}/_{2}$ miles N by E $^{3}/_{4}$ E of Østre Flaks light-ship (C. A. J.); entrance to Mariager Fjord (Th. Mortensen). — **Sa:** PL, Wulffs Flak; AS, Mejlgrund; aV between Samsø and Endelave, 10 m, abundantly; aY at Fyns Hoved; MQ south of Paludans Flak, 11 m; Endelave bay (Thomsen); Hofmansgave (Lyngbye); cU and NZ north of Fyn; at the beacon east of Æbelø. — **Lb:** FY and AX, Bjørnsknude; FZ, Kasserodde; dA, at the beacon Fyrrenden N.

VI. Rhodymeniales.

Fam. 16. Rhodymeniaceæ.

1. **Rhodymenia palmata** (L.) Grev.

Greville, Algæ Brit. 1830, p. 93; Harvey, Phyc. Brit. II, pl. 217 (1849); J. Agardh, Sp. g. o. Vol. II pars II (1852) p. 376; Thuret, Rech. s. la fécond. des Fucacées etc. Seconde partie. Ann. sc. nat. 4ᵉ sér. tome 3, 1855, p. 43, pl. 3, figs. 8, 9. Wille, Morph. og phys. Stud. over Alger. Nyt Mag. f. Naturvid., Bd. 33, II, 1891, p. 99. Buffham 1893, p. 294, Pl. 13, figs. 13, 14; V. M. Grubb, Prelim. Note on the reprod. of Rhodym. palm. Annals of Botany, Vol. 37, No 145, 1923; E. M. Delf and V. M. Grubb, The spermatia of Rhodymenia palmata, Ag. Ann. of Botany, Vol. 38, No. 150, 1924; Ch. Killian, Le développement morphol. et anatom. du "Rhodym. palm". Annales d. sc. nat. 10ᵉ sér. t. 8, 1926; Printz, Algenveg. d. Trondhjemsfjordes 1926, p. 72; M. A. Westbrook, Contrib. to the cytology of tetrasp. plants of Rhod. palm. Ann. of Bot., Vol. 42, No. 165. 1928.

Fucus palmatus L. Spec. plant. II, p. 1162 (1753).
Fucus bullatus O. Fr. Müller, Flora Danica, tab. 770, 1778.
Fucus caprinus M. Vahl, Flora Danica, tab. 1128, 1794.
Fucus delicatulus M. Vahl, Flora Danica, tab. 1190, 1797.
Sphærococcus palmatus Kützing, Phyc. gener. 1843, p. 409. Taf. 63 I, Tab. phyc. 18, Tab. 89, 90.

The frond springs from an orbicular attachment disc, but a smaller or greater number of fronds, besides the primary one, may issue from the same disc, though usually of a smaller size. An attachment disc more than 1 cm in diameter showed in the centre the remains of the decayed primary shoot, near it three fronds produced later, and at the border a great number of small, feebly developed fronds. The frond of the first year has a short cylindrical stipe which is flattened upwards into the wedge-shaped base of the flat frond. This may be undivided or more or less cleft at the top, the first is very often the case in the Danish waters. Young plants are found in summer, e. g. on the stipes or the laminæ of *Laminaria digitata* and *L. hyperborea*, and are easily recognisable by their structure. They must have arisen by germination of tetraspores produced in winter. The development of the young plants has been described by Killian (1926) on the basis of material from the above-named substratum. The growth of the frond stops at the end of summer. In specimens from greater depths and from the inner waters

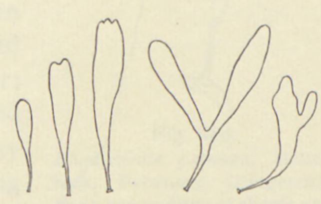


Fig. 564.
Rhodymenia palmata. Young plants growing on the frond of *Laminaria digitata*, August. Nat. size.

the frond of the first year is usually undivided or only feebly divided at the top, but adventitious shoots may be produced at the margins. Broad fronds more or

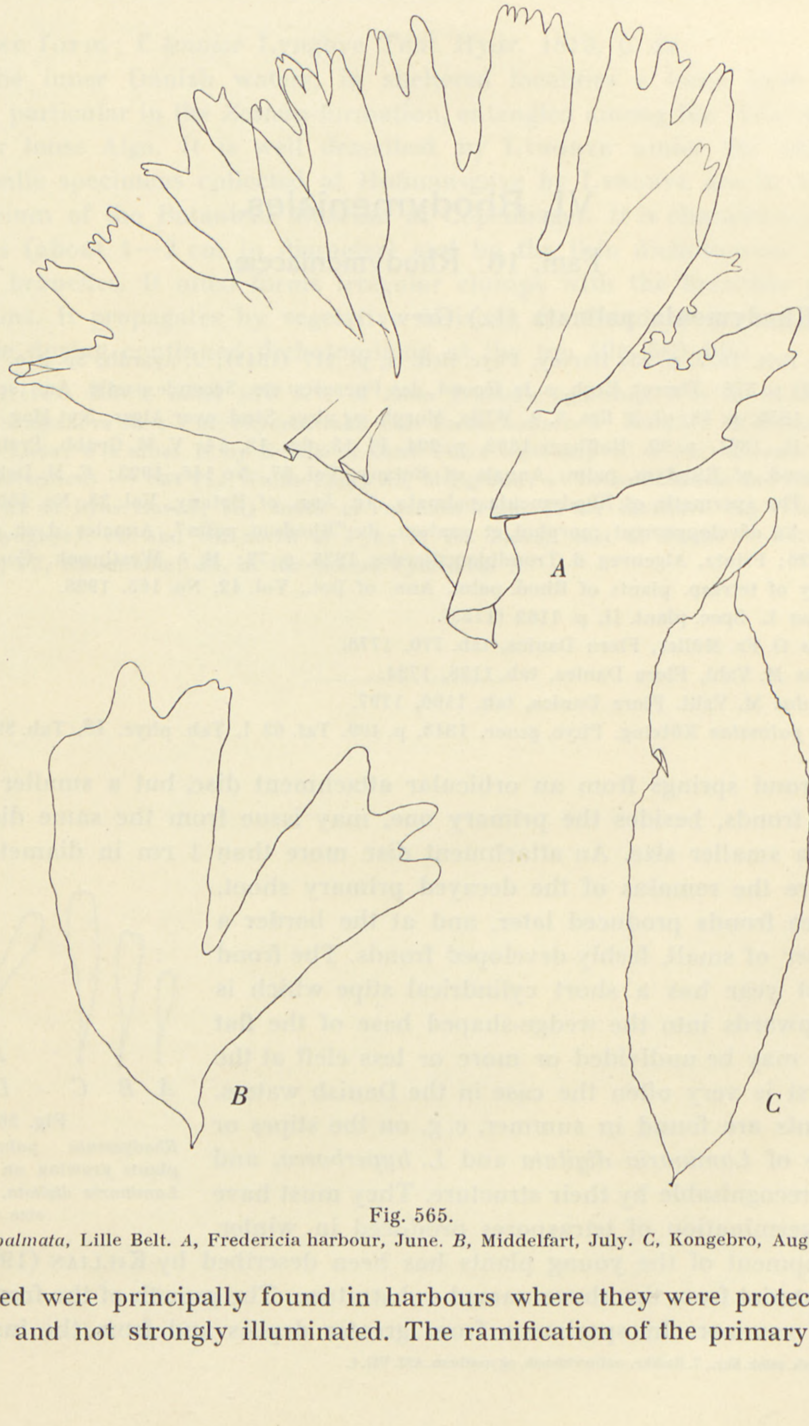


Fig. 565.
Rhodymenia palmata, Lille Belt. *A*, Fredericia harbour, June. *B*, Middelfart, July. *C*, Kongebro, August $^1/_2$ nat. size.

less divided were principally found in harbours where they were protected against the waves and not strongly illuminated. The ramification of the primary frond, and of the secondary segments, takes place by dichotomy or polytomy or, more rarely, in a more irregular manner, the growing power of the upper marginal zone ceasing at one or more points. KILLIAN has shown (l. c. p. 204) that a cleaving of the frond may also take place by longitudinal slits arising under the mechanical influence of the waves either accidentally or in certain predestined places, much as in the *Laminariæ*. It seems, however, that this mode of division is rarely realized in the Danish waters where the species never occurs in places so much exposed to the influence of the waves as on the rocky shores of the Atlantic.

Adventitious shoots arise at the margin of the frond in autumn and winter and grow out in the spring months to new assimilating frond segments. Their number is variable and their arrangement indeterminate. The segments are contracted at the base into a stipe, and this is usually so for the apical segments as well as for the lateral ones, and they have then all the character of adventitious shoots. Sometimes, however, though more rarely, there is only a slight or no constriction at the base of the apical segment or of the upper portion of the frond that has grown out after the last resting period, and the new portion then appears as a direct continuation of the old frond, produced by continued activity of the same marginal meristematic zone. Comp. fig. 566. Such cases were in particular observed among the broad fronds growing in harbours and further in repeatedly dichotomously divided narrow specimens from the Øresund. The difference between the new and the old frond is usually very distinct owing to the brighter colour of the first, and often too owing to the presence of organs of reproduction on the latter. It may happen that the upper portion of the frond dies or is eaten by animals in the course of the first year; adventitious shoots are then produced from the cicatrized border of the resting frond. The marginal fronds may produce new marginal adventitious fronds in the following winter, and the same process may be repeated once more. Three or four generations of shoots frequently occur, from which it can be concluded that the frond may reach an age of three or four years (fig. 566). The frond often attains a length of 20 cm, more rarely 24—27 cm (Lille Belt, Øresund). The frond segments of each year usually measure 10—13.5 cm.

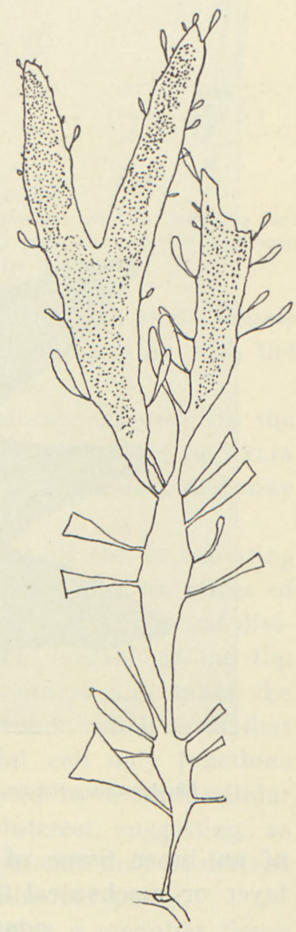


Fig. 566. *Rhodymenia palmata*. Hellebæk, February (Børgesen). Four generations of shoots are to be seen. Nat. size.

As to the structure of the adult frond reference may be made to WILLE (1891). The marginal meristematic zone at the upper end of the frond does not show particular apical cells nor a marginal series of apical cells but consists of a great number of close cells without distinct arrangement. The frond is built up

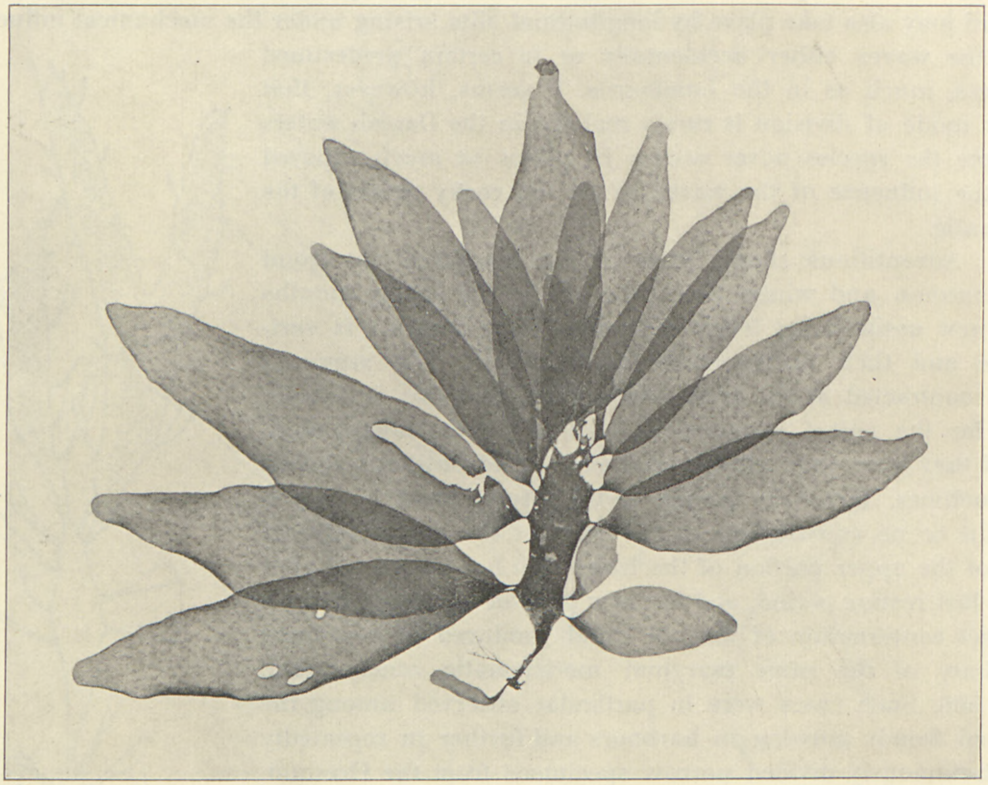


Fig. 567.
Rhodymenia palmata. From Eastern Kattegat, near Læsø Trindel, 19 m. May. Photo, $^2/_3$ nat. size.

of an inner tissue of one or two layers of large thick-walled cells, a medullary layer or mechanical tissue (Wille 1891, p. 104), and an outer assimilating tissue consisting of 1 to 2 layers of smaller cells containing numerous chromatophores (fig. 568). An intermediate layer, (secondary mechanical tissue Wille), is situated between the assimilating and the medullary layers.

Fig. 568.
Rhodymenia palmata. Superficial cells from young plant. 622 : 1.

The young fronds and frond-segments bear numerous hyaline hairs, developed from ordinary peripherical cortical cells from which they are separated by a basal wall situated at the level of the surface of the frond (fig. 569). The hairs appear on the young plants, but only when they have reached a length of about 8 mm. In the older fronds the hairs only occur in the young segments while they are still growing. The hairs are very numerous but are confined to distinct spots, where each superficial cell may bear a hair, while no hairs are found outside these spots (fig. 569, comp. L. K. R. 1911, p. 212). They are easily visible in the living plants, and the spots can be distinguished in dried specimens (fig. 567). The hairs were met with in the months of March to July; they are then shed, and the plants are hairless from August to the end of the winter. The hairs were first described by WILLE (1891, p. 103). V. M. GRUBB took them for trichogynes (1922, p. 151), a view which cannot be maintained, as true procarps have never been ascertained, and as the hairs occur on tetraspore-bearing and on male individuals, while female specimens are unknown; the hairs are purely vegetative organs agreeing with the hyaline hairs of such common occurrence among the Florideæ.

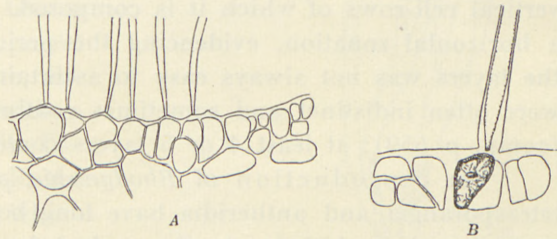


Fig. 569.
Rhodymenia palmata. A, transverse section through a part of a spot of hairs (400 : 1). *B*, base of a hair (630 : 1). (From K. Rosenvinge 1911, p. 212).

The large medullary cells do not contain starch as storage matter. On the other hand the frond contains a soluble carbohydrate which, according to KYLIN (Zeitschr. physiol. Chemie **101** 1918, p. 245), is trehalose and may amount to 14.8 p.c. of the dry weight.[1]

KILLIAN has followed the development of the germinating spores, without doubt tetraspores, which he found on stipes of *Laminariæ*. The spore is divided by vertical and horizontal divisions, forming an hemispherical attachment organ, at the top of which a cell becomes larger than the others and takes the function of the initial cell of the young frond, which is at first fusiform, later flattened. The apical initial cell only functions in the quite young frond; it is early replaced by a multicellular meristeme, but its existence is of great interest, suggesting, as emphasized by KILLIAN, that *Rhodymenia palmata* may be derived from the type with a central axis ("Centralfadentypus").

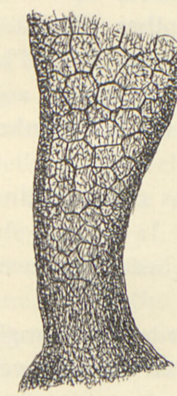


Fig. 570.
Rhodymenia palmata. Stipe of young plant. The large cells of the medullar tissue are to be seen in the upper part of the stipe. About 50 : 1.

The upper portion of the stipe contains a medullar tissue gradually tapering downwards. In a cross section it appears as an oblong or elliptical group of large cells sharply bounded towards the thick cortical tissue composed of radiating cell-rows. This cortex shows stratification in older fronds (comp. JÖNSSON 1891, p. 23, KILLIAN 1926, p. 207). In a specimen from Skagen, which was judged to be two or three years old, the presence of two or three layers in the cortex was ascertained.

[1] According to a recent note by H. COLIN and É. GUÉGUEN the sweet principle of this Alga is a monogalactose of glycerol. (Acad. d. sciences, Paris, July 21, 1930; cited from Nature, No. 3176, Vol. 126).

The attachment disc increases in diameter by marginal growth (comp. KILLIAN 1926, p. 206), but the thickness increases too by continued apical growth of the vertical cell-rows of which it is composed. The large disc mentioned above showed a horizontal zonation, evidencing the periodicity of the growth. The number of the layers was not always easy to ascertain, because the limits between the layers were often indistinct and sometimes confluent, much as in the cortex of *Ahnfeltia* (comp. p. 559); at least 4 or 5 layers could be distinguished.

The reproduction of *Rhodymenia palmata* is remarkable by the fact that tetrasporangia and antheridia have long been known while female sex organs and cystocarps have hitherto been searched for in vain.

The tetrasporangia are produced in irregular patches on both sides of the frond; they arise from superficial cells, being early cut off from a stalk-cell, which remains short, while the surrounding sterile cells divide by transverse walls, forming short cell-rows which make up the greater part of the sori (comp. KÜTZING, 1843, Taf. 46 I). The sporangia are cruciately divided. The development and the cytology have been carefully examined by Miss M. A. WESTBROOK (1928). Reference is made to this publication for details, the principal facts only will be related here. In the prophase of the first division of the tetrasporangium a double spireme stage and a synizesis were ascertained, and although this occurrence "is not absolute proof of meiosis, the constant association of the three in the sporangia of other Florideae suggests that in *Rhodymenia* too chromosome reduction is effected" (p. 164). The number of chromosomes could not, however, be determined with certainty, and the reduction division is therefore not quite settled. In the cortical cells, the number of chromosomes was judged to be greater than twenty.

The ripe tetraspores, according to WESTBROOK, contain numerous starch grains, small discoid plastids and an inconspicuous central nucleus.

The sori arise in the fronds or frond-segments which have been produced the winter before.

The development of the sori probably begins in autumn, for ripe tetrasporangia occur in winter (January to April). But the first stages of the sori were not observed by me. In the fertile specimens gathered in March and April, the sporangia were to a great extent exhausted. It seems that the tetraspore-bearing parts of the fronds normally die after the dissemination of the spores. Sori are therefore not to be found in summer and early autumn; in two cases only emptied sori were still met with in July (**Bw**) and September (**Ks**).

At more northern coasts the occurrence of the tetrasporangia is not limited to the winter, for at Iceland (JÓNSSON) and in Trondhjem Fjord (PRINTZ) they may be met with the whole year, and at the isles of Færöe they were met with in April, May, June and November (BØRGESEN), while at the coasts of England and France (Cherbourg) they only occur in winter.

The antheridia form patches on both sides of the frond similar to the tetrasporic sori but of a paler colour. They were first mentioned and figured by THYRET

(1855, p. 43, figs. 8—9), later by Buffham (1893, p. 294, pl. XIII, figs. 13—14), and more recently E. M. Delf and V. M. Grubb have given an account of their development (1924). According to the latter authors, the development of the male sori begins with a transverse division of the superficial cells. The lower cell thus formed is the basal cell, the upper one the antheridial mother-cell, which can produce in alternate succession at least four antheridia. Male specimens were met with in March and April.

Female sex organs and cystocarps are quite unknown; and as they have certainly been searched for repeatedly by many algologists in this wide-spread alga, it seems probable that they are really wanting. As mentioned above (p. 573), the interpretation of the hyaline hairs as trichogynes cannot be maintained. When the carpogonia are wanting, the question of the occurrence of a reduction division in the developing tetrasporangium will be of great interest. In case the reduction division can be definitely ascertained, a mixie might be supposed to take place at one or other moment of the life-history of the species. If a regular meiosis does not take place, there will be good accordance with the fact that a normal fertilization does not occur. In any case the spermatia are functionless though their structure is apparently quite normal. According to the facts known it must most likely be assumed that the reduction division in the tetrasporangia is initiated but not fulfilled owing to the wanting process of fertilization.

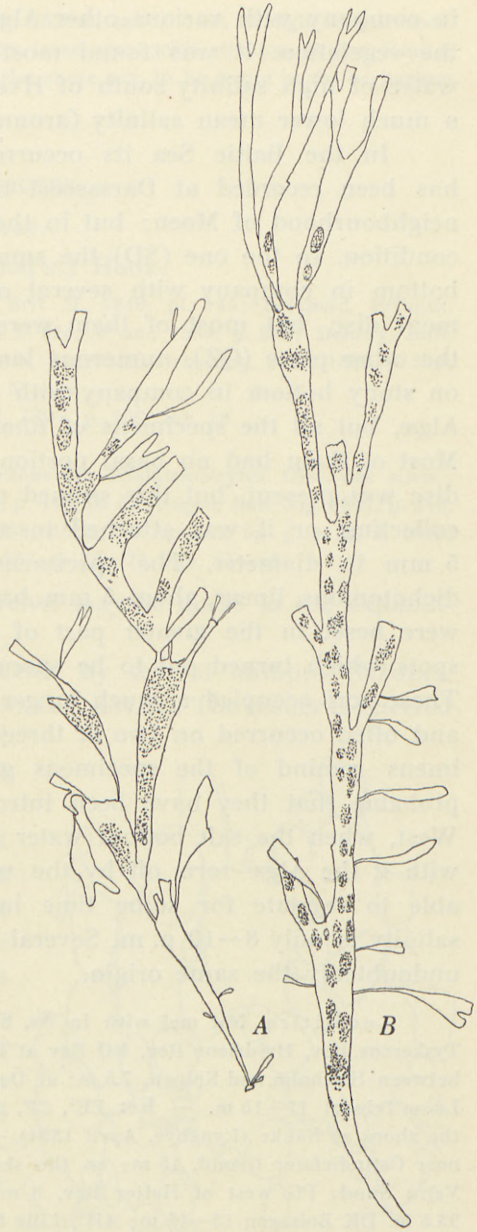


Fig. 571.
Rhodymenia palmata. From the Baltic, QZ off Møens Fyr, 7.5 m, July 1894, ²/₃ nat. size.

Rhodymenia palmata grows on stones and on various Algæ, most frequently on the stipes of *Laminaria digitata* and *hyperborea*, further on *Fucus serratus*, *Furcellaria fastigata*, *Chondrus crispus*, *Phyllophora membranifolia* and on roots of *Zostera*. It occurs most frequently at depths of (5), 7—20 m, more rarely down to 24 m. At slighter depths, 1 m, it has only been met with in harbours (Frederikshavn, Lille Belt). It grows in company with various other Algæ and usually constitutes only a slight part of the vegetation. It was found most abundantly in the Øresund, not only in deep water of high salinity south of Hveen but also at smaller depths in localities with a much lower mean salinity (around Taarbæk Rev).

In the Baltic Sea its occurrence seems rather dubious. It is true that it has been recorded at Darsserort by REINKE and in two localities in **Bm** in the neighbourhood of Møen; but in the two latter places it only occurred in a loose condition. In the one (SD) the small specimens were found in deep water on sandy bottom in company with several other loose Algæ; the specimens had an attachment disc, but most of them were attached to loose specimens of *Furcellaria.* In the other place (QZ), numerous long specimens were found at 7 or 8 metres' depth on stony bottom in company with *Fucus vesiculosus, Fuc. serratus* and other attached Algæ, but all the specimens of *Rhodymenia palmata* were certainly loose (fig. 571). Most of them had no basal portion; in some of them, to be sure, an attachment disc was present, but this seemed not to have been in function at the moment of collecting, or it was attached to a fragment of *Furcellaria* or a little stone only 5 mm in diameter. The specimens were long (up to 28 cm), mostly repeatedly dichotomous, linear, about 5 mm broad; although collected at the end of July they were beset in the greater part of their length with more or less confluent dark spots which turned out to be sporangial sori with checked sporangial mother-cells. These sori occupied a much longer portion of the frond than in the normal fronds and often occurred on two or three consecutive frond segments. Altogether the specimens remind of the specimens growing in the Øresund, and it seems highly probable that they have been introduced into the Baltic Sea by storms from the West, when the salt bottom water overflows the threshold at Saltholm and carries with it the Algæ torn off by the movements of the water. They have then been able to vegetate for some time in the loose condition in a locality where the salinity is only 8—10 p. m. Several other Algæ occurring here in loose forms have undoubtedly the same origin.

Localities. Not met with in **Ns**, **Sk** and **Lf**. — **Kn:** Harbour of Skagen; NV Rev, 7—9 m, Tyskerens Rev, Hvidstens Rev, NØ Rev at Hirsholmene; east of Græsholm, south of Hirsholm, 11 m; between Hirsholm and Kölpen, 7.5 m; at Deget; harbour of Frederikshavn; Tønneberg Banke 16—18 m; Læsø Trindel 11—15 m. — **Ke:** ZE[1], ZF, fH, Fladen, 17—22.5 m; Groves Flak 19 m (Børgesen); on the shore at Nakke (Lyngbye, April 1834). — **Km:** Gjerrild Bugt (Lyngbye, on the shore). — **Ks:** RL, near Ostindiefarer Grund, 15 m; on the shore at Tisvilde (Lyngbye) and Rørvig (E. Rostrup). — **Sa:** Vejrø Sund; PG west of Hatter Rev, 8 m; GD, north point of Sejerø, 11—14 m; PE off Revsnæs, 23.5 m. DK Bolsaxen 13—15 m; AH[1], Lille Grund at Fyns Hoved, 9.5 m. — **Lb:** Fredericia, harbour; Strib, harbour; Middelfart, harbour and 15—20 m (Rasch,!); Kongebro; off Snoghøj, 15—19 m; Fænø Sund; off Stenderup, 13—15 m. — **Sb:** GU, off Asnæs, 19 m; GP, at Halskov Rev, 10—11 m; UE, at Vresens Puller, 7 m. — **Su:** Hellebæk on the shore (Børgesen); Kronborg, on the shore (Nolte, C. Rosenberg, Steenberg, Ørsted); PZ, east of Hveen; TF[1], Staffans Flak, 12—13 m; bM, south of Hveen, 22.5 m; OH and bN, off Vedbæk, 10 m; east of Taarbæk Flak, 12.5 m, (S. Lund); Taarbæk Rev, 12—15 m, abundantly; OG[1], between Trekroner and Middelgrund. — **Bw:** Not observed by me; according to Reinke not met with in the western Baltic except at Darsserort at 20 metres' depth. — **Bm:** On the shore at Stevns (C. H. Ostenfeld); SD, N.E. of Møens Klint, 23.5 m, sand, loose, though several spec. with attachment disc; QZ off Møens Klint, 7.5 m, abundantly, loose, some with attachment disc. Similar specimens collected by Liebman at Møen, undoubtedly on the shore, are to be found in the herbarium of the Botan. Museum of Copenhagen.

Fam. 17. Champiaceæ.

Chylocladia Grev.

1. **Chylocladia kaliformis** (Good. et Woodw.) Hook.

Hooker, British Flora Vol. I, 1833, p. 297; Harvey, Phyc. Brit. II, 1849, pl. 145; Berthold, Pringsh. Jahrb. XIII, 1882; Debray, Bull. sc. du dép. du Nord 2e Sér., 9e an., 1886, p. 258; Debray, Bull. sc. de la France et Belg., t. 22, 1890, p. 405; Hauptfleisch, Fruchtentwickelung, Flora 1892, p. 360; Hassencamp. Bot. Zeit. 1902; Kylin, Studien 1923, p. 37—44.

Fucus kaliformis Good. et Woodw., Trans. Lin. Soc. Vol. III, 1797, p. 206, tab. 18.

Gastridium kaliforme Lyngb. 1819, p. 70.

Lomentaria kaliformis Gaillon, Résumé méth. des classifications des Thalassiophytes. Dict. des scienc. nat. Strasbourg 1828, p. 19; Kützing, Phyc. gen. 1843, p. 440, pl. 55; Nägeli, Neu. Alg. 1847, p. 246, tab. X, figs. 13—21. Flora Danica (Liebman) tab. 2578, 1852; J. Agardh, Sp. g. o. II, 3, 1863, p. 731; Kützing, Tab. phyc. 15 tab. 86, 1865; Wille 1887, p. 76—79, figs. 55—64.

As to the nomenclature of the species, reference may be made to the explanation by Hauptfleisch (1912, p. 308).

The structure of the frond has been treated by several authors (Nägeli, Berthold, Wille, Debray, Hauptfleisch, Hassenkamp, Kylin). The reader is referred principally to the papers of Hassenkamp and Kylin quoted above; here only the most important facts will be adduced. The frond is tubular, articulated with diaphragms at the constrictions. The wall of the frond is composed of one layer of large cortical cells, from the outer edges of which smaller cells are cut off by oblique walls. These small cells do not form a continuous layer but form a reticulate system of outer cortical cells. The large, primary cortical cells are at first angular, nearly isodiametrical, when seen from the face; later they increase considerably in the direction of the longitudinal axis of the frond. — There is not one apical cell at the tip of the frond, as indicated by Nägeli and Wille, but a number of cell-rows meet at the apex, each with an apical cell dividing by transverse walls. Within the cortex run a number of about 16 to 20 longitudinal, narrow cell-rows, and at regular intervals the cavity of the frond is traversed by septa composed of a single layer of cells. The

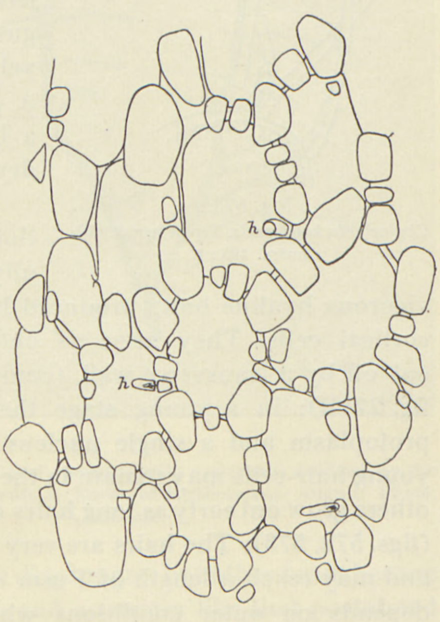


Fig. 572.
Chylocladia kaliformis. Surface view of frond. *h*, hair-cells. 200 : 1.

large cortical cells originally contain one nucleus, later a greater number (comp. KYLIN 1923, p. 39), and numerous very small chromatophores, situated at the outer wall or at the anticlinal walls, or even at the inner wall of the cells; they are orbicular or shortly rod-shaped, often arranged in curved rows. The refractive bodies observed by BERTHOLD (1882, p. 690) in the large cortical cells in specimens growing in sunny localities at Naples, were not met with in the Danish waters, but that is undoubtedly due to the fact that the species here is exposed to a much smaller intensity of light; it always occurs in rather deep water (7—18 m), the sea-water is much more troubled here than usually in the Mediterranean, and the sunlight does not penetrate so deeply, owing to the smaller height of the sun. The blue iridescent gloss of the plant described by BERTHOLD I have never seen; nor does it seem to have been observed at the coasts of the British Islands. The colour of the living plants collected in July and August is bright pink, often yellowish or greenish. A greenish plant took a bright pink colour in drying.

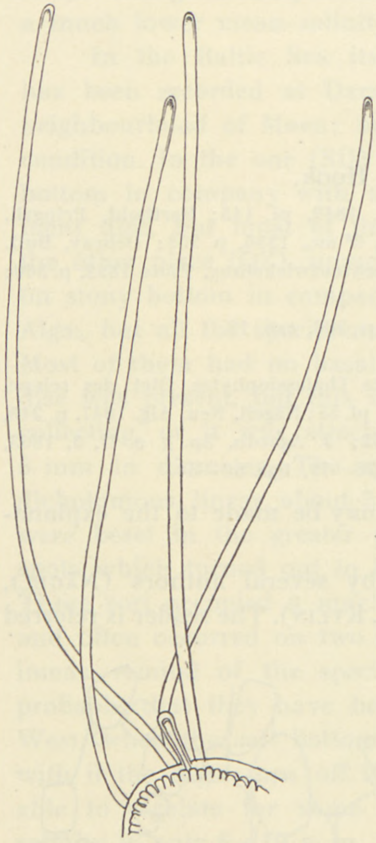


Fig. 573.
Chylocladia kaliformis. Tip of frond with hairs. 195 : 1.

The younger portions of the frond usually bear numerous vigorous hyaline hairs produced by some of the small cortical cells. They arise as outgrowths from these, cut off by a transverse wall (comp. KYLIN 1923, p. 38, fig. 27 d); in a young stage they contain abundant protoplasm and a single nucleus. A number of these young hair-cells may remain in the juvenile stage, while others grow out early as long hairs of the usual structure (figs. 572, 573). The hairs are very thick, about 9—11 μ, and may reach a length of 1 mm or more. It probably depends on outer conditions whether the hair-cells grow out or remain rudimentary. Comp. BERTHOLD (1882, p. 692), who found that their occurrence is largely

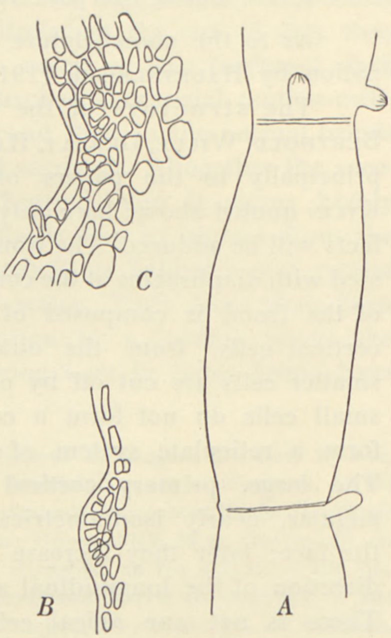


Fig. 574.
Chylocladia kaliformis. *A*, portion of frond with adventitious shoots at the constrictions, above two shoots above the constriction, below a shoot below the constriction and to the left a quite young shoot exactly in the constriction. 63 : 1. *B*, the last-named shoot 200 : 1. *C*, young shoot over the constriction 200 : 1.

determined by the intensity of the light. In the Danish waters the hairs were constantly met with in July and August and were also observed in September.

Ramification. The most common mode of ramification of the frond is lateral, the branches arising at some distance from the tip, in the young furrows, exactly at the level of the diaphragms or a little higher. One, two or three, or rarely more branches may arise in the same furrow, and the branches are therefore often verticillate, but the branches of the same furrow do not arise simultaneously. The development of these branches is altogether acropetalous, but some furrows remain branchless, especially in the branches. According to Debray (1886, p. 15), the branches "proviennent des cellules du diaphragme adhérentes à la couche corticale. Si la paroi présente plusieurs assises de cellules, les petites cellules extérieures sont soulevées et séparées les unes des autres par le bourgeon se formant au-dessous d'elles". It is, however, not obvious from the description of Debray, which is not illustrated by drawings, whether it refers to *Ch. Kaliformis* or to a related species. At any rate, my obervations, which are, however, not very thorough, do not agree with that of Debray. True, the branches often arise exactly in the middle of the furrow, at the level of the diaphragm, but other branches are evidently placed at a little distance above this level, and an origin like that postulated by Debray is consequently precluded. My observations seem to accord better with the assumption that the branches take rise from divisions of superficial cells (fig. 574).

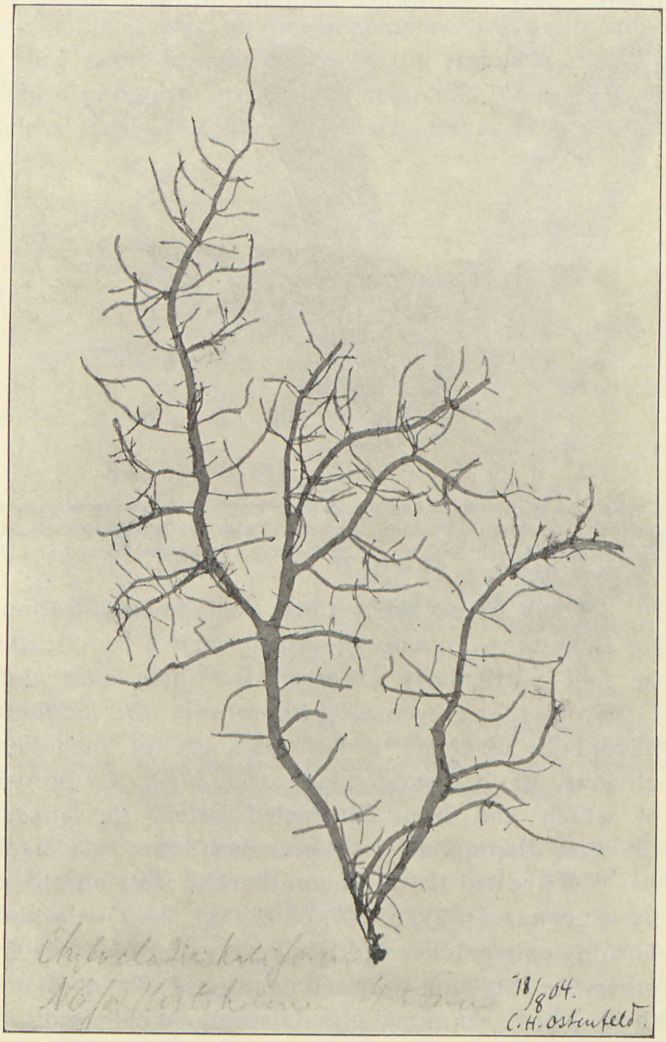


Fig. 575.
Chylocladia kaliformis. Dried specimen with cystocarps dredged by the late Professor C. H. Ostenfeld, North of Hirsholmene. August. Photo, $^{2}/_{3}$ nat. size.

In older portions of the frond adventitious branches arise in indeterminate places. They seem to arise, like the primary ones, by divisions of one or a number of superficial cells. The adventitious shoots may be rather numerous in older fronds; they are thinner than the primary ones.

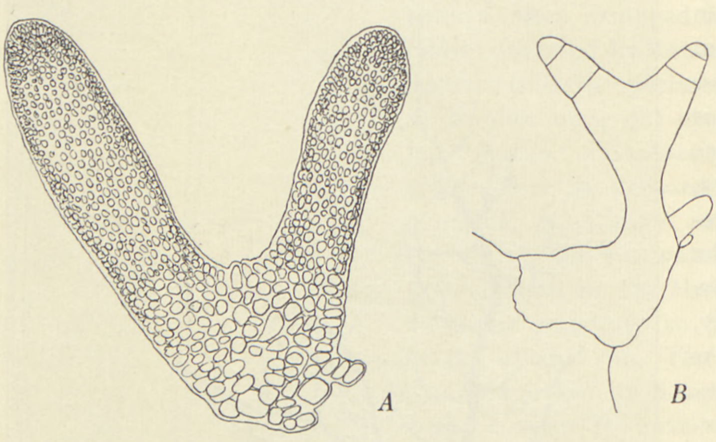


Fig. 576.
Chylocladia kaliformis. Young plants growing on a cystocarp-bearing specimen of *Chylocladia kaliformis.* August. *A*, with two fronds springing from the same attachment disc. 105 : 1. *B*, showing a dichotomy of the frond. 70 : 1.

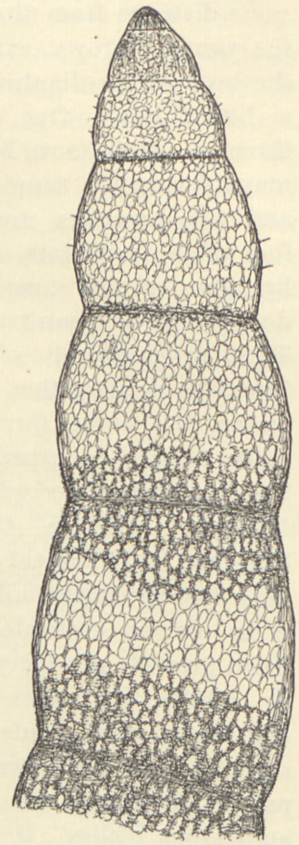


Fig. 577.
Chylocladia kaliformis. Upper end of frond of male plant with annular patches of antheridia-producing cell-rows. August. 30 : 1.

There exists yet a third mode of ramification, namely by dichotomy. Debray described such a ramification which he had particularly observed in *Chylocladia mediterranea* (1886, p. 13). I seems to be rare in *Ch. kaliformis*, for I have only observed a few instances of dichotomy, most obvious in a young plant (fig. 576), the growing-point of which had been bifurcated before the appearance of the first diapraghm; both branches show two diaphragms[1].

Reproduction. The antheridia were shortly described by Buffham (1891, p. 249, pl. 15, figs. 3—4) who found them forming pale patches as irregular rings around the frond, but otherwise they have not been mentioned; Kylin dit not observe them. I have examined a male specimen collected in August at Hirsholmene and preserved in alcohol by Mr. Boye Petersen. The ring-shaped patches detected by Buffham arise near the apex of the frond, in the transverse furrows at the level of the diaphragms. They are originally narrow, occupying only the furrow itself but increase early at their upper and lower margins and then form rather broad belts with irregular borders. In the young rings and at the borders of the older ones a great number of very small cells bud off from the edges of the cortical cells. These

[1] I have observed the same ramification in *Ch. kaliformis* var. *squarrosa* at Biarritz; some joints were found to be bifurcate.

cells divide actively and form close cell-rows growing inward from the edges of the cortical cells which are thus covered by a reticular layer the meshes of which diminish gradually in diameter by the growth of the creeping cell-rows, and the older parts of the fertile layer may finally be continuous, covering also the central parts of the cortical cells. From the upper side of the creeping cell-rows new small cells are early bud off, forming very short upright cell-rows the end-cells of which produce each a spermatium. The spermatia are shortly obovate, about 4 μ in diameter and contain a large nucleus (figs. 578 *C, D*). The spermatial layer is covered by a thick gelatinous layer (comp. BATTERS l. c.) which renders it very difficult to obtain good thin sections showing the development of the antheridia.

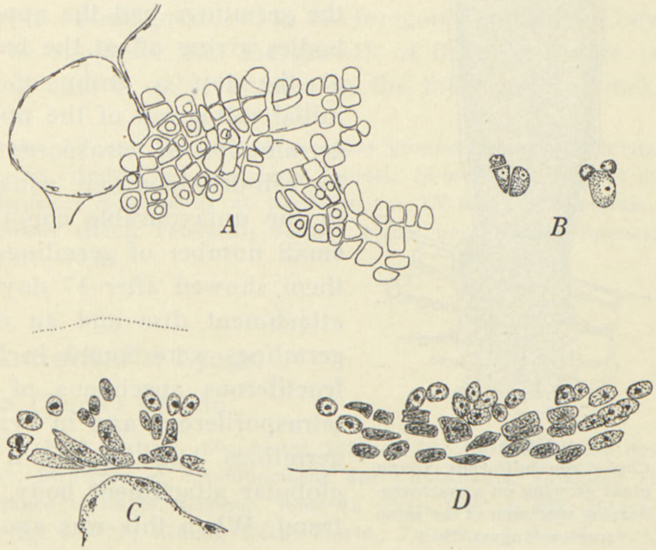


Fig. 578.
Chylocladia kaliformis. Antheridia-producing cell-rows. *A*, seen from the outside. *B*, isolated antheridia-bearing cells. *C* and *D*, transverse section of the antheridia-producing layer. 625 : 1.

The development of the carpogonial branch and of the cystocarp have been examined by several authors (JANCZEWSKI, SCHMITZ, HAUPTFLEISCH, HASSENKAMP and, latest and most exhaustively, by KYLIN (1923)). As I have nothing to add, I shall content myself by referring to the excellent paper of KYLIN, adducing only the principal facts. The curved 4-celled carpogonial branch is borne on one of the large cortical cells. This supporting cell has early cut off two lateral cells which become auxiliary mother-cells. These cells (or one of them) bud off an auxiliary cell, before the fertilization. The fertilized nucleus of the carpogonium divides in the carpogonium, which forms two protuberances fusing with the two auxiliary cells. The auxiliary cell buds off outwards a cell, the first gonimoblast cell which is divided by radial walls into a number of pyramid-shaped cells which divide by a cross wall into an inner, smaller, and a larger outer cell; the latter is the young carpospore, the inner cells fuse together with the auxiliary cells. By further fusions of the basal cells with the auxiliary cells and with cells of the inner fruit-wall a large fusion cell arises which bears the carpospores on the outer side. The large globular cystocarp is surrounded by a wall without apical pore, built up of 3 or 4 layers of cells.

The tetrasporangia are irregularly spread in the cortex. As shown by KYLIN (1923, p. 43), they arise from large cortical cells of the 3rd or 4th order which are not

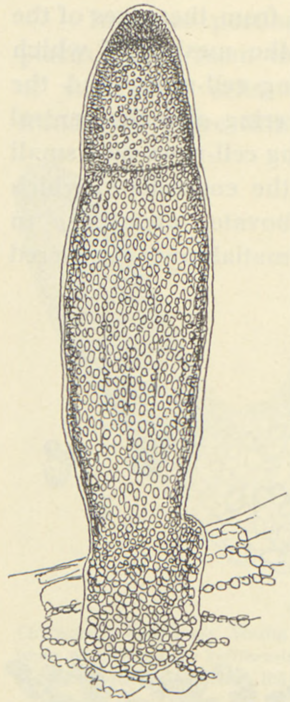


Fig. 579.
Chylocladia kaliformis. Young plant growing on a cystocarp-bearing specimen of the same species. August. 75 : 1.

terminal cells but segment cells, and are therefore connected with at least two neighbouring cells by primary pits. The ripe tetrasporangia project into the central cavity (comp. KÜTZING, Phyc. gen., tab. 55 IV).

The germination of the tetraspores begins, according to KYLIN (1917, p. 5), by formation of vertical walls by which the spore is divided into four quadrant cells which are then further divided by horizontal walls. After 6 days the germlings had the appearance of multicellular globular bodies giving off at the base some 4 rhizoids, and showing at the top a group of smaller, meristematic cells, the initial cell-group of the upright frond. I have examined the germination of tetraspores and carpospores in cultures, but the cell-divisions were usually irregular, without doubt owing to the unfavourable conditions in the cultures, and only a small number of germlings resulted. The best developed of them showed after 17 days a thick, more or less orbicular attachment disc and an erect shoot issuing from it. Older germlings were found in Nature, the youngest growing on fructiferous specimens of *Chylocladia kaliformis,* both in tetrasporiferous and in cystocarp-bearing individuals. These germlings had usually a thick, hemispherical or nearly globular attachment body, and springing from it an upright frond. When this was about half a mm high, it was cylindrical without constrictions, and with an outer layer consisting of small, rather uniform cells. Not unfrequently two fronds were issuing from the same attachment disc (fig. 576). In the germling represented in fig. 579, which was about 1 mm high, the frond is inflated, hollow with at least one septum and with longitudinal cell-rows in the cavity. The identity with *Chyl. kaliformis* was thus indubitable. These germlings were met with in August and probably originated from spores of the fronds on which they were found growing. More developed young plants, met with in September and October, were only from a few mm to 2 cm high; they were provided with hairs, but only feebly developed or rudimentary.

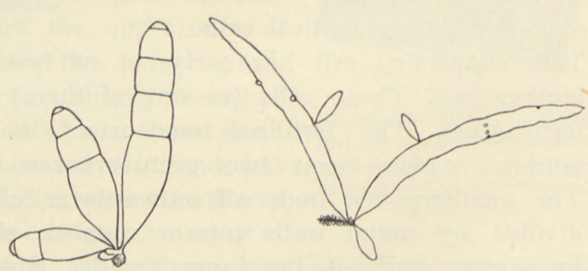


Fig. 580.
Chylocladia kaliformis. Young plants, growing on *Rhodomela* and *Brongniartella*, September. *A*, 3.5 : 1. *B*, 2 : 1.

The species has only been met with in the Northern and Eastern Kattegat. Its absence in the North Sea and Skagerak is certainly due to the want of protected localities. It has been met with at 8—19 metres' depth in water of comparatively high salinity (about 30 p. m.) on gravelly or stony bottom, but is very often attached to other Algæ (*Phyllophora membranifolia, Furcellaria fastigiata, Brongniartella byssoides, Corallina officinalis*) or to dead leaves of *Zostera*. It has only been observed in the months of July to October. Well developed fructiferous specimens, up to 26 cm high, were met with in July and August, but they seem to die away at the end of summer, for in September small specimens only were observed. Germlings were found in Nature already in August, and the small specimens found in September must be supposed to originate from spores produced in the foregoing summer. They were all sterile. It must further be supposed that the growth of the new plants is arrested during winter and spring and is only resumed in the following summer.

Localities: **Kn:** Tønneberg Banke, TP and PO, 16—18 m, stony ground, young specimens, September; TQ, near the light-ship at Læsø Trindel; FF, near Læsø Trindel, 15 m; Nord Øst Rev at Hirsholmene; east of Hirsholmene (Ostenfeld); Nordvestrev at Hirsholmene; TY south of Hirsholm, east of Kølpen (A. Otterstrøm); Trestensrev (Henn. Petersen); various places near Nordre Rønner; 7—11,5 m. — **Ke:** ZG, ZE[1], VY, Fladen, 17—19 m.

Lomentaria Lyngb.

1. **Lomentaria clavellosa** (Turn.) Gaillon.

Gaillon, Dictionnaire des sciences natur. Vol. 53. Extrait, Strasbourg 1828, p. 19; Le Jolis, Liste des Alg. mar. 1864, p. 132; F. Debray, Structure et développement des Chylocladia, Champia et Lomentaria. Bull. scient. de la France et de la Belgique, tome 22. Paris 1890, p. 399; Hauptfleisch, Flora 1892, pp. 325—350, figs. 58—77; Killian, Entw. Florid., Zeitschr. f. Bot. **6**, 1914, pp. 246—248; Kylin, Studien, 1923, pp. 44—49.

Fucus clavellosus Turner, Trans. Lin. Soc. VI, 1801, p. 133, pl. 9, Hist. Fucorum I, 1808. tab. 30.

Gastridium clavellosum Lyngbye 1819, p. 70, tab. 17.

Chondria clavellosa C. Agardh, Spec. alg. Vol. I, 2, 1832, p. 353; Hornemann, Flora Danica tab. 2200, 1834.

Chylocladia clavellosa Grev. in Harvey's Manual 1841, p. 71; J. Agardh, Sp. g. o. II, 2, 1852, p. 366.

Chrysymenia clavellosa J. Agardh, Alg. m. medit. 1842, p. 107; Harvey Phyc. Brit. I, 1846, pl. 114.

Chondrothamnion clavellosum Kützing, Tab. phyc. XV, tab. 81, 1865.

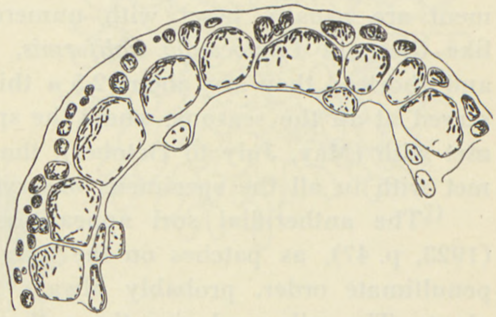


Fig. 581.
Lomentaria clavellosa. Cross section of frond. 420 : 1.

As emphasized by earlier author's e. g. Kylin (1923, p. 44) there is much accordance between *Lomentaria clavellosa* and *Chylocladia kaliformis* as to the structure of the frond. The cortex forming the wall of the hollow frond consists, at least in older portions, of two layers of cells, the outer layer of smaller cortical cells being here continuous. The medullary longitudinal filaments (fig. 581) are more irregular and often connected with each other by lateral pits. Diaphragms are wanting.

The fronds spring singly or several from a flat or cushion-shaped attachment disc (fig. 582). The branches arise at some distance below the apex; they are sometimes opposite, more frequently alternate, biseriate and the fronds are therefore often flat, but the branches may also issue from all sides of the branches. When the branches are regularly opposite or alternating, distichous at regular intervals, it seems probable that the branches correspond to the verticils in *Chylocladia*, and the regions where they are inserted to the diaphragms. Adventitious branches with indefinite position may occur later; they are much smaller than the primary ones. Some shoots grow out and obtain a similar length and character to those of the main shoot, others remain short, but there are all transitions between the long and the short shoots. I have once met with a branchlet ending in an attachment disc (fig. 583); it occurred as a branch of the second order at some distance from the base in a specimen growing on the Bryozoan *Valkeria uva*.

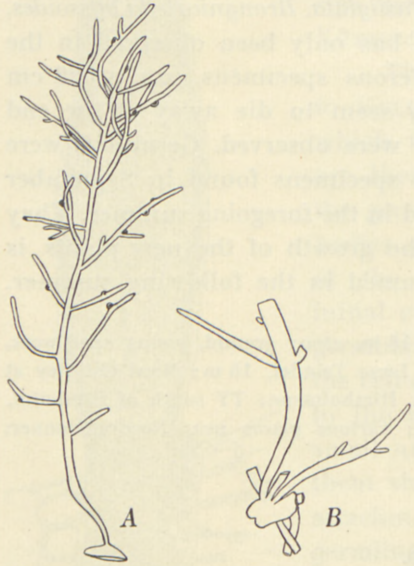


Fig. 582.
Lomentaria clavellosa. *A*, small plant with cystocarps from Skagerak off Lønstrup, August. 3.3 : 1. *B*, lower portion of plant growing on *Desmarestia aculeata*, Hirsholm, October. 4.7 : 1.

The principal branches come near to the main frond in length and thickness; the latter attains a diameter of 1 to 1.5 mm. The branches of higher orders are much narrower, often very thin. Specimens referable or approaching to f. *sedifolia* have not been met with at the Danish coasts; the specimens growing here are always very slender.

The young portions of the frond still in development are usually beset with numerous hyaline hairs, like those in *Chylocladia kaliformis*, but much thinner and shorter; they are about 2.5 μ thick. They were observed at all the seasons, where the species was generally met with (May, July to October), though they were not met with in all the specimens observed.

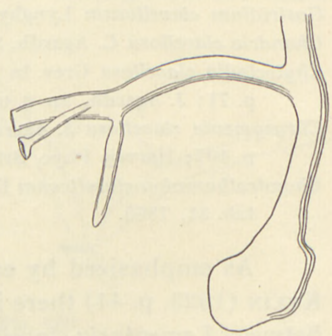


Fig. 583.
Lomentaria clavellosa. A branch ends in an attachment disc. 12:1.

The antheridial sori appear, as shown by Kylin (1923, p. 47), as patches on the branches of the last or penultimate order, probably always in particular male plants. The cells producing the antheridia (spermatangia) bud off from the small outer cortical cells as small colourless cells rich in protoplasm and containing one nucleus (mother cells of the spermatangia Kylin l. c., fig. 33). Specimens with antheridia were observed once in Skagerak, on the 1st of August, and once in Northern Kattegat, on the 13th of July.

The development and structure of the carpogonial branch and of the cystocarp have been treated by HAUPTFLEISCH (1892) and KYLIN (1923). Reference may be made to the description of KYLIN. The tri-cellular carpogonial branch arises as an outgrowth from a primary cortical cell (supporting cell) which becomes multinuclear. Two auxiliary cells are usually present the mother-cells of which bud off from the supporting cell, but one only is developed after fertilization. After the entering of a sporogenous nucleus in the auxiliary cell, a cell buds off from its upper side, and from this cell several gonimolobes are produced. The wall of the cystocarp has a well developed pore at the top. For more details see the papers quoted.

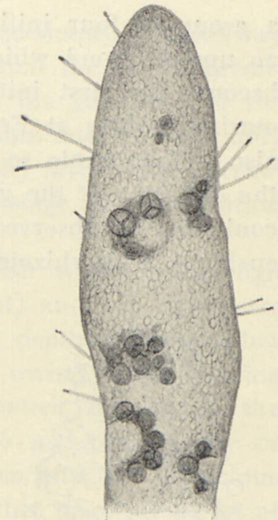


Fig. 584.
Lomentaria clavellosa. August. Tip of tetraspore-bearing frond. 30 : 1.

The tetrasporangia are embedded in the cortex, and form groups at the bottom of depressions in the cortex of the younger parts of the frond; the sporangia do not project inwards into the cavity of the frond (fig. 584). They are tetrahedrally divided.

The germination of the spores has been studied by KILLIAN (1914, p. 246), but owing to difficulties with the cultures he was not able to follow the first stages of the development of the germlings. The youngest stage figured by KILLIAN is an orbicular disc showing in the middle

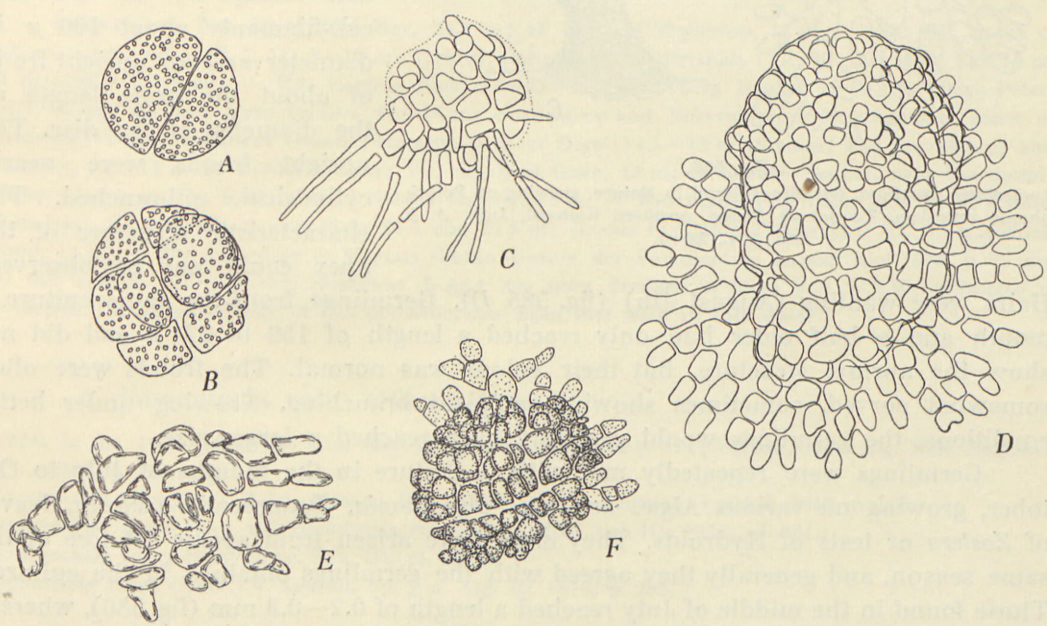


Fig. 585.
Lomentaria clavellosa. Germlings obtained in cultures. *A—C* and *E—F* 8 days old. *D* 15 days old. 560 : 1.

a group of four initial cells. The middlemost part of the disc projects and forms an upright frond which is first cylindrical, later vesicular, and the four apical cells become the first initial cells of the frond. In my cultures in the laboratory of marine biology at Frederikshavn in 1928 and 1929 the conditions were evidently also unfavourable to the germination, for most of the spores did not germinate, the divisions of the germinating spores were not regular, and the four initial cells could not be observed. After 7 or 8 days the germlings had the shape of discs or cushions with rhizoids issuing from the margin. The cell-divisions were more or less irregular, and sometimes portions of the original spore-cell did not take part in the divisions producing the germling. A group of initial cells could not be detected, but the cells often showed a very apparent arrangement in rows, an evident proof of the presence of a meristeme (fig. 585).

After 17 days the germlings had grown much larger, having usually an orbicular disc composed of radiating cell-filaments about 100 μ in diameter and an upright frond of about the same length as the diameter of the disc. The upright fronds were nearly cylindrical, unbranched. The characteristic structure of the apex could not be observed. Hairs were wanting (August 4th) (fig. 585 *D*). Germlings from the same culture a month and a half older had only reached a length of 150 to 224 μ and did not show the normal structure, but their colour was normal. The fronds were often somewhat curved, sometimes showing incipient branching. Growing under better conditions, the germlings would probably have reached a larger size.

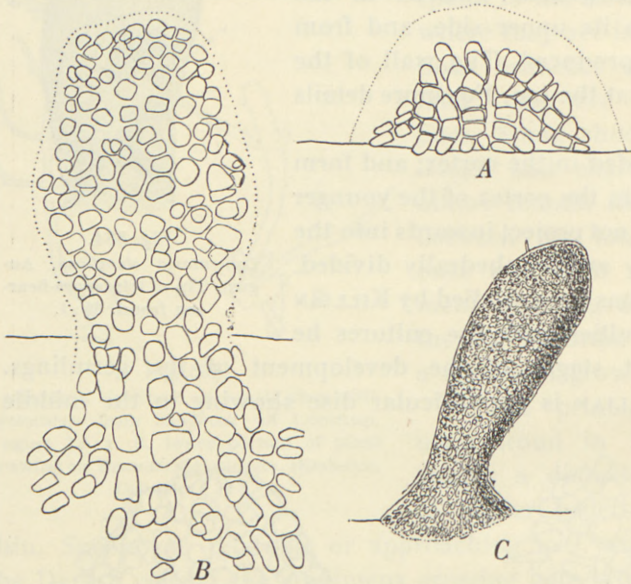


Fig. 586.
Lomentaria clavellosa. Germlings found in Nature, growing on Polysiphonia urceolata, Tønneberg Banke, northern Kattegat, July. *A*, *B* 560 : 1, *C*, 200 : 1.

Germlings were repeatedly met with in Nature in the months of July to October, growing on various Algæ, as e. g. *Polysiphonia*, *Desmarestia aculeata*, leaves of *Zostera* or tests of Hydroids. They must have arisen from spores set free at the same season, and generally they agreed with the germlings obtained in the cultures. Those found in the middle of July reached a length of 0.2—0.3 mm (fig. 586), whereas germlings met with in August reached a length of 2 mm. The largest specimens of the young plants gathered in October reached in the various localities lengths of 2.5 mm, 7 mm and 2 cm, but smaller specimens, partly disc-shaped without any upright shoot, occurred with them. It must be concluded that the spores germinate in the middle and at the end of summer, and that the germlings or the majority of them remain small and feebly developed in autumn and grow out only in the following summer; but it seems quite probable that, under favourable external conditions, the earliest developed germlings may reach the stage of fructification in the same season in which they have arisen.

Lomentaria clavellosa only occurs in the northern Danish waters with high salinity (North Sea, Skagerak, northern and eastern Kattegat) and has only once been met with, many years ago, in the Great Belt at a great depth. On the other hand it has not been met with in the Limfjord, undoubtedly owing to the varying temperature in this area. It grows at depths of 9 to 31 metres, deepest in the North Sea (24.5—31 m) and the Eastern Kattegat (14—26.5 m), on gravelly or sandy bottom with small stones or on stony bottom, very often attached to various Algæ, e. g. *Halidrys*, *Corallina offic.*, *Polysiphonia* spp. etc., further on dead leaves of *Zostera*, on various Hydroids, *Flustra foliacea* and shells of molluscs. It has not been observed in winter and early spring and has probably a small size in this period. The specimens collected in May were only 2—3 cm high and sterile. The maximum of development is reached in July and August when the specimens may reach a length of up to 18 cm (Groves Flak) and are fructiferous, with ripe tetrasporangia and cystocarps at least after the middle of July.

Localities. **Ns:** ZQ, jydske Rev, 24.5 m; aF N.W. of Thyborøn, 31 m. — **Sk:** SY, north of Løkken, 13 m; ZK (0, 3, 7, 11) 8—19 m; various places N.W. of Hirtshals (YK, YL, XO etc.), 13—15 m, off Hirtshals (Børgesen). — **Kn:** Herthas Flak, 19—22.5 m; Tønneberg Banke, 16—19 m (Boye Petersen!); fG and dS near Læsø Trindel, 15—16 m; Nordøstrev and Norvestrev at Hirsholmene; south of Hirsholm, 11 m; Trestensrev (Henn. Petersen), N.E. of Deget 11.5—13 m (Stamm) and Borrebjergs and Laursrev, 7.5—11 m at Frederikshavn; VU, north of Læsø, 15 m; at Nordre Rønner, near the double broom, 11—14 m; TM, N.W. by N of Nordre Rønner, 15 m. — **Ke:** Fladens lightship in S by E, 1 mile, 23 metres; EX and EV, Groves Flak. 26.5 and 22.5 m; Groves Flak 19 m (Børgesen); EU, Lille Middelgrund, 14 m. — **Sb:** According to Magnus (Botan. Unters. der Pommerania Exped. Kiel 1873, p. 66 and 74) this species (*Chrysymenia clavellosa* J. Ag.) has been dredged in Store Belt W.S.W. of Romsø at 51 metres' (27 Faden) depth; it has not otherwise been met with in this water.

2. **Lomentaria rosea** (Harv.) Thur.

Thuret in Le Jolis, Liste des Alg. mar. de Cherbourg 1864, p. 131; Farlow, Mar. Alg. New England, 1881, p. 155.
Chrysymenia Orcadensis Harv., Manual Brit. Mar. Algæ. Sec. edition, London 1849, p. 100.
Chrysymenia rosea Harv. var *Orcadensis* Harv. Phyc. Brit. Vol. III, 1851, pl. 301.
Chrysymenia rosea Harv. Phyc. Brit. III, pl. 358 A.
Chylocladia rosea (Harv.) J. Agardh, Sp. g. o. Alg. III 1876, p. 298.

This rare and imperfectly described species has only been met with once, in July 1892 in the eastern Kattegat, at 22.5 metres' depth. The two dried specimens

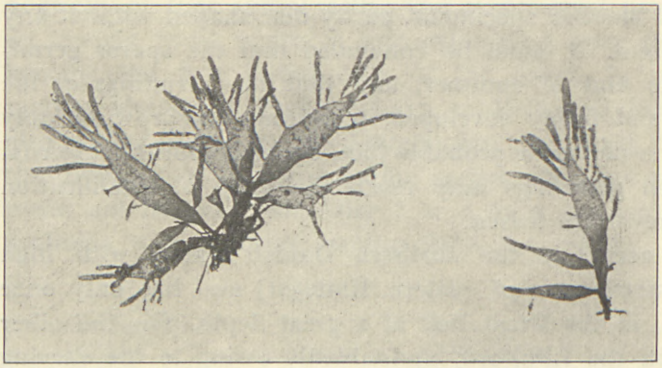


Fig. 587.
Lomentaria rosea. Photo, $^3/_2$ nat. size.

represented in fig. 587 are the only ones collected in the Danish waters. As the structure and fructification of the species have been very little mentioned in the literature, only little can be adduced here on these matters. The specimens have a pink colour. The main shoots are lanceolate, the branches mostly opposite, comparatively narrow; the lowermost lanceolate, but most of them linear, 0.5—0.8 mm broad, sometimes a little broadened upwards. All the shoots are narrowed at the base.

The anatomical structure of the frond seems to be similar to that of *L. clavellosa*. The outer, small-celled cortical layer is subcontinuous, as in the above-named species, or interrupted, the small cells being only developed over the edges of the larger inner cells (fig. 588). The long medullary cell-rows running longitudinally within the cortical tissue were also distinguishable in the dried material. Hyaline hairs the tips of which were filled with protoplasm were met with abundantly in the young pinnæ.

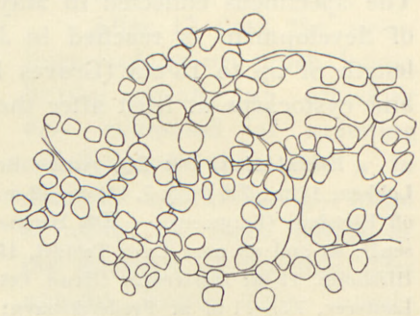


Fig. 588.
Lomentaria rosea. Surface view of a broad frond. 350 : 1.

Both specimens are fructiferous, containing numerous sori of tetrasporangia in the pinnæ. The areas of the frond-wall containing the sori are concave, in accordance with the generic character. The tetrahedrically divided tetrasporangia were ripe in July.

Sex organs and cystocarps seem to be entirely unknown in this species. It has been met with at the coasts of the Northern Atlantic (United States, Iceland, Færöes, British Isles, Helgoland, Norway, Sweden), but from all localities only mentioned with tetrasporangia.

Locality. **Ke:** South end of Groves Flak, 22.5 m, July 12th 1892.

VII. Nemastomatales.

Fam. Rhodophyllidaceæ.

Cystoclonium Kützing.

1. **Cystoclonium purpureum** (Huds.) Batters.

Batters, Catalogue Brit. Mar. Alg., Journ. of Bot. 1902, p. 68.
Fucus purpureus Hudson Fl. Angl. 1762, p. 471 (not seen, teste Batters).
Fucus tuberculatus Lightfoot Fl. Scot. II, 1777, p. 926.
Fucus corallinus O. Fr. Müller Fl. Dan. tab. 709 (1777).
Fucus scorpioides O. Fr. Müller Fl. Dan. tab. 887[1] (1782).
Gigartina confervoides Lyngbye Hydr. 1819, p. 43 (quoad specim. Dan.).[2]
Gigartina purpurascens Lyngbye Hydr. 1819, p. 46 (exclus. var. *γ rostrata*).
Sphærococcus purpurascens Hornemann, Fl. Dan. tab. 1835 (1825). (Primary branches too numerous).
Cystoclonium purpurascens Kützing Phyc. gen. 1843, p. 404, Taf. 58 I; id. Tab. phyc. 18 pl. 15 (1868); J. Agardh, Sp. g. o. II.I, 1851, p. 307; Wille Bidrag, 1885, pp. 17, 30, 33, 76, pl. II figs. 20—22, IV figs. 46, 47, VI figs. 74—76; Schmitz u. Hauptfleisch 1896, p. 370, fig. 222 *C*; A. Henckel, Sur l'anat. etc. des Algues mar. Cystoclonium purpur. et Chordaria flagelliformis; Scripta bot. Petropol. fasc. 19, 1902; Kolderup Rosenvinge, Hyal. hairs, 1911, pp. 206—209, fig. 4; Kylin 1907, p. 131; id. 1917 p. 22; id. Entwick. Florid., 1923, pp. 22—30.
Hypnea purpurascens Harvey, Phyc. Brit. pl. 116, 1846.
Gracilaria purpurascens Nägeli, Die neu. Algensyst. 1847, p. 241.

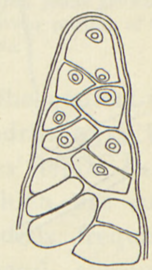


Fig. 589. *Cystoclonium purpureum*. Tip of frond showing the apical cell and its divisions. 560 : 1.

The structure and development of the frond of this common species has repeatedly been studied by Nägeli, Kützing, Wille, Henckel and Kylin. The apical cell of the frond is divided by oblique walls that are inclined alternately to the right and to the

[1] This figure is interpreted in J. Agardh's Sp. g. o. II.I p. 307 as representing *Cystoclonium purpurascens*; in the same work II.II p. 587, however, it is determined as *Gracilaria confervoides* "(fide spec. a Hoffm. datis)". The latter determination cannot be upheld; the figure represents a *Furcellaria* beset with two specimens of an Alga which is probably *Cystoclonium purpureum*. It should be noted, however, that the picture does not correctly represent the base of a *Cystoclonium* fixed to the *Furcellaria*, and the specimen to the left is not fixed to it at all. *Cystoclonium purpureum* is very often fixed to this substratum in Nature, whereas *Gracilaria confervoides* is always fixed to stones.

[2] In Lyngbye's herbarium one specimen only of *Gigartina confervoides* is to be found. It bears the following inscription: "Ex Hindsholm Fioniæ, Jan. 1816, ded. Hofman". It is an old denudated specimen of *Cystoclonium purpureum* easily recognizable by the base which is still preserved. On the wrapper Lyngbye has first written: *Fucus confervoides*; *Fucus* has then been changed into *Gigartina* and (probably later) *purpurascens* has been added to the name *Gigartina*. It is without doubt this specimen which is mentioned by Lyngbye l. c.

left, as shown by Kylin (1923, p. 23), thus producing two rows of alternating segments (fig. 589). The central cell-row is only discernible in the upper end of the frond, later on it cannot be distinguished from the other longitudinal filaments filling up the central part of the frond. The outermost cell-layer has the function of assimilating tissue; it produces numerous long hyaline hairs (comp. K. Rosenvinge 1911, Kylin 1923), which arise in spring and early attain a considerable length, about 1 mm or more, with a diameter of about 10 μ (fig. 590). They form a hyaline clothing on the fronds still growing. When the growth ceases, the hairs are shed and are therefore not met with in autumn and winter.

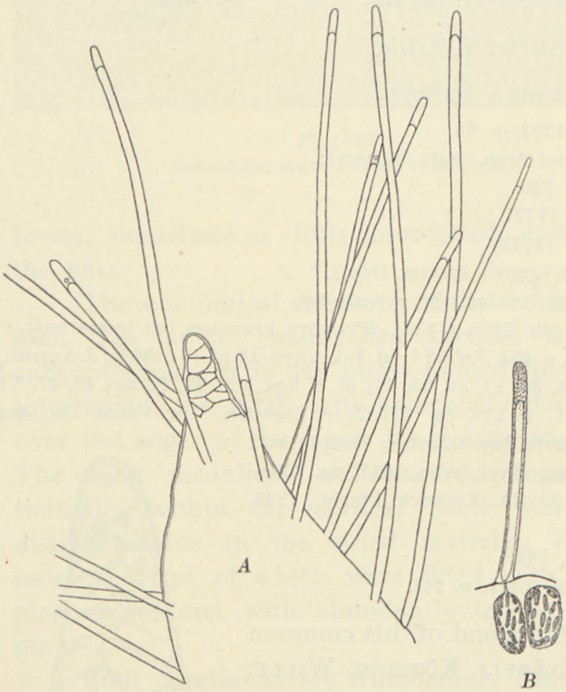


Fig. 590.
Cystoclonium purpureum. *A*, upper end of frond showing hyaline hairs. 200 : 1. *B*, two superficial cells, the one bearing a young hair. 325 : 1. After living plants.

The distinction between the assimilating and the storage tissues is not very sharp. Wille and Henckel (1902, p. 6) count up to 5 layers of the assimilating tissue while Kylin (1923, p. 23) has only one. Within this follows a storage tissue which has also a mechanical function, and the central part of the frond is filled up by the conducting tissue built up by longitudinal filaments, primary and secondary, composed of long cells the transverse walls of which, as shown by Wille (1885, p. 76, pl. VI, figs. 74—76), are perforated by numerous fine threads of protoplasm.

The main stem is very distinct, in particular in the lower part of the frond where it is less branched than above. Near the base, however, a number of horizontal or downward bent branches arise which may reach a considerable thickness but only a length of a few, up to 5 cm (fig. 591). In contact with the substratum they form low hapters which afford a better fastening for the plant (fig. 592). When with increasing age the surface of the plant is very much increased, the primary attachment disc would not suffice to resist the pull caused by the movements of the water. The basal shoots taper gradually towards the top but are not much branched. Upright shoots are sometimes given off from them, and they may thus have the character of stolons but new fronds are usually only produced near the primary ones, and the horizontal shoots have therefore no significance for the propagation of the species.

The tendrils frequently occurring at the ends of the branches have been known for a long time. Lyngbye described them (1819) as peculiar to a particular variety *β, cirrhosa*. They were later mentioned by J. Agardh (Flor. Morph. 1879, p. 10) and in particular by Wille (1885, p. 33) and Henckel (1902, p. 12) who studied their development and structure. They arise at the ends of branches which become long and thin whithout branchlets and are twisted, 5 or 6 worms of a screw often lying close together. The twisted part of the shoot bears a number of short, thick branchlets forming a small bush. The tendrils may remain free or catch fronds of other Algæ or of its own. When growing on *Halidrys siliquosa* the tendrils winding round branches of the host plant are particularly numerous, giving the *Cystoclonium* a very solid attachment. Specimens with tendrils are met with in all the Danish waters; their occurrence seems to depend on external conditions. Wille found them in specimens from a locality with fairly agitated water, and Henckel thought that they might be caused by the contact with an algal frond. This can only be decided by experiments. The tendrils have been met with, from 1 to 20 metres' depth. In the North Sea and Skagerak, which are much agitated, specimens with tendrils frequently occur; but, on the other hand, specimens growing on the moles at Hirtshals and at Hanstholm where the sea is usually much agitated had no tendrils. At the greater depths the influence of the waves can only be feeble, but the water is here agitated by the currents.

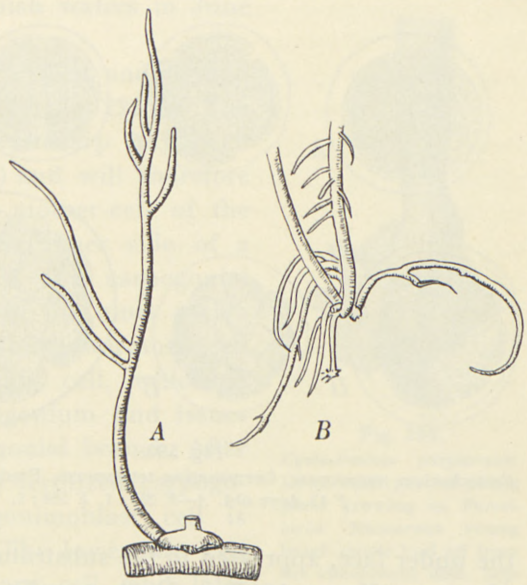


Fig. 591.
Cystoclonium purpureum. *A*, young plant growing on *Furcellaria*. February. 5 : 1. *B*, lower portion of frond. July. Nat. size.

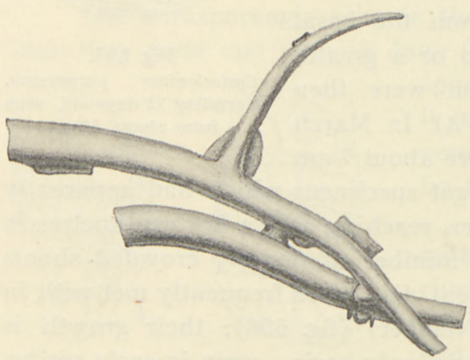


Fig. 592.
Cystoclonium purpureum. Creeping shoots with hapters. 20 : 1.

Wille raises the question whether the cluster of small shoots issuing from the tendrils might give rise to a new individual, but he leaves that undecided (1885, p. 34). Henckel has never found tendrils having the character of stolons, nor have I myself ever found tendrils surviving during the winter and giving rise to new individuals next year.

As ripe spores are produced in summer (July to August) and are able to germinate immediately, young plants must occur already in summer. As shown in fig. 593, the germinating spores divide by orthogonal or more irregularly orientated walls forming a hemispherical body, scarcely larger than the spore. This is the attachment disc. After two weeks, in a culture at Frederikshavn in July, many of the cushions had produced a shoot, one of the superficial cells, not always at the summit of the cushion, taking the character of an apical cell (fig. 593 *F*). Sometimes two shoots arise simultaneously from the same cushion. From the under face, appressed to the substratum, short unicellular hapters spring (fig. 594).

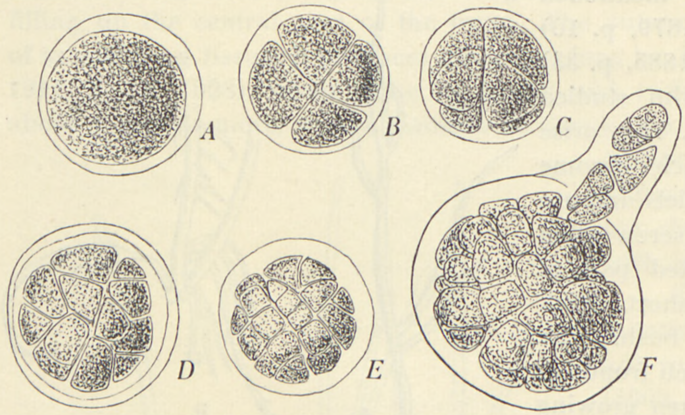


Fig. 593.
Cystoclonium purpureum. Germinating tetraspores, Frederikshavn, July. *F* 13 days old. *A—E* 350 : 1. *F* 560 : 1.

(Compare Kylin 1917, p. 7). A germling in a more advanced stage, agreeing well with those observed in cultures, was met with at the end of September at 16 metres' depth in the Northern Kattegat (fig. 595). The plants which arise from the spores germinating in summer probably reach a considerable degree of development before winter. In the Little Belt I found in February 2—4 cm long plants growing on *Furcellaria.* In some cases one frond only was given off from the basal cushion, in other cases two or a greater number, but some of them were then usually broken off (fig. 591 *A*). In March corresponding specimens were about 7 cm long. In the Northern Kattegat specimens which had apparently arisen from spores in summer, reaching only a few centimetres in length but having a great number of densely crowded shoots springing from the attachment disc, were frequently met with in autumn (September to November) (fig. 596); their growth is arrested during the winter and only begins again in early spring.

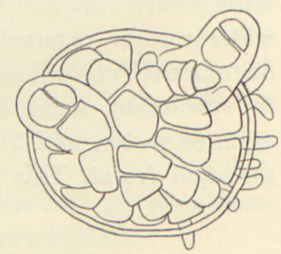


Fig. 594.
Cystoclonium purpureum. Germling 12 days old, seen from above. 560 : 1.

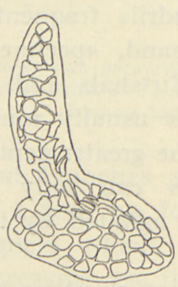


Fig. 595.
Cystoclonium purpureum. Germling found growing on Antithamnion Plumula, September. 75 : 1.

The development of the sex organs has been studied by Kylin (1923). The species is dioecious. The antheridia arise on the surface of younger shoots which may finally be entirely covered by them. They are, according to Kylin (l. c. p. 30), borne on „Spermatangien-Mutterzellen" which are cut off from the cells of the outermost, assimilating layer of cells. Some of the latter, however, remain unchanged (cf. Buffham 1893, p. 293). The spermatia, according to Kylin, contain about 20 chromosomes. The antheridia were met with in the Danish waters in June and July.

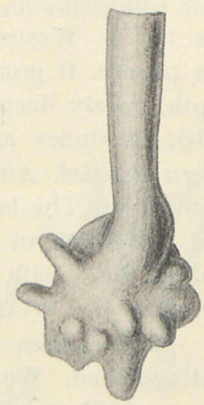


Fig. 596.
Cystoclonium purpureum. Lowermost part of young plant growing on *Furcellaria.* Numerous young basal shoots bud off from the attachment disc. September. 30 : 1.

The carpogonial branch was first described and figured by Schmitz and Hauptfleisch, (1896, p. 369, fig. 222 *C*). The development of the procarp and of the cystocarp has been carefully treated by Kylin (l. c. pp. 25—29) and will therefore only be very briefly mentioned here. The mother-cell of the carpogonial branch is early cut off on the inner side of a superficial cell, but when fully developed the carpogonial branch appears inserted on the inner side of the inner cortex (storage tissue). It is three-celled, and the lowermost cell produces a small lateral cell. The auxiliary cell, which is early developed, is situated near the carpogonium and issues from the same cell which bears the carpogonial branch. After the entrance of a diploid nucleus from the fertilized carpogonium into the auxiliary cell the first gonimoblast cell is formed from the inner side of the latter. The lowermost cell of the gonimoblast fuses with the auxiliary cell, and later similar fusing processes take place between the latter and other cells of the gonimoblast. For further details on the development compare Kylin (l. c.). The structure of the ripe cystocarp has been pictured by Kützing (1843, Taf. 58). Ripe cystocarps were met with in the Limfjord in June, otherwise everywhere in July and August. In September and October they were more or less empty.

The tetrasporangia arise in the cortex and are transversely divided. In a ripe state they were met with in June (Limfjord) and in July to September. The tetraspores germinate immediately after exhaustion, but it may happen that they are not set free and then germinate within the mother plant still surrounded by the sporangial membrane (fig. 597).

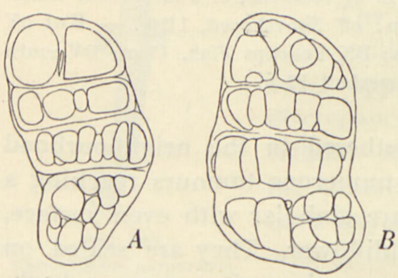


Fig. 597.
Cystoclonium purpureum. Tetraspores segmented within the sporangial wall, September. 200 : 1.

After frutification the fronds die entirely or with the exception of the lowermost portion. The cluster of horizontal shoots issuing from the base of the plant is able to survive through the winter, and new upright fronds then arise from them, or smaller shoots from the foregoing year not having reached the stage of fructification survive through the winter and develop next summer into large fructifying fronds. The species is then perennial, or may at least keep alive and fructify during two years; but many individuals never become perennial because the Algæ or the parts of the fronds to which they are attached die after having fructified.

Cystoclonium purpureum is common in all the Danish waters from the North Sea to the Western Baltic Sea, whereas it has not been recorded in the Baltic Sea proper. It grows in depths from a little under low-water mark to 20 metres' depth, rarely deeper (21.5 m in the eastern Kattegat, 24.5 and 35 m in the Little Belt), on stones and on various Algæ (*Furcellaria, Halidrys, Fucus serratus, Phyllophora Brodiœi, Ahnfeltia* and several others), further on oysters and other shells of bivalves. The largest specimens have been met with in the North Sea, Skagerak and the Northern Kattegat, where a length of 50 cm can be reached. In the inner waters the length does not usually exceed 20 cm, and the largest specimen collected in the Western Baltic was only 13 cm long.

The species is only little variable and no varieties or named forms can be distinguished. We shall merely mention that in exposed localities in the North Sea and Skagerak large specimens may be met with which are remarkable in having a number of long principal branches beset with numerous short branches of the second order in their whole length.

Localities. **Ns:** Not met with at Esbjerg-Fanø and on the groins at the entrance to the Limfjord. Vorupør, 3 m (S. Lund); XR, off Ørhage, 11—13 m; in the bay at Ørhage (Klitmøller), 2 m. — **Sk:** YT off Helshage, Hanstholm, 5.5—13 m, at Roshage, 2 m, mole immediately beneath low-water mark; YM, YN[2], Bragerne 2.5—10.5 m; SY off Løkken; ZK off Lønstrup; several places, XO, VJ etc. off Hirtshals, 5—15 m and abundantly on the mole. — **Lf:** Common from one to 7 metres' depth and from XV and LZ in Nissum Bredning to Hals mole; e. g. Oddesund, Thisted Bredning, Sallingsund, Livø Bredning and Løgstør Bredning. — **Kn:** Common everywhere on stony bottom from Skagen harbour, Herthas Flak, 20 m and Læsø Trindel, 16 m, southwards. — **Ke:** Several places in Fladen, Groves Flak, Lille Middelgrund from 10—22 m, further GJ, OO and Gilleleje harbour. — **Km:** Several places from Læsø Rende to NC off Fornæs, 4—11 m. — **Ks:** Several places from Grenaa harbour to Hastens Grund and D, grønne Revle. — **Sa:** Numerous localities from 0 to 15 metres' depth. — **Lb:** Several places, from 1 to 35 metres' depth, from Bogense harbour to dH east of Hesteskoen, 15 m. — **Sf:** Several places. — **Sb:** Several places, 1 to 19 m. — **Sm:** S.E. of Masnedø, c. 3 m. — **Su:** Hellebæk; Kronborg; PZ, east of Hveen, 13.5 m; Taarbæk Rev, 12 m; off Skovshoved, 11 m. — **Bw:** bY south of Als; cG off Kegnæs; cE, Middelgrund south of Als, 13 m; DX Vodrups Flak, 13 m; DV south of Marstal; LA, south of Lolland, 7.5 m; UL, Øjet 20 m; KY, Femerbelt 12 m.

Some specimens of *Cystoclonium purpureum* gathered in the neighbourhood of Frederikshavn and in the Limfjord were set with numerous tumours reaching a diameter of 2.5 mm or more. The smaller tumours are globular with even surface, the larger more irregular, somewhat resembling cauliflower. They are seated on both the thin and the bigger branches; in the first case they often cause a backward bending of the frond (fig. 598). Small shoots of *Cystoclonium* may issue from the surface of the tumours (fig. 598 *B*). The colour is bright, nearly white, yellow or rose to red-brown.

Such tumours have been shortly mentioned as early as 1808 by Turner (Fuci, p. 18, plate 9, figs. *f, g, h*) who described them as swellings "unconnected with the fruit" and depicted them as irregularly spherical bodies from which small adventitious shoots are given off.

SCHMITZ[1] gave a more detailed description of the tumours, especially their anatomical structure; he showed that the interior of the tumours is built up of a medullar tissue of interwoven cells whereas the cortex is somewhat similar to that of the normal plant. In the cortex rhizoids may appear, sometimes in great numbers. SCHMITZ further stated that almost the whole tissue of the tumours, in particular the cortex, is filled with small, nearly oval bacteria. The bacteria live intercellularly in the middlemost layer of the cell-walls. When they are very numerous, they penetrate towards the surface of the tumour, numerous rhizoids are then produced, the cells are partly disunited and the bacteria can escape into the surrounding water. SCHMITZ supposes that the tumours are galls occasioned by the bacteria.

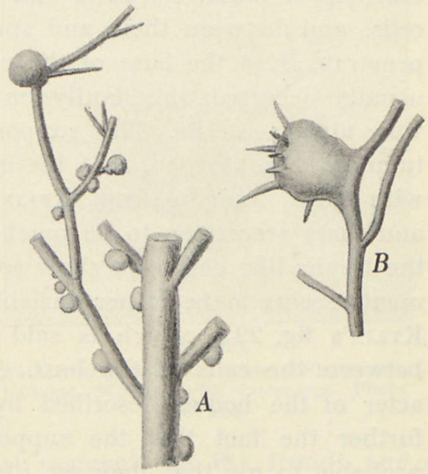


Fig. 598.
Cystoclonium purpureum. Parts of frond with tumours. *A*, 3 : 1.

The tumours have recently been examined by CHEMIN[2] who confirmed the observations of SCHMITZ. He states that the bacteria are "légèrement ovoides et leur grand axe atteint à peine 1 μ". He mentions an attempt at inoculating bacteria from a gall to another individual of *Cystoclonium*, without result however, but nevertheless he agrees with SCHMITZ in considering the tumours occasioned by the bacteria; in all the tumours examined he found bacteria.

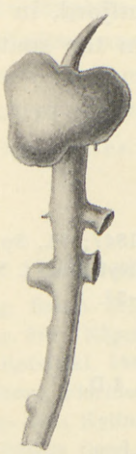


Fig. 599.
Cystoclonium purpureum. Upper end of shoot with hapters and a tumour. 23 : 1.

The tumours from the Danish waters examined by me agree with those described by the authors quoted, as to the outer appearance and anatomical structure; but there is the discrepancy that I have not been able to observe the intercellular masses of bacteria. In the swollen membranes of the tumours, only the homogeneous substance of the middlemost layer was to be seen, no bacteria, even after staining with gentiana-violet, and this was the case, too, in the large tumours with disunited cells. Only scattered rod-shaped bacteria much larger than those described by CHEMIN were sometimes observed. It seems doubtful, therefore, whether the tumours are really caused by bacteria; their etiology must be left for further research.

[1] FR. SCHMITZ, Knöllchenartige Auswüchse an den Sprossen einiger Florideen. Botanishe Zeitung 1892.
[2] E. CHEMIN, Action des Bactéries sur quelques Algues rouges. Bull. de la Soc. bot. de France 1927, p. 441.

In 1907 (Studien, p. 127) KYLIN described a new parasitic Alga, *Choreocolax Cystoclonii*, growing on *Cystoclonium purpureum*. It forms irregular globular bodies, 1—4 mm in diameter, yellow-white, often with a tinge of pink; they have a cortex built up of radial cell-rows and an inner tissue of isodiametrical or irregular larger cells, and between them and springing from them long branched cell-rows which penetrate from the base of the parasite between the cells of the host. The parasite usually occurred abundantly on one and the same individual of *Cystoclonium*; it was always sterile. The supposed parasite bears so much resemblance to the tumours here treated, that the question arises if they might possibly be identical with them. Judging from KYLIN's description, the outer appearance is the same, and there seems too to be much accordance as to the anatomical structure, though the hypha-like cell-rows show some disagreement; but the occurrence of these elements seems to be rather variable. I have not observed stages like that shown in KYLIN's fig. 29 *a*, which is said to represent filaments of the parasite penetrating between the cells of the host. Altogether it must be said that the parasitic character of the bodies described by KYLIN cannot be said to be proved. Considering further the fact that the supposed parasite was always sterile, it seems highly probable to me that they are identical with the tumours here described, and that like these, they are merely luxuriancies caused by some unknown agency. It should be stated that KYLIN did not mention bacteria in the tissue of the tumours.

The tumours have been met with repeatedly in the environs of Frederikshavn, particularly east of Deget (Boye Petersen), off Feggeklit in the Limfjord, in Lille Middelgrund in the eastern Kattegat and near Ostindiefarergrund in the southern Kattegat.

Euthora J. Agardh.

1. **Euthora cristata** (L.) J. Agardh.

J. Agardh, Nya alger från Mexico. Öfvers. af K. (svenska) Vetensk. Ak. Förhandl. 1847; id., Sp. g. o. Vol. II, pars II, p. 385, 1851; N. Wille, Morph. og physiol. Studier over Alger. Nyt Mag. f. Naturvidensk. Bd. 32. II. 1891, p. 107 ff., Tavle II; Kylin, Entw. Flor. 1923, pp. 36—37.
Fucus gigartinus L.? Oeder, Flora Danica, Tab. 394. 1768.
Fucus cristatus L., Turner Fuci I. 1818, Tab. 23, p. 48.
Sphærococcus cristatus Agardh Synops. 1817, p. 29; Lyngbye, Tent., 1819, p. 13, Tab. 4 D.
Rhodomenia cristata Greville Alg. Brit. 1830, p. 89.
Rhodymenia cristata Harvey, Phyc. Brit. III, tab. 307, 1851.
Callophyllis cristata Kützing, Tab. phyc. 17, tab. 93, 1867.

This pretty little subarctic Alga has only been met with in a few places in the eastern Kattegat at 22—25 metres' depth. It will only be briefly mentioned here, as I have no new observations on the morphology and the development. The fronds are rather narrow, mostly alternately pinnate, more rarely secund or subdichotomous and flabelliform. The structure of the frond has been described by WILLE and KYLIN. As shown by these authors, the segments of the frond terminate in an apical cell dividing by oblique walls. The frond has an assimilating tissue consisting of about two layers of small cells while the inner tissue is composed of large thick-walled cells, by WILLE denoted as a mechanical tissue. There is also a feebly developed conducting tissue between the large inner cells.

The antheridia seem to be unknown; in the Danish waters they were not met with.

The procarps arise near the border of the young frond and consist, according to KYLIN (l. c.), of a three-celled carpogonial branch and an auxiliary cell borne on the same cell which bears the carpogonial branch. The development of the cystocarp has not been followed, but KYLIN has given a drawing of a nearly ripe cystocarp and shown that cell-rows grow out from the cystocarpial wall and divide the gonimoblast into smaller portions.

Fig. 600.
Euthora cristata. From Groves Flak, Eastern Kattegat, 24.5 m. With cystocarps. Photo, nat. size.

The tetrasporangia arise in groups in the last segments of the fronds and are cruciately divided; they have not been met with in the Danish waters.

The species has been dredged in the months of May and July, always on stony bottom at considerable depths, consequently in water of high salinity, growing on the hapters of *Laminaria hyperborea* and *L. saccharina* and on Hydroids, such as *Tubulina* and *Sertularia.* The fronds reach a length of 1—3.5 cm. Most of the specimens gathered in May had procarps or more or less developed cystocarps. Ripe cystocarps were met with in July.

Localities. **Ke:** ZF, 26.5 m, and JQ 21.5—30 m, Fladen; EV, 22.5 m and JT, 24.5 m, Groves Flak.

Rhodophyllis Kützing.

1. **Rhodophyllis bifida** (Good. et Woodw.) Kützing.

Kützing, Botan. Zeit. 1847, p. 23, Tab. phyc. **19**, pl. 50, 1869. J. Agardh, Sp. g. o. II, pars II, 1851, p. 388; Nägeli, Neu. Algensyst. 1847, p. 234; Reinke, Lehrbuch d. allg. Bot. 1880, p. 119; Wille, Entwickl. 1887, p. 71, figs. 38—39; Schmitz u. Hauptfleisch (Engl. u. Prantl) 1896, p. 376; Nienburg, Florideenkeiml., Hedwigia **51**, 1912, p. 303; Killian, Entw. Florid., Zeitschr. f. Bot. **6**, 1914, p. 248; Kylin, Entw., 1923, p. 31.

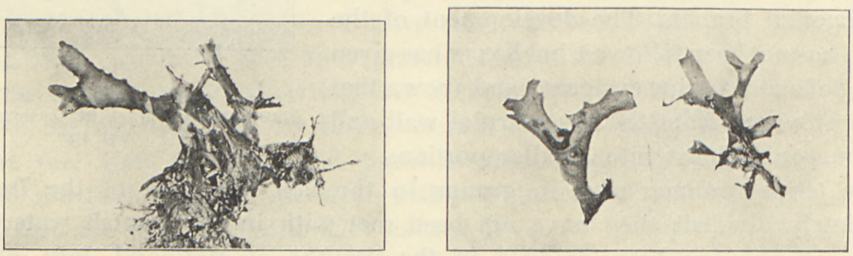
Fucus bifidus Good. et Woodw. Trans. Lin. Soc. Vol. III, 1795, p. 159, pl. 17 fig. 1.

Rhodymenia bifida Greville, Harvey, Phyc. Brit. I, pl. 32, 1846.

The structure and development of the frond have been described by NÄGELI, WILLE, KILLIAN and KYLIN. The tips of the dichotomous frond have a marginal row of apical cells, some of which, the principal ones, divide by alternate, oblique walls. The frond consists of three layers of cells, the middlemost of which is composed of hypha-like filaments forming a net-work with large meshes. Hyaline hairs were not observed.

According to KILLIAN the first stages of the germination of the carpospores and the tetraspores much resemble those of *Lomentaria clavellosa*. An attachment disc is produced by vertical divisions of the spore-cell. One of the cells of this disc, one of the original octant-cells, early becomes larger than the others and gives rise to the leafy frond.

According to KYLIN, the species is monoecious. The antheridia arise scattered on the surface of the frond, 3 to 5 small cells are cut off from a cortical cell, and each of these small cells produces 2 or 3 spermatangia. The development of the procarp and of the cystocarp has been carefully examined by KYLIN. The following facts only shall be mentioned here. The procarps arise near the border of the frond. The three-celled carpogonial branch is borne on a supporting cell which also supports



A *B*

Fig. 601.
Rhodophyllis bifida. From Groves Flak, 19 m, collected by dr. F. Børgesen. *A*, with cystocarps, *B*, with tetraspores. Photo, nat. size.

an auxiliary cell. From the outer side of the supporting cell and the auxiliary cell branched cell-rows are produced which form a cortical layer over the procarp. The auxiliary cell having received a dipoid nucleus from the fertilized carpogonium produces on its inner face the first gonimoblast cell from which a number of carpospore-producing bushes are given off. Fusions take place between the auxiliary cell and the inner gonimoblast cells. The ripe cystocarp has no particular ostiole.

The tetrasporangia are scattered over the surface of the outer segments of the frond. They arise by transformation of primary cortical cells and divide by transverse walls.

Rhodophyllis bifida has only been met with in Skagerak and the northern and eastern Kattegat at considerable depths, 14—27 m, where the salinity is high and the temperature slightly varying. It grows on stony or gravelly bottom, often attached to Hydroids or Algæ (*Halidrys*). The largest specimens, up to 3 cm long, were found in August and September whereas the specimens gathered in May were only 3 mm high. Cystocarps and ripe tetrasporangia were met with in August and September.

Localities. **Sk:** XO and YK N.W. of Hirtshals, 11—15 m. — **Kn:** Herthas Flak, 20—22.5 m (!, F. Børgs.); TO, Tønneberg Banke, 18 m. — **Ke:** Groves Flak, IT, EX, EV, 22.5—26.5 m, Groves Flak (F. Børgs.), 19 m.

Fam. 19. Plocamiaceæ.

Plocamium Harv.

1. **Plocamium coccineum** (Huds.) Lyngb.

Lyngbye, Tent. 1819, p. 39, tab. 9 B; Kützing, Phycol. gen. 1843, p. 449, Taf. 64; Harvey, Phyc. Brit. I, pl. 44, 1846; Nägeli, Neu. Algensysteme 1847, p. 228, Taf. X, figs. 22—37; J. Agardh, Sp. g. o. Alg. Vol. II.2, p. 395, 1852; Kützing, Tab. phycol. Bd. 16, Taf. 41; Schmitz, Untersuch. 1883, p. 26, Taf. V, figs. 37—38; Buffham 1884, p. 338, 1891 p. 249, Plate 16, figs. 8—9; Phillips, Developm. of the cystocarp in Rhodymeniales, Ann. of Bot. 11, 1897, p. 352; Oltmanns, Morph. u. Biol. 1904, pp. 597, 646, 661; Kylin 1923, pp. 49—53.

Fucus coccineus Hudson, Flora Anglica. Tom. II, 1778, p. 586, Goodenough and Woodward, Transact. Lin. Soc. 1797, III, p. 187.

The structure of this common Atlantic species has been described by Kützing (1843), Nägeli 1847, Oltmanns (1904) and Kylin (1923). The ramification and the cell-divisions at the tips of the frond were carefully explained by Nägeli who stated that in the vegetative pinnæ the apical cell is first divided by transverse walls, whereas they "beendigen ihr Wachsthum meist durch shiefe Wände"... "Die Sporenäste und Keimäste dagegen wachsen durch schiefe Wände in der Scheitelzelle" (l. c. p. 228). Kylin says (1923, p. 51) that he has not observed the oblique divisions of the apical cells, and it must be admitted that the apical cell of most of the vegetative pinnulæ are divided only by transverse walls. Nägeli's statement is, however, correct, at least for the feebler vegetative and for the male pinnulæ. In the lowermost, feeblest pinnula in a row, the last dividing walls of the apical cell are oblique, alternating (fig. 602), whereas the upper pinnulæ are divided by transverse walls to the very end of their growing activity, and in the tetrasporiferous pinnulæ the apical cells early begin to divide by oblique walls; the lateral ones are even divided only in this manner (fig. 603). In a female plant with young procarps, I found only transverse divisions in the apical cell of the pinnulæ.

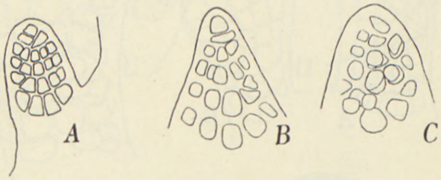


Fig. 602.
Plocamium coccineum. Lowermost sterile pinnulæ. 350 : 1.

As to the anatomical structure and its development reference may be made to the quoted paper of Kylin. We shall merely emphasize that the frond contains a central row of long cells rich in protoplasm, and is built up of an inner tissue of large parenchymatous cells which can be designated as a storage tissue, as it is rich in starch grains, and an outermost layer of small cells, which is essentially an assimilatory tissue; its cells contain numerous small chromatophores. Hyaline hairs are not produced.

Antheridia were not observed in the Danish specimens. According to Buffham (1891) and Kylin (1923, p. 53) they form a layer on the surface of the pinnulæ of the last and penultimate order.

The procarps arise in great numbers at the edges of the young branches of the flattened frond, at the inner as well as the outer edges. Their development has been described by SCHMITZ, PHILLIPS and KYLIN. Referring the reader to KYLIN's paper, I shall only mention that the carpogonial branch is 3-celled and that the supporting cell (Tragzelle) according to SCHMITZ and KYLIN develops directly into an auxiliary cell, while PHILLIPS thought that the auxiliary cell was cut off from the supporting cell after fertilization. The first gonimoblast cell is cut off from the outer side of the auxiliary cell; it gives rise to several lateral cells which produce each a gonimolobe. The wall of the globular cystocarp consists of 3—4 cell-layers.

The tetrasporangia are produced in particular pinnæ (stichidia) which are very different from the vegetative ones. They are flattened, simple and lanceolate or branched with nearly opposite or alternate, divaricate branches. The tetrasporangia are included, biseriate. OLTMANNS (1904, p. 661) compares them to the stichidia in *Tœnioma* and says that they are situated beside the central axis. The latter assertion, however, is not correct, for there is no axial cell-row in the fertile part of the stichidia, owing to the fact that the apical cell of this organ is divided by oblique segment walls, as pointed out by NÄGELI. The first segments of the fertile pinnæ are cut off by transverse walls, but after the formation of e. g. 4 segments by this mode of division, the apical cell divides for the rest of its active period by alternating oblique segment walls. The segments cut off from the wedge-shaped apical cell are first divided by a periclinal wall. The outer daughter cell divides by anticlinal cell-walls and gives rise to the marginal portion of the cortex or wall of the stichidium. The inner daughter cell divides by two periclinal cell-walls by which are cut off two peripheral cells which by anticlinal cell-divisions give rise to the cortex on the two faces of the stichidium, while the middlemost cell is a young tetrasporangium. The sporangia are therefore contiguous and form a continuous zigzag line along the longitudinal axis of the stichidium. The wall of the stichidium consists of only one layer of cells. When the stichidia are branched, the insertion of the branches is high, the breadth of the branches is greatest at the base and diminishes upwards. The branches are fructiferous from the very base. The uppermost cells continuing the zigzag row of sporangial mother-cells remain sterile.

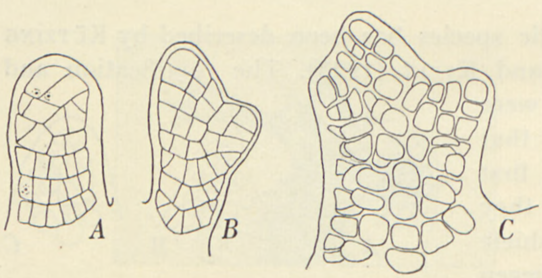


Fig. 603.
Plocamium coccineum. Young stichidia. *A*, 560 : 1, *B—C* 350 : 1.

As is well-known, the sporangia divide by three parallel walls. The primary nucleus is first divided into two, a transverse wall is produced in the middle of the cell, and the two daughter nuclei enter into the resting stage before the next divisions take place (fig. 604 *C*).

Buffham reports (1884, p. 338) that he has met with "a fine plant, divided near the base, bearing tetraspores on one half and coccidia on the other". If a similar case should be met with again, it would be of interest to ascertain whether the plant is really a single individual or if its origin might possibly be due to the fusing of two distinct individuals.

The germination I have not observed; but according to Kylin the germination of the carpospores begins with the formation of a disc-shaped body ("Keimscheibe") (1923, p. 53, fig. 34 e).

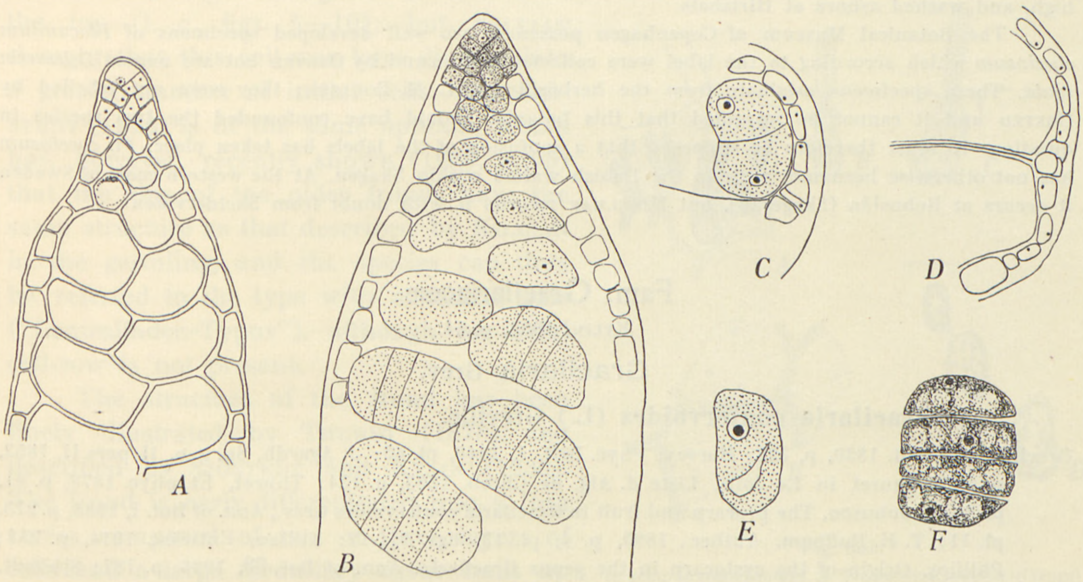


Fig. 604.

Plocamium coccineum. From Hirtshals, September (*A*) and from the Færöe Islands, May, collected by F. Børgesen. Stichidia. *A* and *B*, optical longitudinal sections. *C* and *D* cross sections. *E*, undivided sporangium. *F*, ripe sporangium. 350 : 1.

Plocamium coccineum has only been met with in the North Sea and Skagerak. It has only been collected in the months of June to October, but this is due to the fact that dredgings in these waters have not been made in winter and spring. It has been found at depths from 2 to 18 metres in Skagerak, and a small specimen was found in the North Sea at 27 metres' depth. It grows on stones and on various Algæ (*Laminaria hyperborea, Rhodomela, Phyllophora membranifolia, Furcellaria*).

The Danish specimens agree with the typical North European form. Though the species has not been collected in winter and spring, it is evident that it is perennial. In specimens gathered in June the new shoots had a brighter colour than the older ones, and the old portions of larger plants are often largely covered with *Membranipora pilosa.*

The fronds reach a length of up to 10 cm. Tetrasporangia and cystocarps frequently occur in August; they were also met with in September, but the stichidia were then partly emptied and thrown off. Young stichidia were observed in June.

Localities. **Ns:** Washed ashore at Römö (C. M. Poulsen); eR, 9 miles NW 1/2 N of Lodbjerg lighthouse, 27 m, a small incomplete specimen 7 mm long, October. — **Sk:** Bragerne, 2.5 m, on Rhodomela, 4 cm, sterile, July; Dana St. 2900, east of Bragerne, 9 m, 1.5 cm high, sterile, October; washed ashore at Løkken (Mrs. Witthøft), 4 cm in diameter with ripe cystocarps; ZK[7] abreast of Rubjerg Knude, 18 m, 4—6.5 cm high and two other places off Lønstrup, about 8.5 m, on Phyllophora membranifolia; repeatedly washed ashore at Lønstrup; off Hirtshals, 12 m, F. Børgesen, on *Laminaria hyperborea*, 7—8 cm in diam.; Bredegrund and Møllegrund off Hirtshals, 9—15 m, several specimens, up to 7.5 cm high, and washed ashore at Hirtshals.

The Botanical Museum of Copenhagen possesses two well developed specimens of *Plocamium coccineum* which according to the label were collected in Øresund by Ørsted but are named *Delesseria alata*. These specimens originate from the herbarium of C. M. Poulsen; they were not labelled by Ørsted and it cannot be imagined that this botanist should have confounded the two species in question. It must therefore be supposed that a confusion of the labels has taken place. *Pl. coccineum* has not otherwise been met with in the Danish waters within Skagen. At the western coast of Sweden it occurs at Bohuslän (Skagerak), but Kjellman records it with doubt from Skelderviken.

Fam. Gracilariaceæ.

Kylin, 1930, p. 54.

Gracilaria Grev.

1. Gracilaria confervoides (L.) Greville.

Greville, Alg. Brit. 1830, p. 123; Harvey, Phyc. Brit. I, 1846, pl. 65; J. Agardh, Sp. g. o. II pars II, 1852, p. 587; Thuret in Le Jolis, Liste d. Alg. de Cherb. 1863, p. 134; Thuret, Ét. phyc. 1878, p. 81, pl. 40; T. Johnson, The procarp and fruit in Gracilaria confervoides Grev., Ann. of Bot. I, 1888, p. 213, pl. 11; T. H. Buffham, Anther., 1893, p. 4, pl. 13, figs. 11, 12; Killian, Entwick. 1914, p. 254; Phillips, Origin of the cystocarp in the genus Gracilaria. Ann. of Bot. **39**, 1925, p. 787; Sjöstedt, Florid. Studies, Lunds Univ. Årsskr. **22** no. 4, 1926, pp. 51—64; Kylin, Entwick. 1930, p. 55.
Fucus confervoides L. Sp. plant. ed. 2, II, 1763, p. 1629.
Gigartina confervoides Lam. Thal. 1813, p. 48; Lyngbye Tent. 1819, p. 43.

The closely placed cylindrical fronds spring in a fairly great number from a fleshy flat disc. Harvey says that there is "a small disc accompanied by fibres" (Phyc. Brit. pl. 65, Manual, sec. edit. 1849, pl. 16), and his figure shows a "radix fibrosa". Other authors mention only a disc, and I have myself not seen any fibres in the Danish specimens. The disc has a parenchymatous structure, being composed of vertical or ascending cell-rows. The cells were in summer filled with numerous starch-grains. The disc increases in circumference by marginal growth and may reach a diameter of at least 0.5 cm; it becomes slowly thicker by continued growth of the vertical cell-rows of which it is composed. The periodicity in the growth may cause a stratification; the presence of one secondary layer could be ascertained in an older disc examined.

The upright cylindrical fronds reach a length of up to 32 cm, though most of the specimens collected scarcely exceeded 20 cm in length. The ramification is pronouncedly lateral, the branches arising at a long distance below the apex. All the shoots taper upwards.

As to the structure of the tip of the frond, the authors do not agree. Killian (1914) described the germination of the carpospores and found that the spore divides by vertical walls, forming an orbicular disc increasing by continued anticlinal and periclinal cell-divisions. The central part of the disc becomes vaulted, and one of the central cells develops more vigorously than the others; it becomes the initial cell of the primary upright frond issuing from the disc. The young frond has then a single triangular initial cell at the top (l. c. figs. 5—10); but Killian thought that this cell was later divided into a greater number of initial cells, and Sjöstedt (1926) is of the same opinion. Kylin has, however, recently shown (1930, p. 55) that the tips of the older fronds have the same structure as that described by Killian in the germling, and the species can thus be referred to the type with a central axis ("Centralfaden-Typus"), although an axial cell-row is not present.

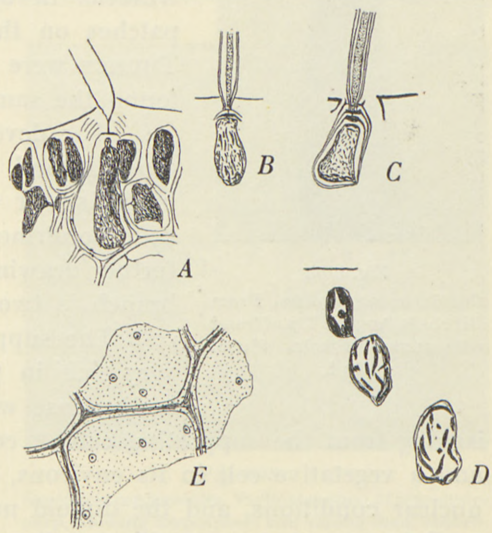


Fig. 605.
Gracilaria confervoides. A, Transverse section of frond with a hair. *B* and *C*, basal portions of hairs. *D*, cortical cells. *E*, medullar cells showing secondary pits seen from the face. *A*—D 560 : 1. *E* 420 : 1.

The structure of the frond has been finely illustrated by Thuret (1878) and described by Sjöstedt and Kylin (1930). The frond is early differentiated into a thin cortex composed of two or three layers of cells and a large medullary tissue built up of large, round, isodiametrical cells not lengthened in a longitudinal direction. These cells are connected by numerous pits, partly secondary, and are without any rhizoids (fig. 605 *E*). The young cortical cells contain one nucleus while the older and inner cells may contain a greater number. Each cortical cell contains several chromatophores which are long, linear, ribbon-shaped, bent and sometimes branched; they are most easily seen in the inner cortical and the outer medullar cells (fig. 605 *D*).

The young parts of the shoots bear numerous hairs (fig. 605). They were first briefly mentioned by me (1911, pp. 206, 208). Later Phillips observed the hair-producing cells but misinterpreted them as carpogonia (1925), whereafter Sjöstedt (1926) gave a description of the development and structure of the hairs (in *Gr. compressa*). They arise early (in *Gr. confervoides*) from primary cortical cells which remain undivided and therefore by continued growth become larger than the surrounding dividing cortical cells (fig. 605 *A*). The hair-bearing cell is connected with the hair by a narrow pit the transverse wall of which is situated a little lower than the surface of the frond. KYLIN thought that the hairs are rarely developed, albeit the hair-bearing cells frequently occur. I found numerous and very well developed hairs in July and August (fig. 606).

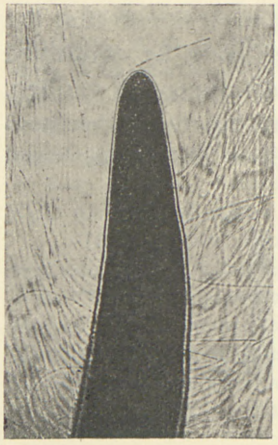


Fig. 606.
Gracilaria confervoides. From Hirtshals, August. Tip of frond with numerous hairs. Photo. 70 : 1.

The antheridia occur in particular individuals; they arise, as shown by THURET (1863, p. 134 and 1878, pl. 40, figs. 1—3) in globular crypts sunk whithin the surface of the frond, the antheridia-producing cells clothing the cavities, whereas in other species of the genus these cells form patches on the surface of the frond. The observations of THURET were confirmed by BUFFHAM (1893), and I have found the same in Danish specimens.

The development of the carpogonial branch, the gonimoblast and the cystocarp has been exhaustively treated by SJÖSTEDT (1926, pp. 54—63), and his observations have been confirmed by KYLIN (1930, pp. 55—59) who has given further drawings. According to these authors, the carpogonial branch is two-celled and developed from a primary cortical cell. The supporting cell of the carpogonial branch becomes very rich in protoplasm and multinucleate, and the same is the case with the basal cells of the vegetative branches issuing from the supporting cell. A connection takes place between the carpogonium and a vegetative cell in its environs, but not with one predesigned in structure and nuclear conditions, and the diploid nucleus remains in the carpogonium. According to SJÖSTEDT, a true auxiliary cell cannot therefore be pointed out in the genus *Gracilaria*. Further cell-connections take place with the result that a large ramified fusion-cell is produced, of which the carpogonium constitutes an essential part (fig. 607). Shortly after the formation of the fusion-cell, gonimoblast-cells are cut off from several points of its surface. The gonimoblast consists in an advanced stage of an inner parenchymatous layer, forming a placenta surrounding the fusion cell and an outer layer consisting of radiating cell-rows the outer cells of which are transformed into carpospores (fig. 608). At the periphery of the cystocarp particular long, radiating tubular cells are developed, springing from the parenchymatous tissue and penetrating with their apex into the pericarp which is separated from the gonimoblast by a split (fig. 608). As shown by SJÖSTEDT, they enter into connection with the cells of the pericarp and take up nutriment from them. The pericarp has

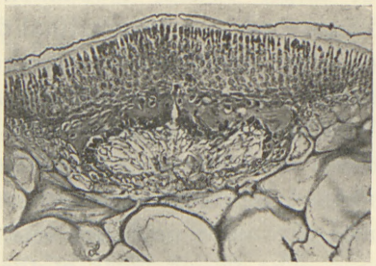


Fig. 607.
Gracilaria confervoides. Young cystocarp, showing the fusion cell, the parenchymatous placenta and the young carpospore layer. Photo. 100 : 1.

a well developed pore at the top. For further details of the structure and development of the cystocarp compare the quoted papers of SJÖSTEDT and KYLIN.

The tetrasporangia are developed in particular individuals; they arise in the cortex by transformation of primary cortical cells. They are cruciately divided.

The species has been met with in several places at the coast of Skagerak from Hanstholm to Skagen, always growing near land at a depth of about one meter or at most two meters. It grows on stones but is often partly covered by sand. The species is perennial. It has not been observed in the winter months, because I have not visited the coast of Skagerak at that season, but large wintering specimens with emptied cystocarps were met with in April. The attachment disc winters, and the same is the case with a great part of the upright fronds or their lowermost part, and new shoots then arise from the disc or from the lowermost part of the wintering shoots. — Ripe tetrasporangia were met with in June, July and August, and as late as October tetraspore-bearing specimens were met with, but most of the sporangia were emptied. Antheridia were observed in July and August. Ripe cystocarps are common in July and August, and mostly emptied cystocarps were met with in October and as late as April.

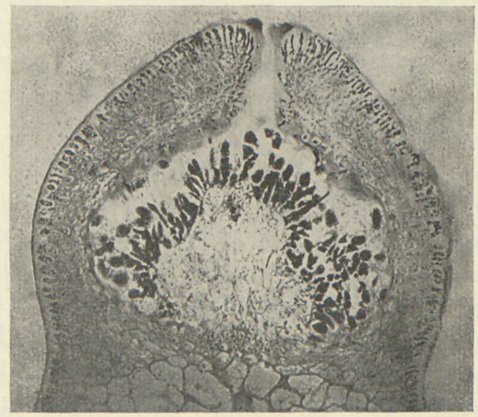


Fig. 608.
Gracilaria confervoides. Vertical section of ripe cystocarp, showing carpospores and among them absorbing tubular cells. Photo. 100 : 1.

Localities. **Ns:** Rømø, on the shore at Havneby (O. Jaap. Schrift. naturw. Ver. Schlesw.-Holstein, Bd. 12, 1902). Hjerting, 15. Aug. 1908 (collector unknown), some incomplete specimens, partly with cystocarps. — **Sk:** Hanstholm, west side of Roshage, near land, 2 metres; on the shore at Svinekløv (P. Petersen); Blokhus (E. Pingel); Løkken; Nørre Lyngby (Ove Paulsen); Lønstrup, 1 m, and numerous specimens on the shore; Hirtshals, on stones near land, 1—2 m, west side and east of the mole; north side of Skagens Gren, in a seine, common on the shore.

Loose forms. *Gracilaria confervoides* has only been met with attached to stones on the north coast of Jutland. Within Skagen it has only been found loose on the bottom in a few widely separated localities. LYNGBYE records *Gigartina confervoides* from the coast of Hindsholm Fioniæ as found by HOFMAN BANG, and several specimens of this species from Hofmansgave are also contained in the herbarium of LYNGBYE, and in that of the Botanical Museum of Copenhagen, all collected by HOFMAN BANG in the years 1824 to 1828, though it is said to be very rare. The species seems, therefore, to have lived here in a loose condition at least for some years, perhaps for a long time. On some of the specimens LYNGBYE has written, that HOFMAN found them after the storm on the first of November 1827. It seems, therefore, that the species occurred only at a certain depth whence it was only washed ashore by violent storms. The specimens from these localities are only slightly different from the typical ones except that they are all without base and sterile, and it can be added that they are all devoid of hyaline hairs. They are about 12 cm long, and the branches are often somewhat bent. HOFMAN BANG referred them to *Fucus scorpioides* Fl. Dan. t. 887. LYNGBYE was much in doubt as to their determination. The anatomical structure agrees with that of *Gracilaria confervoides*, in particular the central tissue built up of large short cells, by which this species is easily distinguished from *Furcellaria fastigiata* and *Ahnfeltia plicata* with which the loose specimens have been compared.

Fig. 609. *Gracilaria confervoides* f. *tenuissima*. Ulfsund, Søren Lund. Nat. size.

Loose specimens were further met with in two localities in the Limfjord, where they occurred on clay-muddy bottom without vegetation. These specimens are only different from the normal ones by the want of base and by being sterile.

F. *tenuissima*. A more aberrant sterile, loose form has been gathered by Mr. SØREN LUND by dredging in Ulfsund on the north side of the island of Møen at 3 metres' depth, where it occurred in company with loose *Cladophora*. The specimens are only 2—3.5 cm long and very thin, 140—200 μ in diameter, while in the normal specimens the main axis often reaches a thickness approaching to one mm. At the first glance it did not seem easy to determine these thin specimens, but an examination of the anatomical structure showed that they must be referred to *Gracilaria confervoides*. The medullary tissue of the terete frond consists of large, almost isodiametrical cells without rhizoids, not lengthened in the longitudinal direction of the frond, and the tip of the frond agrees perfectly with that of the normal frond, being only somewhat thinner. The apical meristem was decidedly active in spring. The fronds have a brown-red colour; they have a firm consistency and are repeatedly branched; 7 generations of shoots were observed. The branches of the consecutive generations are essentially of the same thickness, the youngest branches only somewhat thinner. The branches are more divaricate than in the typical specimens. — It seems probable that these much reduced specimens derive from detached normal specimens accidentally introduced from the Skagerak in these waters in olden time, having been able to keep alive and vegetate in a sterile state by adaptation to the local external conditions, especially the low salinity which probably varies about 1 p. ct.

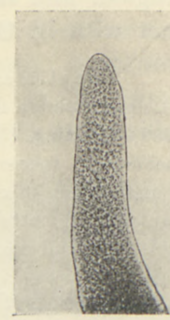


Fig. 610. *Gracilaria confervoides* f. *tenuissima*. Tip of frond. 70:1.

Locality. **Sm:** Ulfsund, off Nymarke Nakke, 600 m from land (S. Lund, April 1930).

General Remarks on the Danish Species of the Gigartinales Rhodymeniales and Nemastomatales.

Reproduction, Alternation of Generations.

Of the 18 species of these groups mentioned above, 11 only have the typical alternation of generations peculiar to the Florideæ. In one of these species the two generations do not occur simultaneously. As shown by STURCH, the sporophytic individuals of *Harveyella mirabilis* occur, at the British shores, in early spring, whereas the cystocarps are only met with in winter (December, January). In the Danish waters and at the west coast of Sweden the behaviour of this species is similar, for the cystocarps have only been observed in December and January, and the tetrasporangia most frequently occur in April to June, in individuals growing on branches and branchlets of *Rhodomela* produced in winter and thrown off in summer. The tetrasporangia are thus developed a little later in the Danish than in the British waters, and latest in the inner Danish waters. It must, therefore, be concluded, that two short-living generations, a sexual generation and a tetraspore-generation, succeeding each other, are produced in the course of one year. Aberrations from this scheme may, however, sometimes occur; e. g. individuals with the two kinds of sex organs and others with tetrasporangia were once found growing simultaneously on the same host plant in October, probably owing to special external conditions. On the other hand, the life-history of the species is different in the Arctic Sea, for it has only been found with sex organs and cystocarps in Scoresby Sound (East Greenland), whereas tetrasporangia were not met with at all, and it seems, therefore, that the sexual generation only is developed in the Arctic Sea.

The behaviour of *Harveyella mirabilis* at the shores of Northern Europe is a rare example of seasonal alternation of generations. SVEDELIUS has first used this term for the life history of *Ceramium corticatulum* in the Baltic.[1] This species has there an ephemeric gametophyte generation in late summer and a winter generation of tetrasporic plants, and SVEDELIUS points out that a similar seasonal alternation of generations has formerly been ascertained in *Chantransia efflorescens* and in *Harveyella mirabilis*. As to the former it must be admitted that no exact proof has been given of the assumption that *Rhodochorton chantransioides* is the sporophytic generation of *Chantransia efflorescens*, as maintained by KYLIN[2] and myself[3], and that the life-history of the species, therefore, needs further experimental and cytological investigation.

[1] N. SVEDELIUS, The seasonal alternation of generations of Ceramium corticatulum in the Baltic. N. A. reg. soc. sc. Upsal. Upsala 1927. — G. SJÖSTEDT, Revision of some dubious Swedish Ceramium types, their classification and ecology. Lunds Univ. Årsskrift, N. F. Avd. 2. Bd. 23, Nr. 12. 1928. — N. SVEDELIUS, The seasonal Alternation of Generations of Ceramium corticatulum. Svensk Botanisk Tidskrift, Bd. 23, 1929.

[2] H. KYLIN, Zur Kenntnis einiger schwedischen Chantransia-Arten. Botan. Studier tillägnade F. R. Kjellman. Uppsala 1906, p. 113.

[3] L. KOLDERUP ROSENVINGE, Mar. Alg. Denm. Part. I, 1909, p. 137.

In *Lomentaria rosea* sex organs are thus far unknown, tetrasporangia only are known; but as the species is rather rare, great importance cannot be attached to this fact.

On the other hand, sex organs and cystocarps are the only known organs of reproduction in *Gigartina mamillosa*, whereas tetrasporangia are unknown. It should be ascertained whether the sporophyte generation is really wanting or whether tetrasporangial sori may perhaps have been confounded with cystocarps.

Rhodymenia palmata is very remarkable by having tetrasporangia and antheridia, whereas carpogonia and cystocarps are unknown. As this species is widely spread, it must be supposed that the last-named organs are really lacking, and the spermatia must then be without function. As a fertilization does not take place and no other mixie has been ascertained, it must be expected at the outset that nuclear division in the sporangium does not have the character of a meiosis. According to Miss Westbrook, a double spireme stage and a synizesis was ascertained by the first nuclear division, but the accomplishment of the reduction division has not been substantiated, and it may be supposed that this process is only initiated but not performed.

It is interesting to note that there are other Florideæ which agree with *Rhodymenia palmata* in having only tetrasporangia and antheridia whereas female sex organs and cystocarps are wanting, viz. *Antithamnion boreale* (Part III, p. 370), *Rhodochorton penicilliforme* (Part III, p. 389), *Rhododermis elegans*[1] and *Halosaccion ramentaceum*[2].

In *Ceratocolax Hartzii* well developed tetrasporangia occur; and the tetraspores are undoubtedly able to give rise to new plants infesting *Phyllophora Brodiæi*, though the first stages of the germination have not been observed. Sex organs too occur, at any rate procarps, which are, indeed, usually badly developed; apparently normal carpogonia with long trichogynes may, however, be met with. Antheridia, too, seem to be produced but they are scarcely quite normal. And the fact that fertilization and cystocarps have never been observed corroborates the supposition that the sex organs do not reach a normal development. The tetrasporangia develop in (winter and) spring, they are ripe in April and May, and after June tetrasporangia-bearing plants are not observed. The individuals as a rule bear either tetrasporangia or sex organs, but as, in one case at least, the presence of nemathecia and sex organs in one and the same specimen was ascertained, it is probable that this is a normal occurrence. It must then be supposed that an alternation of generations does not take place here, but that the individuals produce first tetrasporangia and later sex organs without normal function. As procarps may arise also in spring, it is possible, however, that some individuals produce only sex organs or that these organs can be produced independently of the nemathecia.

[1] Kolderup Rosenvinge, The Marine Algæ from North-East Greenland. Meddelelser om Grønland, Vol. **43**, 1910, p. 105.

[2] H. Jónsson, Mar. Algæ of Iceland, I. Bot. Tidsk. Bd. **24**, 1901, p. 139.

The reproduction of *Phyllophora Brodiæi* and *Ahnfeltia plicata* exhibits instances of a much reduced alternation of generations. In *Phyllophora Brodiæi* it has been shown that the globular bodies, formerly usually considered as a parasite of the genus *Actinococcus*, are much reduced tetrasporophytes of *Phyllophora Brodiæi*. The fronds of this species are all sexual plants usually bearing antheridia and procarps in the same individual. A fertilization process was not seen by the author, but observations of H. Claussen and Kylin suggest that a fertilization and a transfer of a sporogenous nucleus to the auxiliary cell really take place. The auxiliary cell gives off protuberances which do not become gonimoblast filaments but grow out as intercellular cell-filaments which finally give rise to the nemathecial bodies forming cushions outside the surface of the frond. The carposporophyte is abandoned, and in its place a tetrasporophyte is developed. The intramatrical cell-filaments growing out from the auxiliary cell represent the much reduced vegetative part of the tetrasporophyte.

Ahnfeltia plicata is a still more reduced type. Sex organs, fertilization process and cystocarps are wanting. The only organs of reproduction are the nemathecia, which produce monospores in the end-cells of the nemathecial filaments. In the young nemathecia small groups of generative cells appear which give rise to horizontal cell-rows and to secondary nemathecial cell-rows the end-cells of which develop into monosporangia. The groups of generative cells are considered as reduced procarps. These cells or some of them grow out into cell-rows partly in a horizontal, partly in a vertical direction, the latter forming secondary nemathecial filaments producing monospores in the end-cells. The whole complex of cell-filaments produced from the generative cells is considered as corresponding to the sporophytic phase of the typical diplobiontic Florideæ, although it arises without any fertilization process from the *Ahnfeltia* plant. The nemathecium of *Ahnfeltia* can be compared with that of *Phyllophora Brodiæi*, and the monosporangia of the former with the tetrasporangia of the latter. The monosporangia can be interpreted as reduced tetrasporangia which have failed to be divided, in good accordance with the absence of a reduction division.

Loose Forms of normally Attached Species.

The fronds of a comparatively great number of the species treated in the fourth part of this work are able to maintain life for a shorter or longer time after having been disengaged from their support. When living long in a loose condition, the fronds are always sterile. In stormy weather numerous fronds of Algæ are torn away from their substratum. Many of them are washed ashore but a great number are carried by the currents to localities often situated far away from the spot where they were growing and where the external conditions may be rather different from those in their original growing place. The annual species and others with a soft consistency of the frond die shortly after having been loosened; those with a more solid structure are able to keep alive for some length of time. In the Danish waters great quantities of loose Algæ are especially carried along the bottom by westerly storms, when the currents run from the northern areas with comparatively high salinity to the Belt Sea and the Baltic where the salinity of the water is lower, and they may then come to rest in localities where the water is less agitated and the external conditions altogether rather tranquil. In such localities the loose Algæ may find a tolerably permanent place of residence, whether they lie loose on the bottom or they are retained between the rhizomes of *Zostera*-plants or between attached Algæ. Loose forms of several species of Algæ are often found entangled with each other in such places. The power of keeping alive for a long time in a loose condition depends not only on the consistency of the frond but also on its ability to support the different external conditions in the new place (salinity, variation of temperature etc.), and on its power of increasing and branching after having been detached from the substratum. As will be seen in the following, the species here in question show great differences in their power of adaptation to the loose condition.

Phyllophora membranifolia does not seem very willing to vegetate in a loose condition. Detached fronds may be met with, but they are not different from the attached ones and seem unable to grow after having been detached. (Comp. p. 521).

Three loose forms of *Chondrus crispus* were mentioned above (pp. 506—507); they occur rather rarely and in small quantities, and it is doubtful whether they are able to vegetate and propagate in the loose condition. Specimens of f. *incurvata* showing a callus disc at the lower end of the frond cannot have lived long after the disengagement for the callus must be supposed to have been produced on the wound surface where the frond has been loosened, and the aberrant shape of the frond must, therefore, be supposed to have been accomplished by transformation of the frond, not by innovation.

Rhodymenia palmata occurs in a loose condition in the Baltic north of the Isle of Møen (**Bm**), where the species cannot live in the normal, attached state, owing to the low salinity of the water. These specimens have undoubtedly been carried into the Baltic from Øresund when the bottom current through Øresund overflows the threshold at Saltholm; they resemble those growing attached in Øresund. They undoubtedly keep alive for some time, but it is doubtful whether they can propagate for any long period. At any rate, as the species can continually be introduced in this part of the Baltic, it is understandable that it has often been met with in this area, like many other loose Algæ. The great length of the fronds gives evidence of a continued growth in the loose state.

Phyllophora Brodiæi which is very common in all the Danish waters often occurs in a loose condition of various shapes. The most common form is f. *concatenata* which is most frequently met with in the *Zostera* region; it is characterized by long fronds alternately filiform and flat, lanceolate, branched by dichotomy and by proliferations. Nearly related to it is f. *filiformis*, the frond of which is very narrow, almost entirely cylindrical. F. *stellata* has a quite different shape, the dichotomously branched frond bearing at the top of the branches bunches of radiating small, narrow shoots which must be considered as sterilized sexual shoots. These loose forms are probaby able to vegetate and propagate for a long time by continued growth and branching, a multiplication taking place by decay of the oldest parts of the frond.

Ahnfeltia plicata, which, like the foregoing species, is of common occurrence in the Danish waters, also appears in a loose form (f. *tenuior*, p. 568), which is easy to recognize as belonging to this species but, on the other hand, of a very aberrant shape. Its frond is lower and thinner and the branches divaricate. It is common in company with other loose Algæ, in particular between Zostera. It is undoubtedly able to vegetate and propagate by continued dichotomizing and dividing.

Gracilaria confervoides occurs, attached to stones, in the Danish waters only on the shores of the North Sea and Skagerak, but loose specimens have been met with in a few places in the inner Danish waters. A few specimens, not different from the normal ones except by being destitute of base were found in the Limfjord, where they may easily have been introduced by currents from the North Sea. It is more remarkable that loose specimens of the same species have been carried by the currents to two localities in the inner waters situated at great distances from those where the species is normally growing. At Hofmansgave, at the North coast of the island of Funen, loose specimens differing from the normal ones only by somewhat curved branches, but otherwise easily identified by their anatomical structure, were met with in the years 1824 to 1828. They must have originated from specimens introduced by currents from the Skagerak and have kept vegetating at least in that period. Later they have not been observed and have probably sooner or later decayed owing to the unfavourable external conditions. The specimens found at the north coast of Møen, where the salinity of the water is very low (about 8 ‰), are more aberrant in the inconsiderable size and small thickness of the fronds; the anatomical structure of the frond, however, showed with certainty that the fronds belonged to *Gracilaria confervoides*. The fact that the loose specimens were found in a considerable number in this locality suggests that this form f. *tenuissima* is able to vegetate and to propagate by dividing, and it can be concluded that it has been adapted to keep alive during a certain period. Whether it would be able to propagate for an indefinite period must be settled by later investigations.

The most remarkable example of loose Florideæ taking a shape very aberrant from that of the typical species is *Phyllophora epiphylla* f. *Bangii* (p. 540), characterized by its incised frond. It has so far been considered as an independent species, referred even by one author to another genus (*Rhizophyllis*). By examining a great number of specimens of *Phyllophora Bangii* I have been able to prove that it is a loose form of *Ph. epiphylla*, connected with it by rare transitional forms. The typical species only occurs in the North Sea, Skagerak and the Northern and Eastern Kattegat, whereas f. *Bangii* almost exclusively occurs out of this area in water of lower salinity in the inner Danish waters, including the Western Baltic. That it has not been met with in Øresund is probably due to the too low salinity of the surface water in this area. In some specimens (α), the frond is not incised in its whole length but has broader portions with more or less entire border, and in these specimens ramification by proliferations may occur just as in the typical species. Other specimens have not such dilatations of the frond and only branch by lateral ramification, never by proliferations (β, *tenuis* Lyngbye). This form has certainly arisen by branching of the broader form (α). It occurs partly together with the latter, partly alone, in the innermost waters (Great Belt and Western Baltic). It is interesting to note that in the southernmost part of the area of β a new form arises as branches from it, branching just like it by lateral ramification only, but entirely wanting the lacinulæ characteristic of β (fig. 528). — *Ph. Bangii* is able to vegetate and propagate by continued growth and ramification and decay by degrees of the lowermost part of the frond; it can therefore be maintained for a very long time even if renewal by transformation of the typical form only rarely occurs. In this respect it can be compared with the floating forms of *Sargassum* in the Sargasso Sea. The number of specimens of *Ph. Bangii* in the Danish waters is much larger than that of the typical *Ph. epiphylla*.

J. SCHILLER has designated the formations of loose Algæ as "Migrationsformationen"[1] or wandering formations; this designation would not, however, be particularly well-suited to the loose Algæ mentioned here, because they live in localities where the movements of the water are feeble and where the loose Algæ to a great extent are retained and entangled between *Zostera*-plants or attached Algæ; they are, therefore, practically resident on the same spot.

[1] J. SCHILLER, Über Algentransport und Migrationsformationen im Meere. Revue der ges. Hydrobiol. u. Hydrogr. Bd. II, H. 1 u. 2.

Addenda.

Fam. Bangiaceæ.

2. **Erythrotrichia reflexa** (Crouan) Thuret in herb.

Hauck, Meeresalg. Deutschl. u. Oesterr. 1884, p. 22; G. Hamel, Floridées de France. Bangiales. Revue Algologique, Vol. I, 1925, p. 288.
Bangia reflexa Crouan, Algues mar. du Finistère. III, N. 394, 1852.
Porphyra reflexa Crouan, Florule du Finistère 1867, p. 132, pl. 10, fig. 73.

In July 1923 I found in the harbour of Frederikshavn a small *Erythrotrichia* which agreed with *E. reflexa* (Crouan) by its short curved filaments attenuated at both ends. The same species was found again in the following years in several places in the Northern Kattegat.

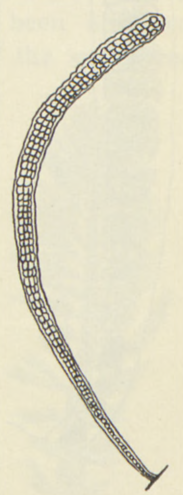


Fig. 611.
Erythrotrichia reflexa from Tønneberg Banke, Northern Kattegat, 19 m, July. The filament is by exception not attenuated at the top.

Only little has been added to our knowledge of *E. reflexa* since it was described in 1852 by the brothers Crouan upon specimens from Brest. Hauck recorded the species from the Adriatic Sea but, according to Hamel (l. c. p. 289), the plant which Hauck has communicated under this name is not *E. reflexa* but *E. obscura*. Hamel records the localities known on the coast of France, and gives some dimensions for the specimens of Crouan: thickness at base 10 μ, in the middle 35 μ and near the top 15 μ.

The Danish specimens, which I have examined in a living state and well preserved, show larger dimensions than those given by Hamel which are in accordance with my observations on examining the original specimens of Crouan and specimens from Bornet collected at Biarritz. The lower part of the frond consisting of a single row of cells showed a thickness of 17—35 μ, and the middlemost part a thickness of 32—63 μ, most often about 46 μ. The plants may reach a length of 5 mm but are usually shorter, about 2 mm

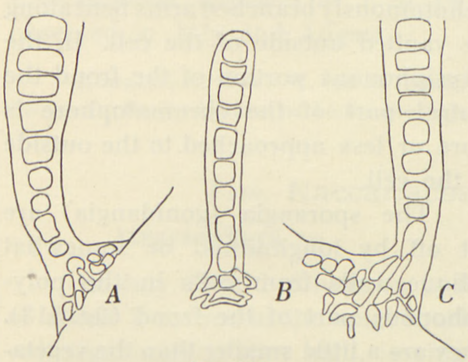


Fig. 612.
Erythrotrichia reflexa. *B*, young plant. *A* et *C*, basal parts of plants. 350 : 1.

or smaller. The thickness gradually increases towards over the middle, longitudinal divisions beginning at various distances from the base. The number of vertical septa in each joint of the middlemost part of the frond may be about 4. Near the top the filament is again tapering; longitudinal divisions are wanting.

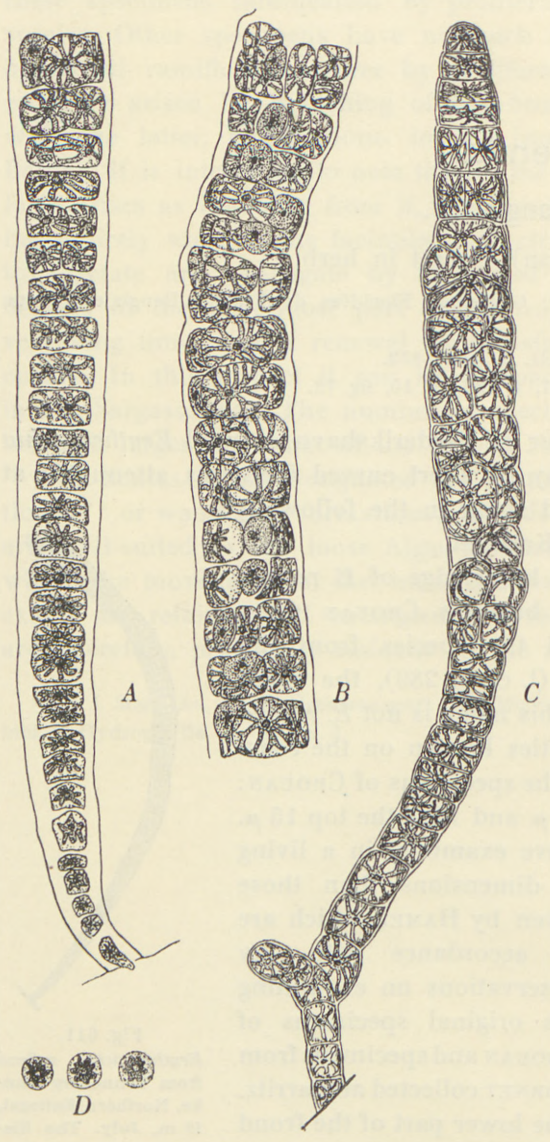


Fig. 613.
Erythrotrichia reflexa. After living plants. In *B* monosporangia are to be seen. In *C*, the basis of the plant was hidden. *D*, monospores. After living plants. 340 : 1.

As nearly all the observed specimens were unbranched, it appeared doubtful whether the Danish specimens ought to be referred to CROUAN's species. One specimen only was found which showed a little branch issuing near the base (fig. 613 *C*). According to CROUAN the fronds are branched or simple, with branches arising near the base, alternate or opposite.

The young plants are cylindrical, monosiphonous, fixed to the substratum (various Algæ) by rhizoids produced by the lowermost cells of the filaments (fig. 612 *B*) and forming a conical attachment organ composed of several closely united branched cell-filaments (fig. 612, *A*, *C*). CROUAN described the "root" as colourless; I found it of the same dark purple colour as the upright filament. Each cell of the filaments contains a stellate chromatophore with a central pyrenoid and long, simple or dichotomously branched arms bent along the vaulted outside of the cell. In the polysiphonous portion of the frond the central part of the chromatophore is more or less approached to the outside of the cell.

The sporangia (gonidangia) are cut off by longitudinal or somewhat oblique walls from cells in the polysiphonous part of the frond (fig. 613). They are a little smaller than the vegetative cells, about 14—16 μ in greatest diameter, often broadly obovate, and are easily recognizable by their dense contents. The stellate chromatophore is not so distinct as in the vegetative cells, but the pyrenoids are easily observed. In the exhausted spores the chromatophore is very distinct (fig. 613 *D*); its arms are shorter than in the vegetative cells. In the living spores the chromatophore was red, while the pyrenoid appeared with a yellowish colour. In a certain position the chromatophore showed an incision on one side where the nucleus probably was situated. The living spores showed no amoeboid changes of shape, but were able to execute gliding movements on the slide.[1]

The Danish plants are here referred to *Erythrotrichia reflexa* although they are almost all unbranched and their dimensions larger than those of the French specimens, and though there seem also to be differences as to the attachment organ. Crouan attributed to his species a "Racine discoide incolore". I have not observed the attachment organ of the original specimens in Crouan's Exsiccate No. 394, but I have seen the attachment organs in specimens of the same species from Biarritz communicated by Bornet (herb. Thuret), and these agreed with those of the Danish specimens; I think, therefore, that Crouan's short description of the attachment disc is founded on some incomplete observation. Colourless attachment organs are otherwise not known in the genus *Erythrotrichia*. As to the nearly complete want of ramification in the Danish specimens, it is noteworthy that only one little branch has been met with, although the species has been observed repeatedly during recent years. On the other hand the greater part of the specimens examined from the collection of Crouan were unbranched, and all the filaments examined of the specimen from Biarritz were unbranched. The greater thickness of the filaments in the Danish specimens is perhaps due to the different external conditions. As long as *Er. reflexa* and its variation is not better examined in different localities, it is impossible to decide with certainty whether the Danish species is the same as that from the coast of France.

The species was found growing on various Algæ (*Polysiphonia urceolata*, *Cystoclonium purpureum*, *Sphacelaria saxatilis* and *Callithamnion Hookeri*) at 1 to 19 metres' depth; it was only observed in July and August.

Localities. **Kn:** N.W. end of Tønneberg Banke; Hirsholm harbour (Henn. Petersen); Frederikshavn harbour; Borrebjergs Rev, Marens Rev.

Fam. Naccariaceæ Kylin 1928.

Atractophora sp.

In July 1929 I found on a stone picked up from a depth of about 2 metres in the neighbourhood of Frederikshavn a small red Alga, only 2 mm high, issuing from a circular disc. As the

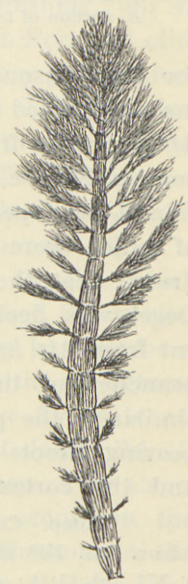


Fig. 614.
Atractophora sp.? 33:1.

[1] Comp. L. Kolderup Rosenvinge, On Mobility in the reproductive Cells of the Rhodophyceæ. Botan. Tids. **40** p. 72.

species was unknown to me I tried to get other individuals in the same locality and in other similar places but without success. The only existing little specimen showing a very characteristic structure, I think it useful to give a short description of it and some figures in order to render an identification of the species possible.

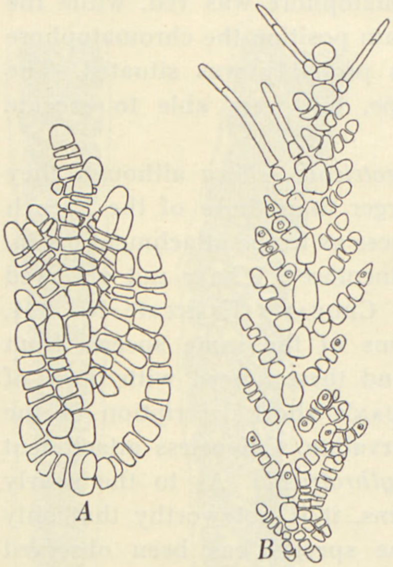


Fig. 615.
Atractophora sp.? *A*, tip of frond. 625 : 1. *B*, portion of branch. 440 : 1.

The frond has a distinct axial cell-row which bears at each joint a whorl of branches, from the base of which downward growing cell-rows issue, which form a thick cortex surrounding the axial cell-row. The branches are mostly pinnate, with opposite branchlets and with limited growth; branchlets of the second order may occur. Many of the end-cells of the pinnæ and pinnulæ bear a hyaline hair. The lowermost branches are simple or feebly branched. Branches of the same kind as the primary axis, with enduring growth, occur. The colour of the plant is brownish-purple, somewhat resembling that of *Plumaria elegans.*

The plant recalls *Atractophora hypnoides* in the general structure[1]; but it differs so much that it cannot be identified with it. As I had no material for comparison, I applied to Mr. E. Chemin at Paris who has most kindly sent me some dried specimens of *Atr. hypnoides* from the north coast of France. An examination of these specimens, some of which were young, confirmed that the plant from Deget was decidedly different from *Atr. hypnoides.* The branches of the latter are similar to the primary axis, bearing shoots on all sides, and the cortex built up of

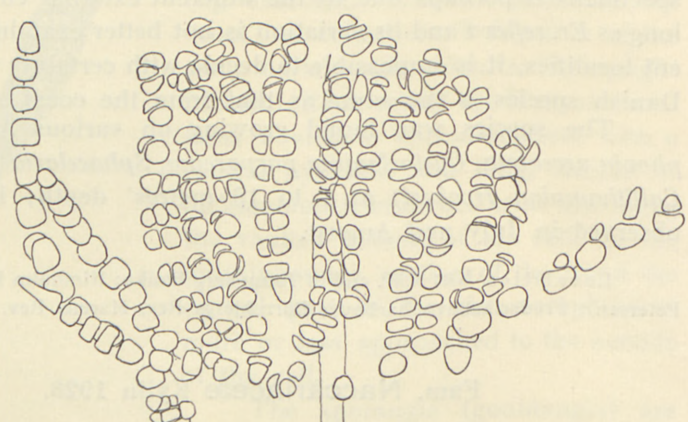


Fig. 616.
Atractophora sp.? Portion of the main axis. The cell-rows of the cortex are a little separated by pressure. The long cells of the axial cell-rows are to be seen in the middle. 625 : 1.

[1] Comp. Crouan, Ann. d. scienc. nat. IIIe sér. t. 11, 1848, p. 371, pl. 11 A; Nägeli, Morph. u. Syst. d. Ceram. 1861, p. 388; Zerlang, Flora 1889; Kylin, Entwick. Florid. Studien. 1928, p. 12; E. Chemin, Sur le développement des spores de Naccaria Wiggii Endl. et Atractophora hypnoides Crouan, Bull. soc. bot. France, t. 74, 1927, p. 274.

the downwards growing cell-rows budding off from the base of the branches has a quite different structure from that of the Danish specimen. In the French plant it remains filamentous, consisting of parallel cell-rows and it has a comparatively small thickness, while the cortical cell-rows in the Danish plant are early divided by numerous transverse and longitudinal walls, the latter being both radial and tangential, with the result that the cortex becomes thick and is built up of numerous short cells, whereas the axial cell-row is narrow (fig. 616), in contradistinction to *Atr. hypnoides* where it is very broad. Finally the cortical cell-rows of the latter bear numerous short simple or feebly branched filaments which do not occur in the Danish plant (comp. CROUAN l. c. fig. 3—5). In spite of the differences quoted it seems probable that the Danish plant belongs to a species related to *Atractophora hypnoides*.

Locality. **Kn:** South coast of the isle of Deget near Frederikshavn.

Fam. Rhizophyllidaceæ.

Chondrococcus Hornemanni (Mertens) Schmitz.

This species was first described by MERTENS in 1815 (Göttinger gel. Anzeiger 1815 No. 64) under the name of *Fucus Hornemanni*. It was mentioned and described 1819 by LYNGBYE who writes (1819, p. 35) that it was found in Öresund "ubi ad oram Helsingoræ hanc speciem elegantem et quidem rarissimam cel. Forskaal olim legisse fertur". LYNGBYE named it *Desmia Hornemanni* and gave a very good picture of it (l. c. Tab. 7 C). The original of this figure is to be found in The Botanical Museum at Copenhagen, labelled by MERTENS: *F. Hornemanni*; on the back of the sheet HORNEMANN has written: "legit Forsk: ad oras Helsingoræ". The species was referred to *Sphærococcus coronopifolius* by C. AGARDH in Synops. Alg. Scand. 1817, p. 30, and later united with *Sphærococcus Lambertii* (Suhr) by J. AGARDH (Sp. g. o. II.II. 1852, p. 641) under the name of *Desmia Hornemanni* (Mert.) Lyngb., which name is still kept in his Epicrisis, 1876, p. 357, while KÜTZING referred the species to the genus *Chondrococcus*. There can be no doubt that this Alga has not been found growing in the Öresund. LYNGBYE had evidently his doubts as to the correctness of the locality cited, and J. AGARDH wrote (1852, p. 642): "cum nave forsan transvecta?". SCHMITZ (Marine Florideen von Deutsch-Ostafrika, Engler's Bot. Jahrb. Bd. 21, 1895, p. 171) pointed out that *Chondrococcus Lambertii*, which is common at the Cape, is specifically quite different from the true *Ch. Hornemanni* which occurs in the Northern Indian Ocean. I can fully confirm this distinction. In *Ch. Hornemanni* the pinnæ are generally opposite while in *Ch. Lambertii* the branches are alternate and more distant, and the frond broader. It can be imagined that the specimen described and figured by LYNGBYE has been collected by FORSSKÅL in the Red Sea, but that a confusion of labels has occurred after FORSSKÅL's death, during the last part of the journey or later.

Genera incertæ sedis.

Conchocelis Batters 1892.

1. Conchocelis rosea Batters.

E. A. Batters, On Conchocelis, a new genus of perforating Algæ, in G. Murray, Phycological Memoirs, Part I, London 1892, pp. 25—28, Pl. VIII. G. Nadson, Die perforierenden (kalkborenden) Algen. (Russian with abstract in German), Scripta Botanica Horti Univ. Petropolit. fasc. 18, 1900, pp. 14—19, 36—37. L. Kolderup Rosenvinge, On the Marine Algæ from N. E. Greenland. Meddelelser om Grønland, **43**, 1910, p. 111. H. Printz, Algenveg. d. Trondhjemsfjordes. Skrifter utg. af D. Norske Vid.-Akad. Oslo. 1926, pp. 54, 257.

Batters described in 1892 a perforating red Alga living in the calcareous shells of Molluscs gathered near the coast of Scotland. The frond consists of a horizontal layer of thin, branched interlaced filaments giving off irregular inflations, which are simple or branched, and consist of from two to ten cells, each containing a star-shaped chromatophore. According to Batters the plant appears to be reproduced by means of spores formed in the cells of the inflations, one spore in each cell. He had "seen globular bodies which appear to be spores escape from the cells". In accordance with Bornet he referred the plant to the *Porphyraceæ (Bangiaceæ).*

The plant seems to be widespread for it has been met with repeatedly at the shores of northern Europe and in the Arctic Sea, but it is as yet imperfectly known. Nadson advanced (1900) the opinion that it was not a Rhodohycea but only a red variety of the green Alga *Ostreobium Queketti* Born. et Flah.; this opinion, however, has not been accepted by later authors (Kolderup Rosenvinge 1910, Printz (1926), and it can be taken for granted that *Conchocelis rosea* has been confounded by Nadson with a red variety of *Ostreobium Queketti.* Printz found such a red form of the last named Alga in the neighbourhood of Trondhjem, and I found a similar form in the Northern Kattegat, but they were both quite distinct from *Conchocelis rosea.* After having examined specimens of the latter gathered in East Greenland I maintained, though with doubt, that it could be referred to the *Bangiaceæ*, which classification was principally founded on the lack of pits in the transverse walls and the supposed presence of spores comparable to the monospores of the *Bangiaceæ.* On examining the Danish specimens of the species, I have, in order to gain a better determination of its systematic position, directed my attention in particular to the structure of the chromatophores, the presence or want of a pit in the transverse walls, and the reproduction.

The species is fairly widespread in the Danish waters where it grows in the shells of various molluscs; but it is most easily accessible when it occurs in the calcareous tubes of *Spirorbis* and *Pomatocerus triquetrus*, two Serpulids often attached to *Furcellaria* a. o. Algæ, and the shells of which are frequently pink owing to the abundant occurrence of *Conchocelis rosea.* For a study of the finer structure of this plant the shells of these Serpulids were treated with acetic acid, Carnoy's fluid, Nawashin's mixture or picric acetic acid. The latter treatment was particularly good for demonstrating the nuclei and the pit-connections between the cells.

The peripheral part of the frond is formed of long thin filaments, usually 3—4 μ thick, sometimes only 2 μ or still thinner. Where there is ample room the filaments may be long and straight and consist of very long cells; they may be simple or bear opposite or alternate branches rising rectangularly near the upper end of the cells. The branches are partly different from the long straight filaments by being composed of shorter more or less swollen, spindle-shaped or more irregular cells. (Comp. figs. 617—619). Later the filaments become very much branched and densely felted together, forming a more or less continuous layer within the surface of the shell. The cylindrical cells contain a small number of long ribbon-shaped or perhaps branched chromatophores and, in the middle of the cell, a nucleus which is often rather inconspicuous and feebly stained with hæmatoxylin. The transverse walls are very distinct but it is usually impossible to distinguish a central pit by application of dry lenses; but with high magnifying power a callus button deeply stained with hæmatoxylin on each side of the transverse wall could sometimes be observed (fig. 617 *A*, *E*), a sure sign of the presence of a pit. The structure of the inflated cells is similar to that of the cylindrical cells; the nucleus was in some cases very distinct (fig. 618 *B-F*), the chromatophores shorter. The transverse walls of the inflated cells have the same small diameter as those of the long cells. The contents of the inflated cells is at first not very rich, but later it often becomes dense and rich in granular matter, probably floridean starch, as it takes a red-brown colour with iodine, and the inflations may then resemble the chlamydospores of Fungi (fig. 618 *J*).

A new kind of cell-rows, different from those hitherto mentioned, spring, usually from the inflated cells, but sometimes perhaps directly from the long thin cells. The cells of these rows are different from the others by greater breadth and denser contents. Besides the cell organs they contain much floridean starch which gives the cell a granular, untransparent character. The cells are broader, not only in the middle but also at the transverse walls, which have a much larger diameter than the other cells. The cells of these filaments are cylindrical or a little inflated, almost of the same length as breadth, and they are uniform. These cell-rows are always branched but have a limited growth. The branches are usually more or less curved. As it must be supposed that they normally produce monospores, they will be called fertile cell-rows. In material from different shells they showed, however, certain differences; as I feel doubtful whether these variations are due to differences in the external conditions offered by the various tests in which the plants grow or if they may possibly be expressions of genotypical differences, specimens from various shells will be mentioned separately, and the drawings illustrating them are arranged so that each of the three groups of drawings (figs. 617—619) originates from plants growing in the same shell or, as to those growing in *Spirorbis*, at least from specimens of this Serpulid seated on the same host plant. They are all here provisionally regarded as belonging to the same species, *Conchocelis rosea*.

The specimens shown in fig. 617 grew in *Spirorbis* sp. attached to *Furcellaria fastigiata* gathered near Frederikshavn in July. The fertile filaments are here thick, about 14—16 μ in diameter, and the cells are usually more or less inflated or rounded, with convex outer-walls, of the same length as the breadth or shorter, rarely a little longer. Longitudinal or intercalary transverse or inclined divisions occur here

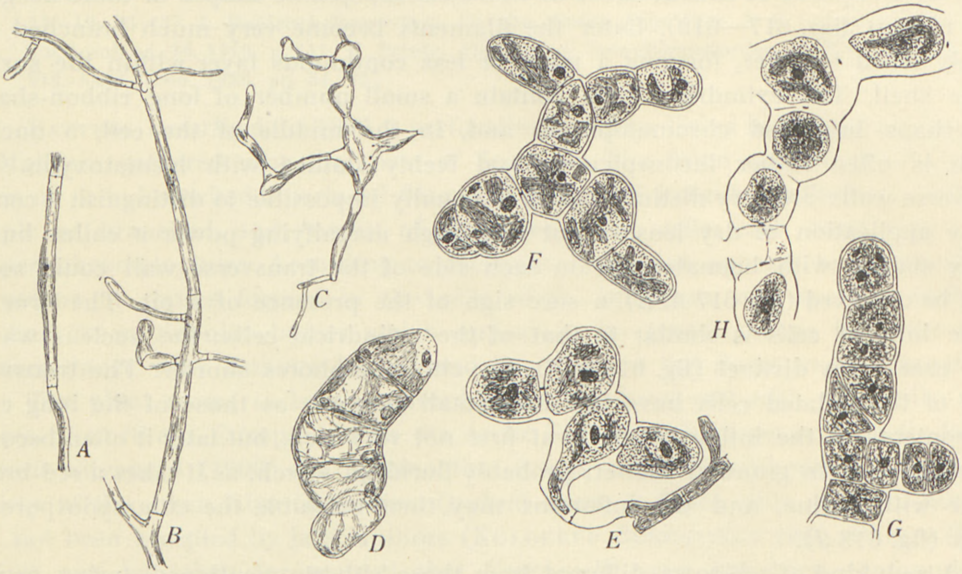


Fig. 617.
Conchocelis rosea, in test of *Spirorbis* sp. from Hjellen near Frederikshavn, treated with picric acetic acid. *A*, cell of long, thin filament, showing nucleus, chromatophores and pit-connections in the transverse walls. *B*, long filament with opposite branches, one with inflated cells. *C*, branched filament with partly inflated cells. *D*, row of broad cells with distinct flat chromatophores lining the wall. *E*, fertile cell-row springing from a thin filament, showing pit-connection in the transverse walls. *F*, branched fertile cell-row. *G*, fertile cell-row, with branch and an oblique intercalary wall. *H*, fertile cell-row the cells of which produce each a monospore. 630 : 1.

and there (fig. 617 *G*). The pit connections in the cross walls appeared distinctly in these specimens which had been treated with picric acetic acid, the callus button in the middle of the wall being intensely stained with hæmalum (figs. *E—H*). A young stage is shown in fig. *E*, where a 4-celled complex of fertile cells is seen in continuity with the thin filament from which it has originated. The larger bushes of fertile cell-rows may somewhat resemble a frond of *Stigonema*, but the outer wall is firm, not gelatinous. The cell-structure is often difficult to observe owing to its dense character. A central nucleus intensely stained with hæmatoxylin was always to be seen but its finer structure could not be observed. Many cells with dense contents suggested the presence of a stellate chromatophore as supposed by Batters and formerly by myself, and the nucleus then seemed situated in the middle of the chromatophore, suggesting a pyrenoid; but on observing well fixed cells with less dense contents, I succeeded in ascertaining that the intensely stained body was not a pyrenoid in a stellate chromatophore but a real nucleus situated in the cytoplasm and surrounded by chromatophores (fig. *E, F*). According to Batters (l. c. p. 26) the "inflations", by which term he denotes the fertile cell complexes, usually consist of from two to ten cells. The branched com-

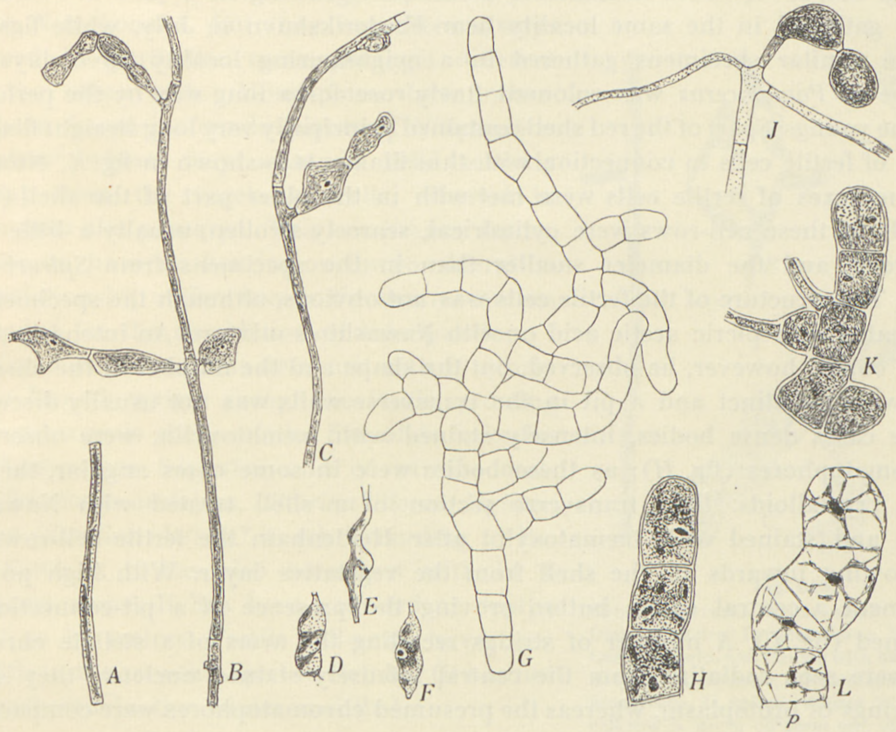


Fig. 618.

Conchocelis rosea. In shells of *Pomatacerus triqueter*. *A—H*, collected at Københavner Rev near Frederikshavn, treated with picric acetic acid, stained with hæmalum. *J—L* from Marens Rev at Frederikshavn. *A*, long cell showing chromatophores and nucleus. *B* and *C*, long filament with branches consisting of inflated cells. *D, E, F*, inflated cells. *G*, branched complex of broad filaments. *H*, end of fertile cell-row. *J*, a couple of inflated cells with dense contents springing from a thin filament. *K*, a fertile cell-row in connection with thin filaments. *L*, four cells of a fertile cell-row from a section through a decalcified shell, showing the central nucleus and radiating plasma-strings, while the chromatophores are feebly stained. *A—F, H—K* 630 : 1. *L* 730 : 1.

plexes of fertile cells here described contain a much larger number of cells, about 50 or more. It is probably such complexes of which Batters treats when he writes (l. c. p. 27) that "the inflations often become detached from the horizontal filaments and are capable of an independent existence", and that he has found them of all sizes and shapes. The continuity of the larger complexes of fertile cells with the thin filaments was not indeed observed by me, and it is probable that their growth can be continued, if their connection with the thin filaments should be interrupted. I have also met with smaller groups of inflated cells consisting of 4 or 5 cells, resembling those figured by Batters but containing flat chromatophores lining the outer walls and one to three dense bodies, perhaps nuclei (fig. *D*). These cell-groups seemed not fully normal. — Fig. *H* shows a row of inflated cells the content of which is contracted and more or less globular, undoubtedly monospores; the callus buttons of the separating walls are very distinct.

Fig. 618, *A—H* show details from *Conchocelis* growing in a tube of *Pomatocerus triqueter* gathered in the same locality near Frederikshavn in July, while figs. *J—L* are from similar specimens gathered in a neighbouring locality three days later. The tube of *Pomatocerus* was coloured finely rose for a long way by the perforating Alga. The youngest part of the red shell contained principally very long straight filaments. A group of fertile cells in connection with thin filaments is shown in fig. *K*. Numerous large complexes of fertile cells were met with in the older part of the shell (fig. *G*). The cells of these cell-rows were cylindrical, scarcely swollen, usually a little longer than broad, and the diameter smaller than in the specimens from *Spirorbis*, viz. 9—11 μ. The structure of the fertile cells was not obvious, although the specimens had been treated with picric acetic acid or with Nawashin's mixture. An intensely stained nucleus could, however, be observed, but the shape and the number of the chromatophores were indistinct and a pit in the transverse walls was not usually discernible. In some cases dense bodies, intensely stained with hæmatoxylin, were observed in the chromatophores (fig. *H*); as these bodies were in some cases angular, they were perhaps crystalloids. In a transverse section of a shell treated with Nawashin's mixture and stained with hæmatoxylin after Heidenhain the fertile cell-rows were seen growing inwards in the shell from the vegetative layer. With high power of enlargement a central callus button proving the presence of a pit-connection was ascertained (fig. *L*). A number of strings recalling the arms of a stellate chromatophore were seen radiating from the central intensely stained nucleus; they seemed to be strings of protoplasm, whereas the presumed chromatophores were comparatively small and feebly stained.

The specimens drawn in fig. 619 grew in *Spirorbis* but agreed as to the fertile cell-rows with those just described from *Pomatocerus*. Fig. *C* shows a two-celled group of fertile cells given off from a spindle-shaped cell. The nuclei were intensely stained, whereas the chromatophores were very indistinct. The fertile cells were cylindric, which is also apparent in fig. *E*, where four globular monospores are to be seen.

The investigations here communicated have shown that there is a distinct difference between 1) a vegetative stage consisting of branched filaments composed of long, thin, cylindric cells and inflated, more or less spindle-shaped cells, both with narrow transverse walls, and 2) fertile branched cell-rows consisting of uniform, broad cells separated by broad cross-walls. The presence of a central pit in the cross-walls has been ascertained, and it has been shown that the cells contain a nucleus and probably always more than one chromatophore. The formation of a monospore in the fertile cells, as presumed by BATTERS, has been confirmed, and it seems that all the cells of the fertile cell-rows are capable of producing a monospore.

The formation of monospores is in good accordance with the reproduction of the *Bangiales*, but the presence of pit-connections between the cells shows that *Conchocelis* cannot be referred to this group, as such connections have never been observed within the *Bangiales*. The plant must therefore be referred to the *Florideæ*, but its relationship within this group is very doubtful. Monospores are known in several *Nemalionales*, but they are there always produced in particular monosporangia different from the other cells. Monospores have otherwise been found in female plants of *Nitophyllum punctatum*[1] where they arise in cells scarcely different from the vegetative cells, situated in groups near the procarps. This occurrence seems, however, to have no bearing on the consideration of the relationship of *Conchocelis*. Further researches are needed for the elucidation of this question.

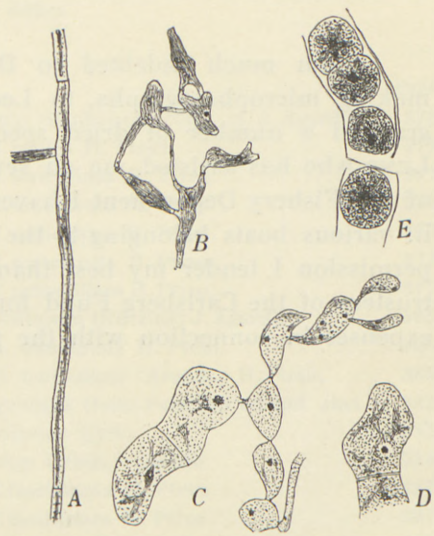


Fig. 619.
Conchocelis rosea. From shell of *Spirorbis* from Deget near Frederikshavn, treated with Carnoy's fluid, and stained with hæmatoxylin. *A*, long cell showing chromatophores. *B*, inflated cells. *C*, spindle-shaped cells; a fertile cell-row is given off from one of them. The nuclei are distinct, the chromatophores only feebly stained. *D*, end-cell of a broad cell-row, a pit-connection is seen in the transverse wall. *E*, Four globular monospores are formed in a fertile cell-row. *A*, *B*, *D* 630 : 1. *C* 510 : 1.

Conchocelis rosea has been met with in nearly all the Danish waters except the Baltic, growing in the calcareous shells of the Serpulids *Spirorbis* and *Pomatocerus triquetrus* and of various molluscs (*Buccinum undatum*, *Littorina littorea*, *Mytilus*, *Cyprina islandica*, *Astarte*? a. o.). According to Dr. JOHS. SCHMIDT it has also been met with in a calcareous stone. It has been gathered at depths from 1 to 32 metres. Fertile cell-rows have been met with in the months April to October (it has not been gathered in the winter months).

Localities. **Ns:** eP, off Lodbjerg light-house, 24 m, in Buccinum undatum. — **Lf:** Nykøbing, in Bucc. und. (Teilmann Friis). — **Kn:** fG, Tønneberg Banke, 15 m; off Aalbæk, 22 m, in Bucc. und.; at Hirsholmene and in numerous places near Frederikshavn, most frequently in Spirorbis and Pomatocerus. — **Kc:** Groves Flak. 23 m and 32 m, in Cyprina isl. (F. Børgesen,!); Søborg Hoved Grund, in Littorina lit., Gilleleje, in Spirorbis. — **Km:** East of Læsø Rende, in Spir.; — **Sa:** 1½ miles N.E. by N. of Sejerø, in Mytilus; Lille Grund, in Spir. — **Sb:** Hov Sand, in Spir.; Lohals, in Spir. Spodsbjerg Mole, in Spir.; off Holmegaard, in Spir. — **Su:** Skodsborg, in a calcareous stone (determ. Johs. Schmidt).

Halosaccion ramentaceum (L.) J. Agardh.

About 50 years ago Mr. O. SMITH sent me some Algæ cast ashore at Lerchenborg, Store Belt. Among these Algæ a specimen of *Halosaccion ramentaceum* is found,

[1] N. SVEDELIUS, Über Sporen an Geschlechtspflanzen von Nitophyllum punctatum. Ber. deut. bot. Ges. **32**, 1914, p. 106.

a very strange finding, as this species has never otherwise been met with in the Danish waters. Since the nearest known localities of this subarctic species are the Trondhjems-Fjord and the Færöe Islands, and as the specimen is quite normal and bears no sign of having been drifting for a long time in the Sea, I consider it most probable that the specimen in question, which has not been labelled by Mr. Smith, has been intermixed by an error among the Algæ found at the coast of Store Belt.

I am much indebted to Dr. Henning E. Petersen who has helped me in making microphotographs, to Lector J. Boye Petersen for having kindly photographed a number of dried specimens reproduced in the text, and to Mr. Søren Lund who has assisted me on several excursions. By the kindness of the authorities of the Fishery Department I have had the opportunity of making researches onboard in various boats belonging to the Fishery Control and Fishery Researches, for which permission I tender my best thanks. And finally I owe a debt of gratitude to the trustees of the Carlsberg Fund for a grant which has enabled me to defray various expenses in connection with the present part of my work.

INDEX

Synonyms are printed in *italics*.

CORRIGENDA

P. 30, l. 9 from top, to be added: 9.5 m.
P. 45, l. 12 from bottom, for E. by N. 1/3 N. read W. by S. 1/3 S.
P. 68, l. 5 from bottom, for Hveen read Hveen, 10,5—19 m.
P. 112, l. 14 from bottom, for **Sa** read **Lb**.
P. 277, l. 14 from bottom, for The fronds read The apical cells of the fronds.
P. 284, l. 6 from bottom, for f. *robusta* Kjellm. read f. *typica*.
P. 375, l. 19 from top, for 10 high read so high.
P. 402, l. 18 from bottom, for *Dasay* read *Dasya*.
P. 467, l. 7 from top, for ***sinuosis*** read ***sinuosus***.
See further p. 150.

EXPLANATION OF PLATE VIII.

Microphotographs.

Figs. 1—3. *Phyllophora Brodiæi.* Sections of nemathecia (from K. Rosenvinge 1929). 1. Auxiliary cell with protuberances. 375:1. 2. Vertical section of nemathecium showing the central cell and a smaller nemathecium on the under face of the frond, evidently arisen by fusion of several small cushions. 64:1. 3. Transverse section of nemathecium showing the central cell. 77:1.

Figs. 4—10. *Ceratocolax Hartzii.*

Fig. 4. From Lille Belt, April. Vertical section of basal part of frond. Cells of the parasite penetrate into some of the cells of the host. 75:1.

Fig. 5. From Store Belt, May. Vertical section of basal part of frond. 124:1.

Fig. 6. Vertical section of base of young frond arisen by germination in aquarium, September 1929. The lowermost cells penetrate as haustoria into the host plant. 76:1.

Fig. 7. From Lille Belt, April. Vertical section of base of plant and the host plant. 76:1.

Fig. 8. From Middelgrund, south of Als, June. Base of plant encompassing the marginal part of the frond of Phyllophora. 80:1.

Fig. 9. At Friis' Sten NW of Læsø, May. Vertical section of nemathecium not yet ripe. 150:1

Fig. 10. From Store Belt, May. Section of branch with supposed antheridia. 166:1.

Fig. 11. *Ahnfeltia plicata.* Vertical section of nemathecium. 120:1.

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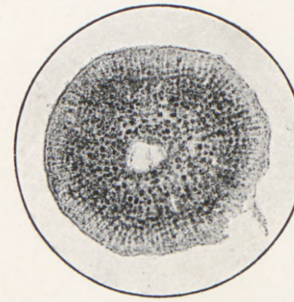

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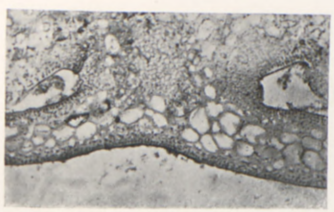

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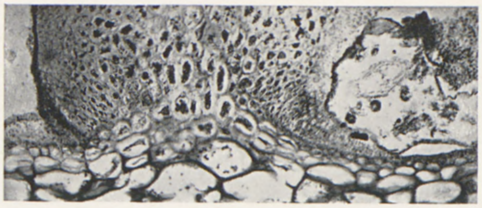

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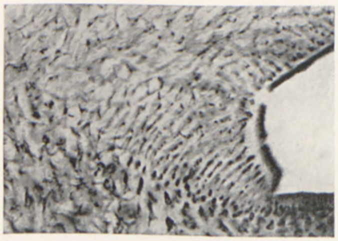

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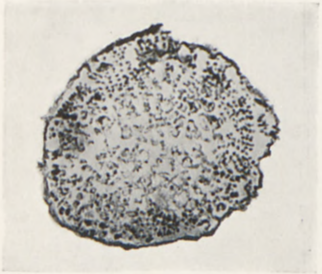

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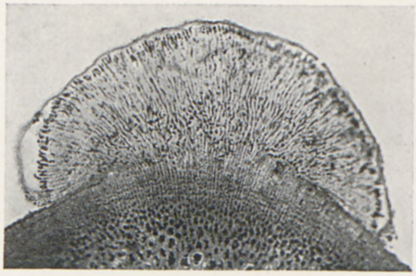

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