# THE MARINE ALGÆ OF DENMARK

# CONTRIBUTIONS TO THEIR NATURAL HISTORY

# PART III RHODOPHYCEÆ III. (CERAMIALES)

BY

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WITH THREE PLATES

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# KØBENHAVN

BIANCO LUNOS BOGTRYKKERI

1923 - 24



# INTRODUCTION

Dince the first part of this publication was issued I have studied the marine Algæ on the Danish coasts almost every summer. During the last two years my investigations have been more extensive. This is chiefly due to the addition made to the area of the Danish flora in consequence of the reunion of North Slesvig with Denmark in 1920. The boundary on the eastern side of Slesvig having been removed from Heilsminde to Krusaa in the interior of Flensborg Fiord, the Little Belt area (Lb) has been augmented by the waters between Heilsminde in the north, and Sønderborg and Pøl at the south-eastern extremity of Als, while the line bounding the Danish part of the Baltic (Bw) on the south must now be drawn from Krusaa through the middle of Flensborg Fiord and thence south of Bredgrund south of Als. Though these waters have formerly been examined by Professor REINKE, and their flora and vegetation dealt with in his well-known work Algenflora der westlichen Ostsee Deutschen Anteils, 1889, I have considered it necessary to study the same waters myself. By the kindness of the fisheries director, Mr. F. V. MORTENSEN, I have been enabled, with the assistance of the fishery control motor-boat, to make investigations and collections in the waters round Sønderborg in June 1921, and in June 1922 to make similar investigations while onboard the control steamer S. S. Falken (fisheries supervisor TROLLE THOMSEN), along the entire eastern coast of South Jutland and likewise in the waters surrounding Funen. In both cases the material was collected partly, by means of a boat, from stone reefs and in other localities such as breakwaters near land, partly by dredgings from ship at a greater distance from land. In the autumn of 1922 there further occurred an exceptional opportunity to make dredgings in the North Sea and the Skagerak in places otherwise very difficult of access, since the marine research ship S. S. Dana was to make fishery investigations in these waters, and especially in places where one might expect to find Algæ. The Marine Research Committee very readily granted me room onboard, and the leader of the cruise, Dr. A. C. JOHANSEN, did everything in his power to further my investigations. As I was obliged to break off my stay onboard on October 7th, mag. sc. Mr. C. A. JØRGENSEN was deputed to carry on my investigations of the flora of the Skagerak and the northern and central parts of the Kattegat until the cruise came to an end on October 19th. Mag. Jørgensen has later, in June 1923, made investigations onboard the Dana in the waters around Bornholm and left the collected Algæ at my disposal.

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In continuation of the list given on p. 22 et seq. I give below a list of the new dredging stations arranged on the same principles as the one already mentioned.

Most of the new dredging places are marked on the charts given on pp. 288 and 290. In the later those places at the shores where investigations and collections have been made are likewise indicated by a mark together with the name of the

place concerned. In deep waters the collections have always been made with a dredge where nothing else is indicated. In most other places an otter trawl has been employed.

As the markings on the charts and in the list show, there was no vegetation at all in the southern part of the North Sea area even where the bottom was stony. This agrees with what earlier German investigations have shown<sup>1</sup> and what I myself found in 1905 at Horns Reef (Part I p. 22, Chart II). Further it was in accordance with what Dr. Johansen had found immediately before my arrival onboard the Dana. In thirty localities between  $6^{\circ}07'$  and  $8^{\circ}16'$  E. and between  $55^{\circ}00'$  and  $56^{\circ}08'$  N. on fishing with otter trawl no vegetation at all was found. It was confirmed, then, by these investigations that this part of the North Sea is a veritable desert as regards bottom vegetation. In the northern part of the North Sea area, where there were stones or at any rate gravel in nearly all the localities examined, the bottom was almost equally bare, being either entirely destitute of vegetation or showing only very sparse vegetation. This result may, however, be partly due to the late season (the latter part of September) for I have formerly found a fairly abundant flora in some parts of this area at the close of July. In the Skagerak, too, the vegetation is on the whole very poor even on stony bottom, and only in a few places, mostly near land, do we find spots with continuous vegetation, especially at Hirshals, but also at Hanstholm, Bragerne and Lønstrup. On the other hand, in the Skagerak one often comes across loose, drifting Algæ carried along by the strong current.

On groins and breakwaters in the northern part of the North Sea area there is an abundant and fairly varied vegetation. At Fanø and Esbjerg the corresponding vegetation is poor in species and, according to REINBOLD<sup>2</sup> and JAAP,<sup>3</sup> the same is the case with the Algæ vegetation on the coasts of Rømø and on the west coasts of North Slesvig; I myself had no opportunity to examine Rømø until August 1923. In the shallow sea between North Slesvig and the islands *Zostera marina* and *Z. nana* grow in low water, but there seem to be no Algæ. Mag. R. Spärck who made dredgings along the east coast of Fanø at a depth of 4—5 m. has kindly informed me that he got numerous oyster shells and mussel shells and not a few stones in the dredge, but that there was no Algæ vegetation. Only a little loose *Fucus vesiculosus* without vesicles and some *Zostera* got into the dredge.

The waters washing the eastern coast of North Slesvig are so similar in character to the adjoining parts of the Little Belt and the western part of the Baltic dealt with in Part I, that they do not require further mention here, the more so since they have been treated in REINKE's above cited work. The depth conditions are shown on Chart II and in map p. 290.

<sup>1</sup> J. REINKE, Notiz über die Vegetationsverhältnisse in der deutschen Bucht der Nordsee. Bericht deut. bot. Ges. 1889 p. 367. TH. REINBOLD, Untersuchung des Borkum-Riffgrundes. Sechster Bericht d. Komm. z. wiss. Unters. d. deutsch. Meere. III Heft.

<sup>2</sup> TH. REINBOLD, Bericht über die im Juni 1892 ausgeführte botan. Untersuch. einiger Distrikte der Schleswig-Holsteinischen Nordseeküste. Sechster Bericht d. Komm. z. wiss. Unters. d. deutsch. Meere. III Heft.

<sup>3</sup> O. JAAP, Zur Kryptogamenflora d. nordfriesischen Insel Röm. Schrift. d. Naturv. Vereins d. Prov. Schleswig-Holstein Bd. 12. 1902.



# List of new dredging stations arranged according to the different waters.

The localities are designated by letters like the foregoing ones (comp. pp. 22-54). Some of the dredgings of the later years have been made by Dr. HENNING PETERSEN, Mag. P. KRAMP or Mr. J. BOYE PETERSEN while I have examined the collected material of Algæ. The dredging stations of Mag. Jørgensen in October 1922 have been designed with the station figures of the S. S. Dana.

#### North Sea. (Ns)

- dU. (Dana St. 2835). <sup>27</sup>/<sub>9</sub> 22. 4 miles N. <sup>3</sup>/<sub>4</sub> E. of Blaavandshuk light-house. 8 m. Fine sand. No vegetation. (Otter trawl).
- dV. (Dana St. 2836). 11 miles S. by W. of Lyngvig light-house. 15 m. Fine sand. No vegetation.
- eG. (Dana St. 2846). <sup>30</sup>/<sub>9</sub> 22. 9 miles S.W. <sup>1</sup>/<sub>2</sub> N. of Bovbjerg light-house. 24 m. Gravel, stones. No Algæ, only a fragment of *Desmar. acul.*
- eH. (Dana St. 2848). <sup>30</sup>/<sub>9</sub> 22. 14 miles W. by S. <sup>1</sup>/<sub>4</sub> S. of Bovbjerg light-house. 27 m. Sand with few stones. No vegetation.
- eI. (Dana St. 2849). <sup>30</sup>/<sub>9</sub> 22. 21 miles W. of Bovbjerg light-house. 34 m. Clay with stones, shells. — No Algæ.
- eK. (Dana St. 2850). <sup>1</sup>/<sub>10</sub> 22. Lille Fiskebanke. 46 miles W. by N. of Bovbjerg light-house. 37 m. — Clay, large stones. Scarce *Hildenbrandia prototypus*.
- eL. (Dana St. 2851). <sup>1</sup>/<sub>10</sub> 22. Lille Fiskebanke. 53 miles W.N.W. <sup>1</sup>/<sub>4</sub> W. of Bovbjerg light-house. 37 m. — Coarse sand mixed with ooze, with shells. — No Algæ.

eF. (Dana St. 2845). <sup>30</sup>/<sub>9</sub> 22. 2,5 miles W. by N. of Bovbjerg light-house. 18–22 m. – Sand, stones, clay. – No vegetation; only *Rhodochorton membranaceum* in Hydrallmannia falcata.

- eE. (Dana St. 2844). <sup>29</sup>/<sub>9</sub> 22. 12 miles N.W. by N. of Bovbjerg light-house. 26 m. Gravel, stones. — Scarce Desmarestia aculeata, otherwise only incrusting Algae (Lithoderma).
- dY. (Dana St. 2838). <sup>28</sup>/<sub>9</sub> 22. 10 miles S.W. <sup>1</sup>/<sub>4</sub> S. of Lodbjerg light-house. 18 m. Clay with single stones. No vegetation.
- dX. (Dana St. 2837). <sup>28</sup>/<sub>9</sub> 22. 11 miles W.S.W. <sup>1</sup>/<sub>2</sub> W. of Lodbjerg light-house. 28 m. Fine sand. — No<sup>\*</sup>vegetation.
- eD. (Dana St. 2843). <sup>29</sup>/<sub>9</sub> 22. S.E. of Jydske Rev. 22 miles W. of Lodbjerg light-house. 41 m. Sand, gravel, stones. — No vegetation; only single specimens of *Desmarestia aculeata* and fragments of a few other Algæ.
- eN. (Dana St. 2853). <sup>1</sup>/<sub>10</sub> 22. Between Lille Fiskebanke and Jydske Rev. 45 miles W. by N. of Lodbjerg light-house. 34 m. Sand, few animals. No Algæ.
- eM. (Dana St. 2852). <sup>1</sup>/<sub>10</sub> 22. Lille Fiskebanke. 55 miles N.W. by W. <sup>1</sup>/<sub>2</sub> W. of Bovbjerg light-house. 48 m. — Gravel, shells. — No Algæ.
- eA. (Dana St. 2840). <sup>28</sup>/<sub>9</sub> 22. 27 miles W. <sup>3</sup>/<sub>4</sub> N. of Lodbjerg light-house. 25–28 m. Coarse gravel. – Very scarce vegetation: single specimens of *Desmarestia aculeata*, *D. viridis*, *Corallina* offic., *Trailliella intricata*, *Chætopteris*, *Laminaria* (young).
- eO. (Dana St. 2854). <sup>2</sup>/<sub>10</sub> 22. 4<sup>1</sup>/<sub>2</sub> miles W. <sup>1</sup>/<sub>2</sub> S. of Lodbjerg light-house. 23 m. Large stones and gravel. Scarce *Phyllophora rubens*, *Lithoderma* and *Lithothamnion*.
- dZ. (Dana St. 2839). <sup>28</sup>/<sub>9</sub> 22. 17 miles W. <sup>3</sup>/<sub>4</sub> N. of Lodbjerg light-house. 36 m. Stones. Scarce Desmarestia aculeata and incrusting Algæ (Cruoria pellita, Lithothamnion lævigatum, Lithoderma).
- eP. (Dana St. 2855). <sup>2</sup>/<sub>10</sub> 22. 8 miles W. by N. of Lodbjerg light-house. 24 m. Gravel and small stones. Scarce *Desmarestia aculeata*, single specimens of *Phyllophora rubens* and *Ph. membranifolia*.
- eQ. (Dana St. 2856). <sup>2</sup>/<sub>10</sub> 22. 8 miles N.W. by W. <sup>1</sup>/<sub>2</sub> W. of Lodbjerg light-house. 27 m. Large and smaller stones. Mostly incrusting Algæ (*Lithoderma, Lithothamnion, Rhododermis elegans*).

- eC. (Dana St. 2842). <sup>29</sup>/<sub>9</sub> 22. Jydske Rev. 23 miles W.N.W. of Lodbjerg light-house. 26 m. Gravel, sand. In four dredgings only single specimens of *Desmarestia acul.*, Furcellaria, *Phylloph. rubens* and *Corallina off*.
- eB. (Dana St. 2841). <sup>29</sup>/<sub>9</sub> 22. 21 miles N.W. <sup>3</sup>/<sub>4</sub> W. of Lodbjerg light-house. 22 m. Gravel with small stones. Two loose specimens of *Laminaria saccharina*.
- eR. (Dana St. 2857). <sup>2</sup>/<sub>10</sub> 22. 9 miles N.W.<sup>1</sup>/<sub>2</sub> N. of Lodbjerg light-house. 27 m. Gravel with stones. Scarce *Desmarestia aculeata*, otherwise only few fragments (*Phyll. rubens, membran., Trailliella, Plocamium coccineum*); stones mostly bare.
- eS. (Dana St. 2858). <sup>2</sup>/<sub>10</sub> 22. 8 miles N. by W. of Lodbjerg light-house. 25 m. Gravel with small stones. No vegetation. (Single small specimens of *Desmar. acul., Phylloph. Brod., Rhodomela*).
- eT. (Dana St. 2859). <sup>2</sup>/<sub>10</sub> 22. 15 miles W. by N. of Hanstholm light-house. 34 m. Gravel, stones. — Scarce vegetation: Laminaria hyperborea and digitata, Phyllophora rubens...
- eU. (Dana St. 2860). <sup>2</sup>/<sub>10</sub> 22. 24 miles W.N.W. of Hanstholm light-house. 50 m. Gravel, small stones (Alcyonidium gelatinosum in abundance). No Algæ.

#### Skagerak. (Sk)

- eV. (Dana St. 2864). <sup>3</sup>/<sub>10</sub> 22. 6 miles N. by E. of Hanstholm light-house. 22–24 m. Stones, sand with shells and clay. Scarce *Desmarestia aculeata*.
- eX. (Dana St. 2865). <sup>3</sup>/<sub>10</sub> 22. 10 miles E.N.E. <sup>1</sup>/<sub>2</sub> E. of Hanstholm light-house; N. of Bragerne. 16 m. — Gravel, stones. — Mostly incrusting Algæ, rather scarce however, further Laminaria hyperborea (scarce) and Phyllophora membranifol.
- Dana St. 2904. <sup>13</sup>/<sub>10</sub> 22. 13<sup>1</sup>/<sub>2</sub> miles N.E. <sup>1</sup>/<sub>2</sub> E. of Hanstholm light-house. 23 m. Stones, shells.
   Very few Algæ. (*Chætopteris, Sphacelaria, Cystoclon., Polys. urceolata, Antithamnion cruciatum, Lithoderma*).
- Dana St. 2902. <sup>13</sup>/<sub>10</sub> 22. 12 miles E. by N. <sup>1</sup>/<sub>4</sub> N. of Hanstholm light-house. E. side of Bragerne. 15 m. — Sand. — Various Algæ, probably all loose (*Laminaria sacch.* and *digit., Fuc. serr., Dilsea, Deless. etc.*). (Young-fish trawl).
- Dana St. 2903. <sup>13</sup>/<sub>10</sub> 22. 12 miles E. <sup>3</sup>/<sub>4</sub> N. of Hanstholm light-house. Near Bragerne. 7 m. Sand, shells. No Algæ.
- Dana St. 2907. 14/10 22. 26 miles N.W. by W. of Rubjerg Knude light-house. 45 m. No Algæ. -
- Dana St. 2906. <sup>14</sup>/<sub>10</sub> 22. 26 miles N.W. <sup>1</sup>/<sub>4</sub> W. of Rubjerg Knude light-house. 70 m. Soft bottom. No Algæ.
- fA. (Dana St. 2868). <sup>3</sup>/<sub>10</sub> 22. E.N.E. of Hanstholm light-house. 18 m. Gravel, shells. Single loose fragments of various Algæ (*Fucus vesiculosus, Halidrys, Furcellaria* etc.) and loose *Zostera* (with rhizomes).
- eY. (Dana St. 2866). <sup>3</sup>/<sub>10</sub> 22. 18 miles E.N.E. <sup>1</sup>/<sub>2</sub> E. of Hanstholm light-house. 15 m. Sand, stones. Very scarce Algæ: *Halidrys, Delesseria alata, Rhodomela, Furcellaria* a. o. and loose *Zostera* with narrow leaves.
- eZ. (Dana St. 2867). <sup>3</sup>/<sub>10</sub> 22. 21 miles E.N.E. of Hanstholm light-house. 15-17 m. Gravel, sand. One specimen of *Halidrys*, single small specimens or fragments of *Dilsea edulis*, *Deless. sinuosa* a. o.; loose narrow-leaved *Zostera*.
- Dana St. 2900. <sup>13</sup>/<sub>10</sub> 22. 21 miles S.W. <sup>3</sup>/<sub>4</sub> W. of Rubjerg Knude light-house. 9 m. Sand. Drifting Algæ (*Dilsea edulis, Fucus serratus, Laminaria sacch.* and *digit., Desmar. acul.* etc.). (Otter trawl).
- Dana St. 2899. <sup>13</sup>/<sub>10</sub> 22. 13 miles S.W. by W. <sup>1</sup>/<sub>2</sub> W. of Rubjerg Knude light-house. 14 m. Sand. Few Algæ (*Furcellaria, Ahnfeltia, Desmarestia acul.* a. o.), mostly loose probably.
- fB. (Dana St. 2869). <sup>3</sup>/<sub>10</sub> 22. 22 miles N.W. <sup>1</sup>/<sub>2</sub> N. of Rubjerg Knude light-house. 47 m. Sand, shells.— Loose Algæ (*Desmarestia aculeata, Laminaria sacch., Chorda Filum* a.o.) and Zostera.
- Dana St. 2912. <sup>15</sup>/<sub>10</sub> 22. <sup>51</sup>/<sub>2</sub> miles W. <sup>1</sup>/<sub>2</sub> S. of Højen light-house. 25 m. Stones, small shells. Incrusting Algæ (*Lithothamnion Sonderi*) mostly on Modiola modiolus.

cK. <sup>26</sup>/<sub>7</sub> 21. North of Skagen; the life-boat station in line with the old church. 28 m.— Soft bottom.— A fragment of *Laminaria digitata*, otherwise no Algæ. — Farther North. 97 m. — Soft bottom. — Some loose Algæ.

### Limfjord. (Lf)

- bU. <sup>27</sup>/<sub>7</sub> 20. Ejerslev-Næse, E. coast of Mors. 3–8 meters. Farthest out oysters and stones with very few Algæ. Nearer land *Zostera*.
- bT<sup>3</sup>. <sup>27</sup>/<sub>7</sub> 20. West of Ejerslev Røn. 7 meters. Firm clay with stones, Mytilus and oysters. Very few Algæ, mostly *Polysiphonia elongata* and *Trailliella intricata*.
- bT<sup>1</sup>. <sup>23</sup>/<sub>7</sub> 20. At the broom, Sæbygaards Hage (Fursund). 2 meters. Stones. Fucus vesiculosus, Corallina officinalis.
- bT<sup>2</sup>. <sup>23</sup>/<sub>7</sub> 20. Knudshoved, at the N.W. end of Fur. 5,5 meters. Great stones. Fucus vesiculosus, Zostera. — North side of the same point, within the broom. 4 meters. — Zostera and stones with Fucus vesiculosus.

# Kattegat, Northern part. (Kn)

- bQ.  ${}^{28}/_7$  11. Skagen, under the land from the lazaretto to the light-house. 2 to 3 meters. Sand and small stones. *Enteromorpha* or *Chorda Filum*.
- cI. <sup>23</sup>/<sub>7</sub> 21. South of Skagen light-house (P. Kramp). 7,5 and 5,5 meters. Sand and small stones. *Ectocarpus siliculosus* abundant, further *Polysiphonia elongata*, and in smaller depth *Chorda Filum*.
- cl<sup>2</sup>. <sup>30</sup>/<sub>7</sub> 21. South of Skagens Gren (Kramp). 9,5 meters. Sand with Zostera. 13—15 meters. — Clayey sand. — Antithamnion Plumula abundantly on Buccinum and Turritella.
- cl<sup>1</sup>. <sup>23</sup>/<sub>7</sub> 21. South side Skagens Gren (Kramp). 9,5 meters. Soft bottom. Some Algæ on the claws of Pagurus and on mollusc shells.
- cH. <sup>20</sup>/<sub>7</sub> 21. Off Skagens harbour (Boye Petersen). Soft bottom with molluscs. Halorhiza vaga, Arthrocladia villosa.
- cH<sup>1</sup>. <sup>22</sup>/<sub>7</sub> 21. Off Klitgaarden, Skagen (Boye Petersen). 4 meters. Soft bottom. Brown Algæ, in particular *Ectocarpus siliculosus* and *Halorhiza vaga*, further *Polysiphonia elongata*.
   2 meters. — Sand with stones. — *Kjellmania striarioides* and *Delamarea attenuata*.
- fC. (Dana St. 2870). 3 miles S.W. by S. of Skagen light-house. 15 m. Ooze with molluscs (mostly Turritella terebra). — Polysiphonia elongata and atrorubescens, Chætopteris on Turritella; Zostera with fruit.
- fD. (Dana St. 2871). <sup>4</sup>/<sub>10</sub> 22. Off Aalbæk. 8 miles S. <sup>3</sup>/<sub>4</sub> W. of Skagen light-house. 22 m. Soft bottom (seine), Pecten islandicus. Lithothamnion lævigatum and L. glaciale on coal, Buccinum undatum o. a.
- fE. (Dana St. 2872). <sup>4</sup>/<sub>10</sub> 22. E. side of Krageskov Rev. 7 m. Sand with Zostera, and various intermingled Algæ.
- Dana St. 2917. <sup>15</sup>/<sub>10</sub> 22. Hirsholm Nordost Rev, just outside the broom. Stones. Rich algal vegetation; *Laminariæ* predominant with *Desmarestia aculeata* and various *Florideæ*.
- fF. (Dana St. 2873). <sup>6</sup>/<sub>10</sub> 22. 4 miles E.S.E. <sup>3</sup>/<sub>4</sub> E. of Nordre Rønner light-house. 8 m. Sand with stones. — Fucus servatus and Furcellaria dominant, further Polyides, Brongniartella, Halidrys a. o.
- dR. <sup>2</sup>/<sub>8</sub> 22. The light-ship at Læsø Trindel S.S.E. 1<sup>1</sup>/<sub>2</sub> miles. 21 m. Stones with *Lithothamnion læve*, other Algæ scarce.
- fG. (Dana St. 2874). <sup>6</sup>/<sub>10</sub> 22. 3 miles W. of Læsø Trindel light-ship. 15 m. Sand, gravel, stones. — Laminaria saccharina, L.hyperborea, Halidrys, Lithothamnia (L.calcareum, glaciale) a.m.o.
- dS. <sup>a</sup>/<sub>8</sub> 22. Læsø Trindel; midway between the light-ship and the broom. Soft bottom (Pennatula). — No Algæ.

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dT. <sup>3</sup>/<sub>8</sub> 22. S. of Læsø Trindel. 20 m. — Soft bottom. — No vegetation. D. K. D. Vidensk. Selsk. Skr., 7. Række, naturvidensk. og mathem. Afd. VII. 3.

- dT<sup>1</sup>. <sup>3</sup>/<sub>8</sub> 22. Nearer the broom. 11 m. Stones. Halidrys, Laminaria saccharina, Furcellaria, Brongniartella, Desmarestia viridis. (Abundant vegetation).
- dT<sup>2</sup>. <sup>3</sup>/<sub>8</sub> 22. S. of the broom. 26 m. Shells, stones. Fucus serratus, Laminaria digitata, Halidrys. Dana St. 2891. <sup>10</sup>/<sub>10</sub> 22. 6<sup>1</sup>/<sub>2</sub> miles S.W. by W. <sup>1</sup>/<sub>2</sub> W. of Læsø Trindel light-ship. 8 m. — Sand, stones. — Fucus serratus and Furcellaria dominant, scarce Halidrys. Further various Algæ; Trailliella abundant, with tetraspores.

#### Kattegat, eastern part. (Ke)

- fK. (Dana St. 2875). <sup>6</sup>/<sub>10</sub> 22. 4 miles W. by N. of Fladens light-ship. 39 m. Sand, shells. No Algæ.
- fI. (Dana St. 2877). <sup>6</sup>/<sub>10</sub> 22. 3<sup>1</sup>/<sub>2</sub> miles W. by N. of Fladens light-ship. 30 m. Sand, stones, shells.
   Few Algæ: Laminaria hyperborea and incrusting Algæ (Cruoria, Cruoriella Dubyi, Lithothamnia, Lithoderma etc.)
- fH. (Dana St. 2876). <sup>6</sup>/<sub>10</sub> 22. 1 mile W. by N. of Fladens light-ship. 17 m. Stones, sand. Laminaria digitata, hyperborea, saccharina, Dilsea edulis, Furcellaria etc.
- Dana St. 2922. <sup>18</sup>/<sub>10</sub> 22. 4<sup>1</sup>/<sub>2</sub> miles S.W. <sup>3</sup>/<sub>4</sub> W. of Fladens light-ship. 30 m. Stones, shells. Laminaria saccharina and hyperborea predominant, further Halidrys, Desmar. acul., Furcellaria, Dilsea edulis, Deless. sanguinea, Brongniartella, Lithothamnion læve, glaciale, various other incrusting Algæ etc.
- fM. (Dana St. 2881). <sup>7</sup>/<sub>10</sub> 22. 10 miles W.S.W. <sup>1</sup>/<sub>4</sub> W. of Fladens light-ship. 23 m. Sand, stones. —
  1) Incrusting Algæ (*Cruoria, Cruoriella Dub., Lithoderma, Lithothamnion glaciale* a. o.
  2) *Halidrys, Desmarestia aculeata.*
- fL. (Dana St. 2880). <sup>7</sup>/<sub>10</sub> 22. 11 miles W. by S. of Fladens light-ship. 33 m. Ooze, sand with small stones. — No Algæ (a small spec. of *Phylloph. membr.*, also one of *Corallina off.*)
- Dana St. 2925. <sup>19</sup>/<sub>10</sub> 22. Store Middelgrund. 14<sup>1</sup>/<sub>2</sub> miles S.S.E. of Anholt Knob light-ship. Lat. N. 56° 33′, Long. E. 12° 05′. 10 m. Stones. *Furcellaria* predominant, with *Laminaria* hyperb., digit., sacchar., Fucus servatus and various other Algæ.

# Kattegat, central part. (Km)

- Dana St. 2919. <sup>17</sup>/<sub>10</sub> 22. 6 miles S.S.W. <sup>1</sup>/<sub>2</sub> W. of Læsø Rende light-ship. Lat. N. 57° 07′, Long E.
   10° 37′. 8 m. Stones. Halidrys abundant, Polys. nigrescens and elongata and various other Algæ.
- Dana St. 2884. <sup>8</sup>/<sub>10</sub> 22. 5<sup>1</sup>/<sub>2</sub> miles N. by E. <sup>3</sup>/<sub>4</sub> E. of Østre Flak light-ship. 9 m. Sand, stones. Zostera in abundance with Furcellaria, further Halidrys, Fuc. servatus a. o. Algæ.

Kattegat, southern part. (Ks)

bR. <sup>16</sup>/<sub>8</sub> 13. Vesterlandsgrund by Gilleleje. — 7,5 meters. — Stones and gravel. — Vegetation partly continuous, partly interrupted by bare spots: Fucus serratus, Furcellaria, Brongniartella, Phyllophora Brodiæi a. o.

Samsø area. (Sa)

cU. <sup>9</sup>/<sub>6</sub> 22. North of Fyn, 55°35′ N, 10°28,5′ E. 9 m. — Zostera with Furcellaria a. o. entangled Algæ. — 7 m. — The same and Fucus serratus.

Little Belt. (Lb)

- cV. 10/6 22. Abreast of Røgle, Røgle Klint S. by W. 19—30 m. At 30 m clay, at higher level small stones. Few Algæ, *Rhodomela*, *Desmarestia aculeata*, *Furcellaria*, *Chorda tomentosa*.
- cX. <sup>13</sup>/<sub>6</sub> 22. Between Strib and Nederballe. 35–44 m. Firm clay. Florideæ (*Cystoclonium*, *Polysiphonia nigrescens*, *Furcellaria*), *Desmarestia aculeata* and *Stictyosiphon tortilis*.
- bS. <sup>21</sup>/<sub>8</sub> 1917. Outer part of Kolding Fjord, off Ellidshøj. C. 4 meters. Soft bottom. Broadleaved Zostera-vegetation with loose Furcellaria and single Fucus vesiculosus and F. serratus.
- cY<sup>1</sup>, <sup>14</sup>/<sub>6</sub>22. Outside the broom at Anslet Hage, 12,5—14 m. Mud. Dead Zostera leaves.

- cY<sup>2</sup>. <sup>14</sup>/<sub>6</sub> 22. The broom at Anslet Hage N.E. <sup>2</sup>/<sub>5</sub> mile. 5–8 m. Dense vegetation of broad-leaved Zostera (flowering), a little loose *Furcellaria* (*f ægagropila*), *Rhodomela* and *Polysiphonia* nigrescens.
- cZ. <sup>15</sup>/<sub>6</sub> 22. Knudshoved Grund (North of Haderslev Fjord), across the bank. 5,5-7 m. 1) plain bottom with single stones, a little Zostera. 2) East border: Zostera-vegetation, a little Furcellaria.
- dA. <sup>15</sup>/<sub>6</sub> 22. The bank E. of the broom Fyrrenden N. 6,5–8 m. Zostera-vegetation with single stones; *Furcellaria*, *Laminaria saccharina*.
- dB. 15/6 22. South of Linderum. C. 5 m. Dense Zostera-vegetation vith Laminaria saccharina.
- dC. 1% 22. South end of Aarø Sund, S. of the broom on the W. side. 8—10 m. Dead Zostera, a little Furcellaria, Rhodomela and Polysiphonia nigrescens. A little further South. 18—19 m. Bare sand.
- dD. <sup>16</sup>/<sub>6</sub> 22. W. of Schønheyders Flak, 21 m. Soft bottom. (Cyprina). No vegetation.
- dE. <sup>16</sup>/<sub>6</sub> 22. Holsts Banke. 8–12,5 m. Sand with stones. Abundant vegetation: Furcellaria, Chætopteris, Phyllophora Brodiæi, Rhodomela, Laminaria digitata, Zostera etc.
- dF. <sup>16</sup>/<sub>6</sub> 22. Starbæk Rev. 1) 5–25 m. Sand. Zostera with Algæ, in particular Desmotrichum undulatum and Chorda Filum; further Fucus vesiculosus, Ahnfeltia, Furcellaria, Polysiphonia nigrescens. – 2) 10 m. – Sand with single stones. – Zostera, few Algæ.
- cA.  $\frac{4}{6}$  21. Outside the beacon at Snogebæk, at the N. end of Alssund. C. 10 meters. Mud with dead Zostera-leaves.
- cB. 4/6 21. W. side of Arnkilsøre, Als, at the beacon. Mud. Zostera with broad leaves.
- cC. 4/6 21. Alssund, a small bank, south of cB. Zostera with Desmotrichum undulatum.
- dH. <sup>17</sup>/<sub>6</sub> 22. Just E. of Hesteskoen. c. 15 m. Sand with stones. Laminaria digitata, Fucus serratus, Delesseria sanguinea, Furcellaria, Rhodomela.
- dH<sup>1</sup>. Same place. 18—19 m. Laminaria saccharina, L. digitata, Delesseria sanguinea, *Phyllophora Brodiæi*.
- dG. <sup>17</sup>/<sub>6</sub> 22. Hesteskoen. (Alssten). 1–2 m. Narrow shoal, consisting of small stones. At the top no vegetation. From 1,5 m. downwards vegetation of *Chorda Filum* and *Ectocarpus*, further single bushes of *Fucus serratus*.
- dJ. <sup>17</sup>/<sub>6</sub> 22. Søndre Stenrøn, by the triple broom. 6–7,5 m. Sand with stones. Zostera, a little Rhodomela.
- dQ. <sup>20</sup>/<sub>6</sub> 22. Bank S. of Lyø, 1<sup>1</sup>/<sub>2</sub> miles south of the S. end. 22 m. Stones (small). Laminaria digitata and L. saccharina, Florideæ, (Phyllophora Brodiæi, Polysiphonia nigrescens, P. elongata f., Rhodomela subfusca f.)

#### Great Belt. (Sb)

- cT. <sup>9</sup>/<sub>6</sub> 22. West of Ryggen, 55°37′ N., 10°41′ E. C. 20 m. In a seine: Laminaria digitata, Delesseria sanguinea, Dilsea edulis (loose).
- cS. <sup>9</sup>/<sub>6</sub> 22. Ryggen, 55° 37′ N., 10° 43,5′ E. 18,5–23 m. Gravel. No vegetation.
- cR. <sup>9</sup>/<sub>6</sub> 22. Ryggen, 55°37' N., 10°44,5' E. 13–13,5 m. Gravel, stones. No vegetation.
- cQ. <sup>9</sup>/<sub>6</sub> 22. N. of Romsø, 55° 36,5' N., 10° 47' E. 22 m. Soft bottom. No vegetation.
- cP. <sup>9</sup>/<sub>6</sub> 22. N. of Romsø, 55° 34,5′ N., 10° 48′ E. 25 m. Soft bottom, Ophiuræ. No vegetation.
- cO. <sup>9</sup>/<sub>6</sub> 22. N. of Romsø, 55° 33′ N., 10° 48′ E. c. 15 m. Soft bottom. No vegetation (a fragment of *Dilsea edulis*).
- cN. <sup>8</sup>/<sub>6</sub> 22. S.W. of Musholm, 55° 26,3' N., 11° 2,3' E. 18 m. Stones. Laminaria saccharina, Deless. sinuosa, D. sanguinea in abundance.
- cM. 8/6 22. N.E. of Sprogø, 55°23' N., 11°0,5' E. 25 m. Mud, stones. No Algæ.
- cL.  $\frac{8}{6}$  22. N.E. of Sprogø, 55°21,5′ N., 11°1,5′ E. 25–27 m. Stones. Delesseria sanguinea, D. sinuosa, Furcellaria a. o.

Baltic, western part. (Bw)

- bZ. <sup>3</sup>/<sub>6</sub> 21. At the beacon south of Sønderborg, at the side of Sundeved. C. 11 m. Coarse sand with stones. Laminaria saccharina, L. digitata a. o. Algæ.
- bV. <sup>3</sup>/<sub>6</sub> 21. N.E. of the N. end of Kobbel Skov (Sundeved), off the point. 6,5–13 meters. Stones. – Furcellaria, Laminaria digitata, several Florideæ (Polysiphonia nigrescens, Rhodomela, Phyllophora membranifolia a. o.)
- bX.  ${}^{3}/_{6}$  21. Off the S. end of Kobbel Skov. 5,5–6,5 meters. Gravel with stones. The same species as in bV and further *Fucus vesiculosus* and *F. serratus*.
- dL. 19/6 22. W. of the broom at Kragesand. 14 m. Clayey sand without vegetation.
- dM. 19/6 22. Same place, E. of the broom. 14 m. Clayey sand with Zostera.
- dN. <sup>19</sup>/<sub>6</sub> 22. Flensborg Fjord. Bank between Holdnæs and Brunsnæs. 9 m. Laminaria saccharina, Zostera.
- bY. 3/6 21. Off Sønderskov. 11,3 meters. First clay with Ophiuræ, then Zostera with Algæ, in particular Furcellaria and Phyllophora.
- cG. <sup>6</sup>/<sub>6</sub> 21. Trindelen, reef from the W. point of Kegnæs. 9,5–11,3 meters. Stones. Several Algæ, Zostera. 11–19 meters. Stones. Laminaria saccharina.
- cD. <sup>6</sup>/<sub>6</sub> 21. Middelgrund (Hans Madsens Grund) south of Als, E. side of the bank, by the triple broom. 7,5—11,5 meters. Sand with stones. Various Algæ, *Laminaria digitata*, *Delesseria sanguinea* a. o.
- cE. <sup>6</sup>/<sub>6</sub> 21. The same bank, a little further south, 13–15 meters. Sand (with stones). Various Algæ.
- cF. <sup>6</sup>/<sub>6</sub> 21. 1 mile S. of Kegnæs light-house. In the channel 19 meters, soft bottom, no vegetation. - 8,5 meters, sand with *Zostera* and Algæ (*Phyllophora Bangii*).
- dK. <sup>17</sup>/<sub>6</sub> 22. Pøls Rev, near the bell buoy. 6–7 m. Stones. Abundant vegetation of *Halidrys*, *Furcellaria* etc.
- dO. <sup>20</sup>/<sub>6</sub> 22. North side of Bredgrund south of Als. 5 m. Bare sand, single spots with stones. — Fucus vesiculosus and F. serratus, scarce Zostera.
- dP. <sup>20</sup>/<sub>6</sub> 22. E. side of Bredgrund. 7<sup>1</sup>/<sub>2</sub> m. Large stony spots covered with vegetation. Fucus vesiculosus, Florideæ (Rhodomela, Polysiph. nigrescens, Furcellaria), scarce Laminaria digitata and Zostera.

# IV. Ceramiales.

# Fam. 11. Ceramiaceæ.

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# Spermothamnion Aresch.

# 1. Spermothamnion repens (Dillw.) K. Rosenv.

Conferva repens Dillwyn, Brit. Conferv. pl. 18 (fasc. 2, 1802 (?)).

Ceramium Turneri Mertens in Roth, Catalecta botan., III, 1806, p. 127, Taf. V.

Conferva Turneri Dillwyn, Brit. Conf. Pl. 100, 1809.

Callithamnion repens Lyngbye, 1819, p. 128, Tab. 40; Kützing, Tab. phyc. XI Tab. 69 I.

Callithamnion Turneri (Roth) C. Agardh, 1828, p. 160. J. Agardh, 1851, p. 23. Harvey, Phyc. Brit. II, pl. 179. Kützing Tab. phyc. XI Tab. 80.

Callithamnion roseolum C. Agardh, 1828, p. 182. J. Agardh, 1851, p. 21.

Ceramium roseolum (C. Agardh) Hornemann, Flora Danica Tab. 2262, 1, 1839.

Spermothamnion Turneri (Mert.) Aresch., 1850, p. 113 (with  $\alpha$ , Turneri,  $\beta$ , roscolum and  $\gamma$ , repens). Bornet et Thuret, Notes algol. fasc. I, 1876, p. 24, pl. VIII figs. 4–5. Hauck, Meeresalg. p. 42.

Spermothamnion roseolum (Ag.) Pringsheim, 1862, p. 15, Taf. IV-VI. Hauck, Meeresalg. p. 44. Reinke Algenfl. 1889, p. 22. H. Kylin, Über Spermothamnion roseolum (Ag.) Pringsh. und Trailliella intricata

Batt., Botan. Notiser 1916. Id. 1923 p. 53.

Herpothamnion Turneri (Mert.) Nägeli, 1861, p. 348, figs. 14-16 and 18-19.

Herpothamnion hermaphroditum Nägeli, ibid. p. 352, figs. 28-29.

Spermothamnion hermaphroditum (Näg.) Janczewski, Développement du cystocarpe d. l. Floridées. Mém. Soc. sc. nat. de Cherbourg. Vol. XX, 1877, p. 115, pl. 3, figs. 7-14.

# α, Turneri (Mertens).

Branches generally opposite, the tetrasporangia usually in corymbiform clusters. Sexual organs usually present.

 $\beta$ , roseolum (Agardh).

Branches generally alternate, the tetrasporangia single or in pairs (small clusters). Sexual organs frequently wanting.

Various opinions as to the denomination and the limitation of this species are still maintained. British authors mention *Spermothamnion Turneri* as common on the British shores but do not mention *Sp. roseolum* as a distinct species occurring there. On the other hand, C. AGARDH and J. AGARDH designate by this latter name the species occurring on the western coast of Sweden which they consider different from *S. Turneri*, a species which they do not record from the Swedish coast. KYLIN follows them in 1907 (Stud. Algenfl. schwed. Westk., p. 149). J. AGARDH (Spec. g. ord. II, 1, 1851, p. 24) quotes the characters by which *Callithamnion roseolum* differs from *C. Turneri*, viz. the ramification which is more rarely opposite, the sporangia which are single or placed in pairs while they are aggregate in *C. Turneri*, the looser and often longer tufts and the longer cells. These characters are, however, very variable, of which one is easily convinced by examination of a greater number of specimens.<sup>1</sup> I can therefore only approve that J. ARESCHOUG in 1850 referred *Call. roseolum* as a variety under *Spermothamnion Turneri*, and it must also be considered that he is justified in referring *Conferva repens* Dillw. to the same species.

<sup>1</sup> Comp. SCHMITZ in HAUCK et RICHTER, Phycotheca universalis No. 657, 1895.

This species of DILLWYN is the first described plant of this form series. It must be granted that the description only comprises sterile plants, but there is no doubt



Fig. 202. Spermothamnion repens. Filament showing the nuclei and the formation of the branches.





that it refers to incompletely developed specimens of *C. Turneri*. Its occurrence on *Fur*cellaria fastigiata which is a favourite substratum of *S. Turneri* speaks decidedly in favour of it. It must therefore be most correct to give the plant DILLWYN's specific name which is 4 years earlier than that of MERTENS.

The Danish specimens may be referred to two forms: f. *Turneri* and f. *roseola*, which are shortly characterized above. The first-named form has only been found in the North Sea, the Skagerak and the northern Kattegat, while in the specimens from the inner Danish waters the branches are rarely or never opposite and the sporangia are placed singly or in pairs on short pedicels. No distinct line of demarcation between the two forms can however be drawn, the characters varying considerably even on the same plant.

As shown by Nägeli (l. c. p. 346), there is a distinct morphological difference between the horizontal filaments, which constantly grow in a transversal direction, and the erect filaments given off from their upper side. New creeping filaments are given off from the flanks of the first named filaments while rhizoids are produced from the under face.

The cells contain numerous nuclei, not only the older cells but also the apical ones which contain a considerable number in thicker filaments. They appear in the apical cells as hyaline globular bodies dispersed in the peripheral part of the dense



Spermothamnion repens. Normal and terminal hapters, 50:1.

protoplasm filling out the cell and not covered by chromatophores. In the other cells the nuclei are smaller and less conspicuous in a living state. In the thinner branches which sometimes occur in f. *Turneri* the number of nuclei may decrease to 3 or 4 (fig. 203) and the same may be the case with the sterile cells supporting the reproductive organs. The branches arise as small lenticular cells cut off by a

Fig. 206. Spermothamnion repens. Hair-cell with several nuclei and numerous small chromatophores. 220:1. concave wall at the upper end of the cell and containing from the first a number of nuclei (fig. 202).

The hapters are numerous; they are frequently produced from a number of consecutive cells of the creeping filaments (comp. DILLWYN I. c., LYNGBYE Plate 40 C). They spring normally from the basiscopic end of these filaments and are as a rule unicellular. When meeting the substratum the cell is expanded in an adhesive disc composed of densely joined dichotomous ramifications of the cell (fig. 204). The hapters may exceptionally be two-celled (fig. 204), and it may also occur that a hapter is produced at the end of a shorter or longer filament (fig. 205).

According to PRINGSHEIM (1862, p. 17, Taf. IV fig. 1 and Taf. VI figs. 1—2) the erect filaments may terminate in a feebly coloured hair and the same may be the case with the involucral branches of the cystocarps. The occurrence of these hairs is however, according to my observations, not normal but a comparatively rare phenomenon which I have observed only in a few specimens. They arise from terminal cells of shorter or longer filaments, these cells becoming much longer, upwards a little thinner. The nuclei persist and become distincter while the chromatophores vanish and appear only as small feebly coloured grains (Comp. Kolderup Rosenvinge, Hyaline hairs. Biol. Arb. tilegn. E. WARMING. 1911, p. 210). Transitional forms between hairs and hapters may occur (comp. PRINGSHEIM and K. ROSENVINGE II. cc.).

The tetrasporangia are in the simplest case solitary and borne on a stalk-cell. This occurs particularly in the f. *roseola*; but a second sporangium is here frequently present, terminal on a lateral stalk-cell given off under the first. In the specimens from the North Sea, the Skagerak and the Northern Kattegat, which are in great part referable to f. *Turneri*, the sporangia are placed in cymoid clusters, the ramification continuing in various

degree. These clusters may be opposite or secund. In the f. *Turneri* verticillate clusters, in ternate whorls, may occur beside the opposite ones. The sporangia contain from the first one nucleus only, while the supporting cell contains several nuclei (fig. 207 B). This comes in existence, as far as I have observed, in the way that the sporangium only receives one nucleus by the division by which it is separated from the stalk-cell. Any disorganization of supernumerary nuclei as in

Martensia a. o. (comp. N. SvE-DELIUS, Bau, Entw. d. Florideengatt. Martensia, K. Sv. Vet. Ak. Handl. Bd. 43, no. 7. 1908) could not be observed. The spores, which arise by tetrahedrical division, contain each one nucleus (fig. 208 A). A cell-wall separating the spores is shown in fig. 207 D. A small number of sporangia containing more than 4 spores, up to 8, was met with on a plant from the North Sea (aF, fig. 207 E). They had the same shape and size as the normal sporangia or were only a little longer. The spores produced seem to be somewhat smaller than the normal ones.

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The antheridia form irregularly ovate stipitate or sessile bodies which may appear on particular plants or branches but more frequently occur in company with the procarps. In the first case they are frequently seriate on the inner side of shorter branches. The antheridia-producing branchlets are divided by transversal walls in a number of segments which remain short except the undermost segment which usually develops into a stalk-cell. The other segments divide by vertical and oblique walls in a number of smaller cells all containing one nucleus only, the outer-



#### Fig. 207.

Spermothamnion repens. Tetrasporangia. A (Hirsholm), sporangia in cymoid cluster. B, young sporangia with one nucleus. C-D (North Sea).
C, sporangia in company with a procarp. D, sporangium without the outer sporangial wall. E, two sporangia and a young procarp; the one sporangium with 8 spores. A-C, 150:1. D-E, 260:1.



Fig. 208. Spermothamnion repens. Sporangia. A (Hirsholm). B, C (North Sea), in company with antheridia and procarps. B, C 150:1.

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D. K. D. Vidensk. Selsk. Skr., 7. Række, naturvidensk, og mathem. Afd. VII. 3.

most of which are smaller and become the antheridia. An axile cell as those figured by Nägeli (l. c. fig. 28) may be present, but only in the under part of the antheridial cluster. The upper segments divide by anticlinal walls in a number of cells,



Fig. 209. Spermothamnion repens. (Hirsholm) Antheridia. B, transverse section of antheridial body. A 63:1. C 350:1. B, D 560:1. meeting almost in the axis of the segment and producing at the periphery a number of smaller cells, the antheridia (fig. 209). The stalk-cell, which usually contains a number of nuclei, produces also by peripheral divisions a number of unicellular antheridia-producing cells (Svedelius' "Spermatangienmutterzellen").

The procarps are situated at the end of short branches, The apical cell of such a branch produces by two transverse divisions two short segments, the uppermost of which undergoes further divisions, giving rise to the procarp, while the undermost and the apical cell remain undivided. By the first of these divisions the upper cell receives only one nucleus while the segment cell, becoming the stalk cell, contains several nuclei (fig. 210 to the left). Only rarely is the stalk cell also uninucleated (fig. 211 *A*). By division of the uninucleated apical cells two cells, each containing one nucleus only, result, the undermost of which is the mother-cell of the procarp.

The development of the procarp has been described by Nägeli (1861), PRINGSHEIM (1862), BORNET and THURET (1876), JANCZEWSKI (1877) and recently

more thoroughly by KYLIN (1923 p. 53-55), to whose description we may here refer. As shown by this author, the cell next to the top divides by longitudinal

walls in a central cell and three pericentral ones the middlemost of which does not divide further. One of the lateral cells gives rise to a peripheral sterile cell (figs.  $211 B, C, G, I^1$ ) and to the carpogonial branch which becomes opposite to the median pericentral cell. The undermost cell-wall of the carpogonial branch is often oblique (fig. *B*, *E*, comp. JANCZEWSKI p. 115), the undermost cell being nearer to the lateral cell from which the carpogonial branch is given off. All the cells of the procarp are uninucleated from the first. The nucleus of the young carpogonium divides into two, the upper of which enters into the trichogyne where it appears



Fig. 210. Spermothamnion repens. Young procarps bearing branches showing the first divisions and the nuclei. 500:1.

as a rather hyaline body with a distinct nucleolus (figs. D, E). As shown by KYLIN, two small sporogenous cells are cut off from the fertilised carpogonium and these cells fuse with the two auxiliary cells which are cut off from the two lateral peri-

central cells; one of these sporogenous cells is seen in fig. F. The cells of the carpogonial branch were often found fused together after fertilisation, most frequently

so that they all took part in the fusion (figs. F, G). The interpretation of the case represented in fig.  $I^2$  is somewhat uncertain. A fusion cell is seen under the carpogonium and on either side of the fusion cell a small cell has been cut off. It has the appearance that the sporogenous cells have been cut off not from the fertilized carpogonium but from the upper sterile cell of the carpogonialbranch. It seems however that this case must be interpreted in another way. The cell



Fig. 211.

Spermothamnion repens. Development of procarps. A, young procarp-bearing filament; the stalk-cell is uninucleated. B, the carpogonial branch is formed; its first cell is partly hidden behind the second one. C, procarp seen from the dorsal side; D, E, lateral view; the trichogyne nucleus is visible. F-K after fertilisation. F, a sporogenous cell is visible. G, the cells of the carpogonial branch fused together; young gonimoblasts. I procarp seen from the ventral side,  $I^1$  at a lower,  $I^2$  at a higher level of the same procarp. The pericentral cell to the left has produced a sterile cell and an auxiliary cell, for the rest see text. K, lateral view; the auxiliary cell in beginning division. D, E 455:1, the other 284:1.

situated to the left of the carpogonial branch in fig.  $I^2$  is evidently the first cell of this branch, being attached to the pericentral cell to the left in fig.  $I^1$ . The fusion



Fig. 212. Spermothamnion repens. Carpospore. 350 : 1.

cell has undoubtedly arisen by fusion of three cells. The upper of these cells must have been the carpogonium or more exactly a part of the carpogonium, undoubtedly containing the sporogenous nucleus, while the small cell situated over the fusion cell must be the rest of the carpogonium, probably without any nucleus. If this interpretation is true, the two small lateral cells must be true sporogenous cells, on the way to fusion with the auxiliary cells just cut off from the peripheral cells (comp. fig.  $I^1$ ).

350:1. The upper sterile cell in the procarps may sometimes divide and grow out in a sterile filament. JANCZEWSKI (l. c. p. 117) found it sometimes replaced by a cluster of antheridia. The statement of PRINGSHEIM (l. c.

p. 19) that it may sometimes develop into a "Sporenmutterzelle" (carpospore), is certainly erroneus. I once observed two procarpia situated one over the other, ori-

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ginating without doubt in the following way: the first uninucleated apical cell (comp. fig. 210) has produced two uninucleated segments each developing into a procarp. The procarp of the undermost procarp protruded obliquely at the side.

The development of the gonimoblasts has been described by KYLIN (l. c.). The ripe carpospores contain one large nucleus (fig. 212). During the development of the cystocarp a number of involucral branches grow out under its base; there are usually 3 or 4, more rarely up to 8.

When sexual organs are present, they almost always occur on the same plant and further in combination with sporangia; the three kinds of reproductive organs are as a rule to be found in the immediate neighbourhood of each other on the same system of branches or branchlets, in various combinations. Usually the procarps are terminal in such complexes of branches, and branchlets bearing antheridia or sporangia are given off under them. A cytological study of such plants is much needed (comp. KYLIN 1916).

The species is widely distributed in the Danish waters except those with slightest salinity (the Baltic around Møen and Bornholm and the Sound south of Helsingør). It occurs scantily in the Limfjord but has otherwise not been met with in the fjords except the Isefjord where it has been found in the entrance. It attains its greatest development in the North Sea and the Skagerak where it has been found in almost all the places investigated and frequently in great abundance. It occurs here in dense tufts up to 5 cm high and may be referred to f. Turneri; it is usually fructiferous in summer and frequently bears sexual organs together with sporangia. Similar specimens are found in the Northern Kattegat, scarcely however exceeding 3 cm in height, and transitions to f. roseola are frequently met with, the sporangiabearing branchlets bearing only a very small number of sporangia. In the more southern waters the species is usually sterile, even in summer; in some places, however, it has been found with tetraspores, but nowhere with sex organs (except once at Helsingør), The branches are rarely or not at all opposite and the sporangia are placed singly or in pairs on the pedicels. Also in the southern waters transitional forms may be met with; e. g. specimens collected at Lohals in Sb have partly numerous opposite branches and well developed corymbiform sporangial clusters.

Spermothamnion repens grows epiphytically on various Algæ, principally on Furcellaria fastigiata, also frequently on Phyllophora membranifolia, Ahnfellia plicata and Corallina officinalis, further on several other Florideæ, on Fucus serratus and Laminaria hyperborea and digitata, and finally it has been met with growing on Buccinum undatum. It is perennial, but most of the upright filaments perish in the autumn, and the tufts are therefore only 2—10 mm high in winter. It is fructiferous only in summer, June to September (October). Ripe sporangia have been found in all these months, ripe cystocarps only in July to September. The species has been met with from low-water mark to 31 meters' depth (North Sea); in the Kattegat it has been observed down to 25 meters', in the more southern waters only to 13 meters' depth.

Localities. Ns: ZO, jyske Rev. 24.5 met.,  $\mathcal{E} \cap +^1$ ; aF, 31 m.  $\mathcal{E} \cap +^1$ ; Klitmøller (Hornemann); XR, off Ørhage and within Ørhage, on stony bottom with Mytilus edulis, sterile (fixed to the pebbles or loose?). — Sk: YT and YU at Hanstholm, 2–13 m,  $\stackrel{*}{\to}$  () +; eY, 18 miles E.N.E.  $\frac{1}{2}$  E. of Hanstholm light-house, 15 miles N. of Bragerne 16 m; YN<sup>2</sup>, S.E. of Bragerne, 10,5 m  $\stackrel{\circ}{\to} \bigcirc +$ ; Bulbjerg (J. P. Jacobsen); SZ and SY, N. of Løkken, 13 m +; washed ashore at Løkken,  $\mathcal{J} \bigcirc +$ ; ZK off Lønstrup, several places, 1-19 m,  $3^{\circ}$   $\bigcirc$  +, or only +; XO and VJ and several other places near Hirshals, 1-15 m,  $3^{\circ}$   $\bigcirc$  +, or only +; Tannisbugt, washed ashore (V. Schmidt); Højen, between first and second shoal. - Lf: LZ, Nissum Bredning; Oddesund, 6,5 met.; MH, Thisted Bredning; I, Venø Bugt; in all places sterile. -Kn: Harbour of Skagen; Krageskov Rev; Hirsholmene,  $\mathcal{F} \cap +$ ; Frederikshavn, harbour and several places in the neighbourhood, e. g. Deget; YP and UD,  $3 \bigcirc +$ ; VT, +, ZP, UC, TL, +, near Nordre Rønner; Vesterø Havn; GM, near Engelskmands Banke, +; Tønneberg Banke, 15,5 m, +; FE, Trindelen, 10 m, +. - Ke: FD, E. of Læsø; VY and ZE<sup>2</sup>, Fladen 15-18 m; XA, S.E. of Kobbergrund; E. end of Anholt; 14<sup>1</sup>/<sub>2</sub> miles S.S.E. of Anholt Knob lightsh. 10 m (C. A. J.); HZ, Store Middelgrund; GI, Ostindiefarer Grund; off Gilleleje, +; Nakkehoved (Lyngbye), +. – **Km**: 6 miles S.S.W.  $\frac{1}{2}$  W. of Læsø Rende light-ship, 8 m; 51/2 miles N. to E. 3/4 E. of Østre Flak light-ship, 9 m (C. A. J); BO, Stensnæs; BN, W. of Asaa; YY, ZC<sup>1</sup> and ZD Kobbergrund; XD, S. of Læsø; XB, S. of Kobbergrund; VN, S.E. of mouth of Randers Fjord; Gjerrild (Lyngbye); BJ, Gjerrild Flak; BH, off Gjerrild Klint. - Ks: EP, Pakhusbugt Anholt; OP, EM and EJ, Lysegrund; HP, S. of Lysegrund; Hesselø (Lyngbye); OS<sup>1</sup>, Hastens Grund; FP. Jessens Grund, 4 m, +: GG and GF, Sjællands Rev: D, N. of Grønne Revle, 11.5 m, +; EH, W. of Lynæs. - Sa: Begtrup Rev, +; FT, N. of Samsø; FX, off Dyngby Hage; MP, Falske Bolsax; MQ, S. of Paludans Flak; AJ<sup>1</sup>, N. of Æbelø, +; AH<sup>1</sup>, N. of Fyns Hoved; Hofmansgave (Lyngbye, Hofm. Bang., C. Rosenberg). - Lb: AX, Bjørnsknude; Linderum; DB, Lillegrund (Reinke, !); CD, Helnæs Hoved Flak; DA, off Bøjgden; CC, Hornenæs, +; LG, off Vidsø, Ærø; DX, Vodrups Flak. Does not occur in the middlemost part of the Belt between AX and Linderum. - Sf: UV, N of Ærø. - Sb: AG, W of Romsø; AF, Møllegrund off Kerteminde; harbour and bay of Kerteminde; NU, off the Strandskov by Bogense, 11,5 m; reef at Korsør; Lohals, harbour, +; UU, Snøde Rev. - Sm: CQ, N.N.E. of Kogrund: Q off Vesterskovs Flak. — Su: BQ, off Ellekilde, 5,5 m; Hellebæk; near Helsingør (Liebman),  $\mathcal{E} \bigcirc +$ ; Kronborg (Lyngbye). — Bw: cF, south of Kegnæs, Als, 8,5 m; dK, Pøls Rey; DU, off Dimes Odde; LC, off Gulstav, 11,5 m; KZ, of Kramnisse.

# Trailliella Batters.

# 1. Trailliella intricata Batters.

E. A. L. BATTERS, Some new Brit. mar. Algæ. Journ. of Bot. Vol. 34, 1896, p. 10; id. in Journ. of Botany, Vol. 38, 1900, Tab. 414, fig. 14. H. KYLIN, Über Spermothamnion roseolum (Ag.) Pringsh. und Trailliella intricata Batters. Botan. Notiser, Lund, 1916, p. 87. KOLDERUP ROSENVINGE, Om nogle i nyere Tid indvandrede Havalger. Bot. Tids. 37, 1920, p. 127. Kylin, Bot. Notiser 1922 p. 346.

Spermothamnion Turneri f. intricata Holmes et Batters, Annals of Botany, Vol. 5, 1890, p. 96.

Spermothamnion roseolum Kylin, 1915, p. 4.

non Callithamnion intricata Ag. Syst. Alg. 1824, p. 132, id. 1828, p. 182, Kützing, Tab. phyc. Vol. 11 pl. 62.

It is remarkable that this species which now occurs abundantly in several places has not been observed, as it seems, before 1890 and has been described for the first time in 1896. In mode of growth, it somewhat resembles *Spermothamnion Turneri*, but differs by smaller dimensions, by the want of opposite branches, by the presence of gland cells and by the structure of the hapters.

There is no essential difference between the horizontal and the vertical filaments. The cells contain a single nucleus, which is easily pointed out by fixing and

<sup>1</sup>  $\mathcal{J}$  designates antheridia,  $\bigcirc$  cystocarps, + tetrasporangia.



Fig. 213. Trailliella intricata. Upper ends of filaments. 300:1.

Fig. 215.

Trailliella intricata. Terminal hapters. 82:1.

are frequently curved a little upwards between the hapters; they usually bear near the hapters a number



The upright filaments are sparsely and irregularly branched; there may be two generations of branches. The

tapering cell which at its under end bears a whorl of repeatedly branched fila-

branches are scattered; they arise a little below the upper end of the filaments and are cut off by a watch-glas-shaped wall (fig. 213). The filaments are of almost equal thickness in their whole length, only a little tapering at their upper end; the diameter is  $25-38 \mu$ , the length of the cells 1-2,5times as long as the diameter, more rarely up to 3 times as long. The long cells are a little constricted at the transversal walls. Hapters may exceptionally be found terminal on the filaments (fig. 215).

The arrangement of the gland cells is irregular; in the horizontal filaments they are particularly produced on the upper convex side. In the upright filaments they have a tendency to be alternating, but no regularity exists and some cells bear no gland cell (comp. KYLIN 1915).

The plant has always been found sterile in the Danish waters till October 1922 when Mr. C. A. JØRGENSEN found tetrasporiferous specimens in two localities

ments closely connate in a conical attachment disc (fig. 214). The rhizomes ittle upwards between the near the hapters a number

Fig. 214. Trailliella intricata. Creeping filament with hapter. 260:1.

iodine. The horizontal filaments are fixed to the substratum through pluricellular hapters, consisting of a downward

staining agents in the apical cell and the young segment cells (fig. 213). As shown by BATTERS and KYLIN, the cells contain numerous disc-shaped, or elongated chromatophores. The fully developed cells contain numerous starch-grains. The pits connecting the cells are very distinct. Most of the articular cells bear at their upper end a small gland cell, in optical section triangular, seen from the face roundish. As shown by KYLIN (ll. cc.) they contain a substance which by addition of hydrochloric acid produces iodine.

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in the Skagerak and the northern Kattegat. The tetrasporangia are formed, as shown by BATTERS, in the upright filaments by longitudinal division of a somewhat swollen cell into two parts of unequal size, the larger forming the tetrasporangium, the other part remaining sterile. The longitudinal wall is often somewhat inclined, the lower end of the sterile cell being broader than the upper. While the sterile cells contain numerous coarse starch grains, the developing tetrasporangium becomes dark-red and with more fine-granular contents. The tetrasporangium is first divided by a horizontal, slightly inclined wall and then by two nearly vertical walls. The ripe spor-

angium is much swollen; it opens by a split opposite to the sterile cell. As shown in fig. 215 bis the sporangium is connected with the sterile cell through a pit in the middle of the longitudinal wall. The sporangia may be solitary or 2 to 6 together and then variously orientated, always separated from the apex of the filament by a varying number of sterile cells. The sex-organs are unknown.<sup>1</sup>

BATTERS thought that this Alga was identical with *Callithamnion intricatum* J. Agardh. If he has founded this supposition only on the short descriptions of C. AGARDH (Syst. Alg., 1824, p. 132) and J. G. AGARDH (Spec. g. ord. II pars I, p. 19), it must be said that these descriptions are too incomplete to allow of an identification, and the plant represented in KÜTZING'S Tab. phyc. 11. Band, Tab. 62,II is evidently another species, being much coarser and showing no gland cells. Two specimens in the herbarium of the Botan. Museum of Copenhagen from J. AGARDH, determined as *Callithamnion intricatum* and collected at Koster Bahusiæ and at Kullaberg, turned out to be *Spermothamnion repens*.



Fig. 215 bis. Trailliella intricata Batt. Parts of filaments with tetrasporangia. A 390:1. B 230:1.

As long as the sex-organs are unknown the systematical position of the genus remains uncertain. The position and development of the tetrasporangia remove it from the other genera of *Ceramiaceæ*; the genus in this respect somewhat reminds one of the *Rhodomelaceæ*.

The species has been found more or less abundantly in numerous places in the Limfjord and the northern part of Kattegat, and recently in several places in the North Sea and Skagerak. It was first met with in the Western part of the Limfjord in 1901 but has not been observed there before that year, although numerous

<sup>1</sup> KYLIN has recently (Botan. Notiser 1922 p. 346) given a drawing of a tetrasporiferous plant after a slide from BATTERS kept in the herb. AGARDH in Lund, not being acquainted with the drawing given by BATTERS in Journ. of Botany 1900.

dredgings have been made in the same part of the fjord in 1890, 1893 and 1899. In the Kattegat it was not observed till 1909, when it was met with in the neighbourhood ot Frederikshavn, although these waters were very carefully explored after 1889. It is therefore very probable that the species has immigrated into the Danish water about the year 1900, a supposition which is in accordance with the observations of KYLIN on the west coast of Sweden (1916, p. 91), where *Trailliella* was found in three localities on the coast of Bohuslän in 1902—1906, while it was not met with by the earlier investigators, e. g. by STRÖMFELT who made large collections (of *Spermothamnion*) on the same coast in 1885—1887. At Helgoland it has also been recorded in later years (comp. KUCKUCK, Zeitschr. f. Bot. 8 p. 135). In July 1907 I found *Trailliella intricata* abundantly on various Algæ and Ascidia at Arendal on the south-eastern coast of Norway, and in July 1916 at Anuglen on the West coast of Norway, near Bergen.

Trailliella intricata is almost always epiphytic, growing on various algæ, e. g. Furcellaria, Corallina officinalis, Phyllophora etc. but it also grows on Mytilus, Trochus, Hydroids and on pebbles, from low-water mark to 28 meters depth.

Localities. Ns: eA and eR, off Thyborøn, 28 and 27 meters. — Sk: eY and eZ, east of Hanstholm, 15—17 meters; 13 miles S.W. by W. 1/2 W. of Rubjerg Knude light-house, 14 meters, with tetraspores, Oct. (C. A. Jørgensen);  $(2^{1}/_{2}$  miles N.E. by N. of Skagens reef light-ship, 90 meters, loose, C. A. J.) — Lf: Nissum Bredning: Harbour of Thyborøn; Rønnen near Lem Vig (1901); ZU, near the latter, 4 meters; XV, N. of Rønnen (1901); off Hesdal, Kobberød; ZT, off Østerbol, 4 m, abundantly on loose Furcellaria; ZV, 5 m: ZY, 4,5 m; XU, 4 m; Nissum Bredning 1908 (Th. Mortensen); Oddesund. XT, south side of Jegindø Tap, 5 m; Sallingsund, various places, abundantly; aT<sup>1</sup>, off Alsted, Mors, 5 m; Knudshoved, Fur; N. side of Fur; W. of Eierslev Røn, 7 m; off Feggeklit, 4 m. — Kn: Harbour of Skagen; fE, E. side of Krageskov Rev, 7 m; various places at Hirsholm, c. 11 m (1909 H. E. P.); near Kølpen, 4 m (H. E. P.); Laurs Rev; harbour of Frederikshavn; E. of Nordre Rønner; ZA, Tønneberg Banke, 12—18 m (1904); fG, 3 miles W. of Læsø Trindels light-ship; various places near the same 11—21 m;  $6^{1}/_{2}$  miles S.W. by W.  $1/_{2}$ W. of Læsø Trindels light-ship, 15 m, abundantly, with tetraspores, October (C. A. J.) — Ke: ZE<sup>2</sup>, near Fladens light-ship, 15 m (1904); 1 mile W. by N. of Fladens light-ship, 17 m, abundantly, Octob.;  $14^{1}/_{2}$  miles S.S.E. of Anholt Knob, light-ship, 10 m (C. A. J.). — Km:  $5^{1}/_{2}$  miles N. by E.  $3/_{4}$  E. of østre Flak light-ship, 9 m (C. A. J.).

# Callithamnion Lyngbye emend.

# Key to the Danish species of Callithamnion.

1.	All cells uninucleate.
	2. Branches generally biseriate; hairs wanting; heaps of paraspores on
	the upper side of the pinnulæ C. Hookeri.
	2. Branches generally spirally arranged; no paraspores.
	3. Pinnulæ with terminal hairs C. Brodiæi.
	3. Pinnulæ usually without terminal hairs.
	4. Main axes vigorous, corticated; cystocarps round C. roseum.
	4. Main axes feeble, usually not corticated; cystocarps lobed C. Furcellariæ.
1.	The older cells contain several nuclei.
	2. Branching pseudodichotomous; pinnulæ blunt, usually with terminal
	hairs C. corymbosum.
	2. Branches generally spirally arranged; pinnulæ pointed, never with hairs <i>C. tetragonum</i> .

# 1. Callithamnion Hookeri (Dillw.) Agardh.

C. Agardh, 1828, p. 178; Harvey, Manual Brit. Alg. 1841, p. 106; J.-Areschoug, 1850, p. 103, tab. IV F (forma a); J. Agardh, 1851, p. 51; Harvey, Phyc. Brit. Vol. III, 1851, pl. 279; Kützing, Tab. phycol. XI tab. 94 a, 1861; Kylin, 1907, p. 150.

## f. Areschougii nob.

Areschoug, l. c. forma a, Alg. scand. exsicc. No. 311; Kylin, l. c. f. typica.

Callithamnion pyramidatum Liebman, Bemærkn. o. Tillæg, Krøyers Tidsskrift II, 1839, p. 479, Tab. VI fig. 1, ex parte.

In several places in the Danish waters a *Callithamnion* has been met with which agrees exactly with *Callithamnion Hookeri a* Aresch., as described by ARE-



Callithamnion Hookeri. Upper end of sterile shoots. A 150:1. B 70:1.

Fig. 217. Callithamnion Hookeri. After a living plant. 160:1.

SCHOUG and KYLIN, ll. cc., and bearing, like the Swedish plants, heaps of paraspores but no or scarce tetrasporangia and never sexual organs. The Scandinavian specimens have certainly justly been referred to *C. Hookeri* Harvey; but as they differ from the British specimens by the presence of paraspores and by the absence of sexual organs they might be regarded as representing a particular form of the species.

The Danish specimens ordinarily reach only a length of 1,5-2 cm; but they may become up to 3 cm high (Skærbæk). The stem and the main branches are very distinct, not bent in zigzag, covered with down-growing cortical filaments. The ramification is mainly pinnate, the consecutive cells bearing each a branch alternating with the foregoing. Vigorous branches generally show a pinnate ramification, the pinnulæ lying all in the same plane, and being rather diverging. The lateral branches do not generally reach the level of the top of the main axis, and the outline of the shoot is therefore lanceolate, pointed above (comp. fig. 216). Exceptions may how-

D. K. D. Vidensk. Selsk, Skr., 7. Række, naturvidensk. og mathem. Afd., VII. 3.

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Fig. 218. Callithamnion Hookeri. Young plants. 145:1.

ever be met with (fig. 217). The pinnulæ become thinner towards the end, but they are not pointed.

In growing fronds with pinnate ramification, the dividing walls are inclined and alternating (figs. 216, 217, comp. KYLIN, l. c. fig. 30 c); in the pinnuæ they are transversal. The lateral branches, the pinnæ, are branched in the same way as the main axis, from the base or so that the first lateral branch of the second order is placed on the  $2^d$  or  $3^d$  article or even higher (fig. 216). According to KYLIN (l. c. p. 151), the branches of the second order are, when developed, orientated in the same plane as the lateral branch and the mother axis, but, when arising, they are placed in a plane perpendicular on the named plane, thus to the right and to the left, and the later position is arrived at by the turning of the lateral branch. My observations are not sufficient to warrant or disprove with certainty this statement, but at all events it

must be said that its validity is not general. The case represented in fig. 216 B is in general favourable to the supposition of KYLIN, however, it will be seen that there are some irregularities, e. g. in the 5<sup>th</sup> and the 10<sup>th</sup> branch from the base; and in other cases the plane of ramification of the youngest branched lateral branches coïncided with that of the mother branch. Deviations from the pinnate ramification





Fig. 219. Callithamnion Hookeri. Part of mains axis with cortication. 70:1.

Fig. 220. Callithamnion Hookeri. With paraspores. (Frederikshavn). A 70:1. B 145:1.

occur rather frequently, in branches of different order (fig. 216 *B*), principally in the most vigorous main axes, which may bear branches on all sides. J. AGARDH states that the lower branches are given off on all sides, and that I have also found in some cases; but in other cases, the main stem was pinnate from the base, and the same was found in a young plant (fig. 218).

The descending filaments constituting the cortex of the stem and the main branches are produced from the base of the cells of the axes and from the base of the branches given off from them; they may completely hide the original cell-filament of these axes. Here and there adventitious filaments are given off from the descending

filaments, principally from the base of the branches (fig. 219).

All cells contain a single nucleus and numerous chromatophores which in the young cells are small lengthened discs (fig. 217), in the older ones long bended, partly branched ribbons.

All the fructiferous specimens bear heaps of paraspores agreeing with the description of KYLIN, l. c. They are more or less obliquely ovate and contain an indefinite number of spores, e. g. 10—12, resembling the tetraspores; they are placed on the upper pinnæ or pinnulæ, usually on their



Callithamnion Hookeri. With heaps of paraspores. (Kerteminde). A, nearly ripe heap. B, younger stage. C-G, still younger stages, the heaps of paraspores partly replaced by vegetative branches. 200:1.

upper side in a number of one or two on the first or on the first and the second joint, more rarely in a number of three or four. In the latter case they are not always placed on the upper side of the branch but partly on the flanks or on the under side, and not rarely it happens that two heaps are placed on the same joint and then one under the other (fig. 221 *B*) or beside the other (fig. 220 *B*) or in oblique direction under the other, or they may be opposite, on the upper and under side of the cell (fig. 220). One of the heaps may be replaced by a vegetative branch. The position of the heaps of paraspores is the same as that of the tetrasporangia which in the plants from the Atlantic shores are placed not only on the upper side of the pinnules but also "utroque latere inordinate" (J. AGARDH, l. c. p. 52, comp. HARVEY l. c. pl. 279, fig. 4, KÜTZING l. c. pl. 94 fig. b).

The fact that the heaps of paraspores have a position similar to that of the tetra-

sporangia might suggest that they are transformed tetrasporangia which have been divided in a greater and indistinct number of cells. This supposition, however, is only little probable; at all events the transformation might then be supposed to begin at so early a moment that it was impossible to decide whether the young organ were really a sporangium. The sporangia are early distinguished by their regular outline and by the double firm membrane (fig. 222). The heaps of paraspores are a special form of vegetative propagative organs, more related to the vegetative



Fig. 222.

Callithamnion Hookeri. Parts of plants with tetrasporangia. In C the same branch bears a tetrasporangium and a heap of paraspores. D and E, intercalary sporangia. A, B 145 : 1. C-E 200 : 1.

cells than the sporangia. This conception is confirmed by the fact that transitional stages between the named organs and vegetative shoots frequently occur (fig. 221) and that they may, as named above, be replaced by vegetative shoots (fig. 221 C-E).

Tetrasporangia were found in some cases in parasporebearing plants, but in small number (Hirsholm, Frederikshavn, Grenaa, Kerteminde, Skærbæk). They are usually placed on the first or on the first and the second joint of a pinnula. Curiously enough, intercalary sporangia may sometimes be met with, arising from an intercalary cell in a pinnula (fig. 222 D). In such cases one of the spores is connected with the underlying cell by a pit, another spore with the cell above. Intercalary spo-

rangia are hitherto unknown as a normal occurrence in the Ceramiaceæ, as far as I know.

The specimens from all the localities with one exception, occurring in depths from 0 to 30 meters, most frequently from 0 to 10 m, agree with KYLIN's f. *typica*, having proportionally short cells, 2-3-4 times as long as broad, and well developed cortex on the principal axes. Specimens from YV in the Samsø area, 15 meters depth, remind one of f. *elongata* Kylin, l. c. by its longer cells, 5-6 times as long as broad; but the pinnulæ are scarcely less diverging than in the typical form. The frond is more slender and the cortex is very feeble or almost wanting. These characters are perhaps caused by the greater depth at which the plant was found growing. The

heaps of paraspores were not more lengthened than in the other specimens but frequently bilobate (fig. 223).

The species has been found repeatedly sterile in April and May, frequently growing on *Furcellaria*, further on *Fucus* serratus, Delesseria sanguinea and Rhomela subfusca. Twice it has been found with paraspores in May, but otherwise with paraspores in the summer months (June to August) and in November. Tetrasporangia were met with in June, August and September.

Localities. **Kn:** Hirsholmene, littoral region and 9 meters (Henn. Petersen, !); Frederikshavn, harbour and Bussserev (!, Henn. Petersen); Østerø harbour, Læsø. — **Ke:** IO, Fladen, 10—11 meters; fl, Fladen, 30 meters, small specimen (C. A. J.); OO, Søborghoved Grund, 8,5 m. — **Ks:** Harbour of Grenaa; OT, Hastens Grund, 9,5 m. — **Sa:** YV; the light-buoy at Hatterbarn N.  $2^{1/2}$  miles, 15 meters (slender form, see above). — **Lb:** Skærbæk harbour off Kolding Fjord, with paraspores and tetraspores; DB, Lillegrund, (slender form, sterile). — **Sb:** Kerteminde, harbour. — **Su:** Ellekilde Hage (Boye Petersen); Hellebæk,washed ashore; near Helsingør (Liebman, *Call. pyramidatum*). — **Bw:** dK, Pøls Rev, 6—7 m.

2. Callithamnion Brodiæi Harv.

Harvey in Hooker, English Flora, Vol. V part 1, 1833, p. 340; Manual, 1841, p. 105, Phyc.
Brit. Pl. 129, 1849. J. Agardh, 1851, p. 57, III, 1876, p. 34. Kylin, 1907, p. 162.

Phlebothamnion Brodiai Kützing, Spec. alg. 1849, p. 655, Tab. phyc., 11. Band, Tab. 100<sub>II</sub>, 1861.

Fig. 223. Callithamnion Hookeri. Slender form from 15 meters depth (YV). 47:1.

Only some few specimens of the species here mentioned have been met with, growing on *Furcellaria fastigiata* collected on the Nordvestrev by Hirsholmene, in company with four other species of Callithamnion, Spermothamnion repens and others. They agree perfectly with the quoted figures and descriptions of AGARDH, KÜTZING and KYLIN, and it is probably justly that the name of HARVEY has been assigned to them though it is not excluded that two species might have been confounded under that name. Referring especially to the paper of KYLIN, a description of the Danish specimens may be given here.

The specimens reach only a length of 1,5 cm at most. The main axes are very

distinct, straight, not bent in zigzag, corticated below. The thickness is  $130-150 \mu$  below, over the cortication about 75  $\mu$ . The cells are  $1^{1}/_{2}-5$  times as long as broad. From the cells of the cortical filaments growing down in the outer walls small adventitious filaments are given off (fig. 224), probably more numerous in larger specimens. The lateral branches are as a rule much shorter than the main axes



Fig. 224. Callithamnion Brodiæi. Part of tetrasporiferous plant. 62:1.

the result being that the outline of the main branches become narrow, hastate or pyramidate.

The branches are given off on all sides, as a rule one from each joint; they are usually placed in a spiral line, however not in the whole length of the shoot, the angle of divergence is about  $\frac{1}{3}$  or  $\frac{1}{4}$ , the spiral turning to the right or to the left in different shoots (fig. 227). In a long branch the branches were arranged from the base in a spiral turning to the right with an angle of divergence of  $1/_3$ , then irregularly, after that in a spiral to the right with an angle of divergence of 1/3 and finally secundate. The ramification of the lateral branches is usually similar to that of the main branches. The first branches of the second order are frequently alternating to the right and to the left or irregularly arranged, and it is only at a higher level that the regular spiral arrangement commences. In the main branches this ramification may be repeated several times, but the branches become gradually feebler and the later branches have limited growth, are divaricate and more irregularly branched, often secundate, bearing only branches on the upper side (fig. 228). As will be seen, this description

agrees with that of KYLIN. Secundate pinnulæ are also mentioned and figured by HARVEY (Phyc. Brit. Pl. 129), but as many and as regularly arranged secundate pinnulæ as in HARVEY's figs. 2 and 3 I have never seen in the Danish specimens.

In the main branches dividing walls of the apical cell are inclined, and the axis is at first bent in zigzag but later it becomes straight. In the unbranched or feebly branched pinnulæ the dividing walls are transversal.

The cells contain a single nucleus in the young and the later age, and numerous long ribbon-like, more or less branched chromatophores.

Characteristic of the species is the great development of hyaline hairs at the tip of the branchlets, as already figured by KÜTZING and KYLIN. The hairs are rather

short  $(7-9 \mu \text{ thick}, 160-290 \mu \text{ long})$ . The pit connecting the hair with the bearing cell is very distinct. The hair-bearing cell cannot function as apical cell but it may produce a branch which sometimes grows out approximately in the same



Callithamnion Brodia: Parts of tetrasporiferous plant. 158:1. Callithamnion Brodia: Parts of male plant. A 77:1. B 220:1.

direction as the mother axis, the hair being pushed aside (fig. 225 C). In the observed cases the hair was pushed towards the dorsal side of the filament. The process may be repeated in the same filament.

The tetrasporangia are placed on the branches of higher order, principally on the upper side of the branchlets, on the first joint, on two or three consecutive ones or more irregularly. There are frequently two on the same joint and then the younger below the older or obliquely beside and below it (fig. 225). The undermost sporangium may be placed on the middle of the joint which may also be the case with a single sporangium (225 C). A seriate arrangement as regular as in HARVEY's figs. 3 and 4 is only met with exceptionally in the Danish specimens (fig. 225 *B*). The sporangia were 70—76  $\mu$  long, 61—65  $\mu$  broad; they are discharged through a transversal split above.

The antheridia are produced on the surface of long cushions on the upper side of the branchlets which are much divaricate in the male specimens. The cushions are composed of two or more small bushes on each joint fused with each other and with those of the neighbouring joints. The outer cells only of these bushes produce spermatia while the under cells remain sterile.

The procarps are placed on a branchbearing cell opposite to the branch. They have the same structure as in *Call. corymbosum*. In an unfertilised carpogonium the trichogyne was feebly swollen at the base (fig. 227). There are two nearly globular gonimoblasts and under each of them a smaller one which may produce carpospores as well developed as the large ones. The cell bearing the cystocarp is frequently shorter than the other cells in the same filament.

As pointed out by Nägeli (Morph. Ceram., 1861, p. 372), Call. Brodiati CROUAN (Alg. mar. du Finistère, no. 154, Florule du Finistère, p. 138) is not identical with HARVEY's and KÜTZING'S species. In the specimen of the Exsicc. I found the ramification generally pinnate in the pinnæ and the pinnulæ as well, the cells much shorter and thicker and hairs totally wanting. CROUAN's plant has been described as Maschalosporium gallicum (Call. gallicum Sauvageau, Alg. mar. Golf. Gascogne, Journ. de Botanique t. XI 1897, p. 63). It is probable that HARVEY's description included also this species (comp. Phyc. Brit. pl. 129 fig. 3-4), but it seems to have been worked out principally after specimens of the species mentioned here under HARVEY'S name. I have had no occasion to examine authentical specimens.



Callithamnion Brodiæi. Upper ends of female

plants; *A*, with fully developed, *B*, with young procarp. *a* auxiliary mother-cells; the first cell of the carpogonial branch is not visible. *A* 270:1. *B* 200:1.



Fig. 228. Callithamnion Brodiæi. Part of cystocarp-bearing plant. 70:1.

C. Brodiæi cannot be confounded with any of the species found at the Danish shores. C. corymbosum is the only species bearing equally numerous hairs but these hairs are much longer than in C. Brodiæi.

Localities. Kn: Nordostrev by Hirsholm, 7-9 meters depth, on Furcellaria fastigiata, July 1904; one specimen with cystocarps met with at the same place in August 1922 (C. A. Jørgensen).

# 3. Callithamnion tetragonum (With.) Ag.

C. A. Agardh, Spec. Alg. Vol. II sect. I 1828, p. 176; J. Agardh, 1851, p. 53; Harvey, Phyc. Brit. pl. 136, 1849; Kylin, 1907, p. 158.

Conferva tetragona Withering, Arrang. Brit. Pl., 3<sup>d</sup> edit. Vol. IV, 1796, p. 405.

Dorythamnion tetragonum Nägeli, 1861 p. 344-345.

Callithamnion brachiatum Bonnem., Harvey, Phyc. Brit. p. 137, 1849.

This species is here taken in a somewhat wider sense than generally accepted. The typical, first described *C. tetragonum* is characterized by its thick pinnulæ, having



Callithamnion tetragonum Ag. From Devonshire, ex herb. J. G. AGARDH. 47:1.

Fig. 230. Callithamnion tetragonum (f. brachiata). From Cherbourg. 47:1.

their greatest thickness above the base  $(80-140 \ \mu \ according$  to HAUCK, 75–100  $\mu$  after KYLIN), consisting of barrel-shaped cells and suddenly acuminate. In the very nearly related *C. brachiatum* the pinnulæ are thinner  $(40-80 \ \mu)$  and consist of cylindrical cells 2–3 times as long as broad. This form is, certainly rightly, regarded as a form of *C. tetragonum* by several authors (J. AGARDH, l. c.; HAUCK Meeresalg., p. 83; GRAN, Kristianiafjord, p. 26); it forms further a transition to *C. fruticulosum* Ag., as principally known from the Scandinavian coasts. J. AGARDH has already stated that the latter is related to *C. tetragonum*, and GRAN (l. c.) declares that the Norwegian specimens determined by him as *C. tetragonum*  $\beta$ , brachiatum, show much

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resemblance to C. fruticulosum. KYLIN (1907, pp. 154–162) points out the accordance in the morphological structure existing between these three forms which he considers as distinct species, and he further describes a new, fourth species, C. spiniferum characterized principally by thinner pinnulæ,  $25-40 \mu$  thick, and consisting of longer cells, 5–8 times as long as broad, while in C. fruticulosum the pinnulæ, according to KYLIN, are  $40-60 \mu$  thick and consist of cells 3-5 times as long as broad.

I cannot acknowledge the right of distinguishing these four forms as species, at all events not with the delimitation given by KYLIN. The specimens found at the



Fig. 231.

Callithamnion tetragonum var. divaricata. A, pinna. B, branch-system with tetrasporangia. C, branch with tetrasporangia and an arrested procarp p. A, B 70:1. C 200:1.

North coast of Sealand agree perfectly with J. AGARDH's description of C. fruticulosum and with specimens from AGARDH (from Kullaberg), and the dimensions of the cells in the pinnulæ correspond also with those attributed to this species by KYLIN, viz. 3-5,5 times as long as broad; but the thickness of the pinnulæ is the same as that attributed to C. spiniferum, viz. 23-42  $\mu$ . In specimens found in the Northern Kattegat, the pinnulæ are thicker and of a structure more resembling that of C. brachiatum, but in some of the specimens the pinnulæ were up to 123  $\mu$  thick and consisted of cells only 1,2-2,7 times as long as broad, thus resembling those of the typical C. tetragonum; the cells were, however, not barrel-shaped and the pinnulæ were thickest at the base. My investigations have led me to consider all these supposed species as forms of one species which must bear the name of the first described form, the typical, Atlantic *C. tetragonum* (With.). This apparently rather variable species may very likely comprise a number of elementary species, but as it is impossible for me to distinguish them, it is preferable to distinguish varieties or forms within the larger species.

The typical *C. tetragonum* has not been found at the shores of Denmark. But plants that must be regarded as forms of this species have been met with in two distinct groups of localities, the one in the neighbourhood of Frederikshavn and Hirsholmene in the Northern Kattegat, the other at the North coast of Sealand



Fig. 232.

Callithamnion tetragonum var. divaricata. From Hirsholmene. A, part of stem with branches. B, branch. C, branch with procarp; the two auxiliary mother-cells are visible. A 50:1. B 47:1. C 260:1.

from Gilleleje to a place a little north of Helsingør. As the specimens from these two groups of localities are different from each other, they may be mentioned particularly.

The species is easily distinguished from the other Danish species by its pointed pinnulæ which never terminate in a hair and by the cells being multinucleated to the top or with the exception of a few of the uppermost cells.

# Var. divaricata.

The species has been found several times in the neighbourhood of Frederikshavn and at Hirsholmene but only in a few and small specimens, 1,5–2,5 cm high. They pretty much agree with var. *brachiata* in the structure of the pinnulæ, but these are more divaricate than in that variety. The pinnulæ have their greatest thickness at the base and gradually taper upwards. Their greatest thickness is somewhat variable; it was greatest in a specimen met with in November in Busserev at Frederikshavn, viz.  $50-124 \mu$ , frequently over  $100 \mu$ . In small specimens found in the same locality in July it was only  $49-63 \mu$ . The length of the cells was in the first case 1,25-2,7, in the latter case 2,5-3 times the breadth, and similar dimensions of the pinnulæ were found in specimens from Marens Rev (January) and Hirsholmene (July). In the pinnæ with arrested growth, the last pinnulæ were more or less divaricate (figs. 231-232).

The tetrasporangia are placed on the inner side of the pinnæ, usually beside and at a lower level than the branches. Tetrasporiferous pinnæ with arrested growth may form corymbiform clusters. The sporangia are nearly globular,  $62-70 \mu$  long,  $51-59 \mu$  broad. In sporangiferous specimens, undeveloped procarps may be found in the same pinnæ as the sporangia (fig. 231 C).

Found with ripe tetrasporangia in July and November, with ripe cystocarps in July.

Localities. Nordostrev by Hirsholm, in Furcellaria, 7,5-9,5 m; Busserev and Marens Rev by Frederikshavn.

Var. fruticulosa J. Agardh.

Kolderup Rosenvinge 1920, p. 7.

Callithamnion fruticulosum J. Agardh, Symbolæ, Linnæa, 15. Bd. 1841, p. 46, Spec. gen. ord. Alg. II p. 56, 1851; Kylin, Algenfl., 1907, p. 154. Non Roth, Catalecta II, 1800, p. 183, nec Lyngbye, Hydr., 1819, p. 124.

Callithamnion Hookeri (Dillw.) b. Areschoug, Phyc. scand. 1850, p. 104.

Phlebothamnion fruticulosum Kützing, Tab. Phyc. 11, 1850, pl. 95.

Callithamnion Baileyi Harv., Ner. Bor. Amer. II. 1853, p. 231, pl. 35 B; Farlow Mar. Alg, N. Engl., 1881, p. 127, pl. XI, figs. 1-2.

Phlebothamnion Baileyi (Harv.) Kützing, Tab. phyc. 11, 1850, pl. 95. Callithamnion spiniferum Kylin, l. c. p. 159.

When J. AGARDH has named this plant C. fruticulosum, it might be observed that it is not identical with the plants which have formerly been designated by this name. J. AGARDH has himself identified ROTH'S species with C. versicolor Draparn., and C. fruticulosum Lyngbye is at all events also a different species. I do not doubt that our plant is identical with C. Baileyi or with one of the forms of this variable species of which HARVEY declares, l. c. p. 232 that "the most robust forms, with shortest joints, approach inconveniently near to C. tetragonum, from which species the more delicate ones appear widely different." In North American specimens from FARLOW and SAUNDERS I found cystocarps and antheridial-cushions resembling those in the European species.

As mentioned above, I cannot regard *C. spiniferum* as a species distinct from *C. fruticulosum*, the dimensions of the pinnulæ offering no distinctive characters. According to KYLIN (l. c. pp. 157-162), the dimensions of the gonimoblasts and the
tetrasporangia should in *C. spiniferum* be greater than in the last named species; in the Danish specimens, these organs reach the dimensions stated for *C. spiniferum*, the goni-

Fig. 233.

Callithamnion tetragonum var. fruticulosa. From Hellebæk. Upper part of sterile branch. The first branch of the second order is marked with  $\times$ . 200:1.

moblasts being  $130-227 \mu$  in diameter, and the sporangia being  $74-81 \mu$  long,  $46-61 \mu$  broad.

As stated by KYLIN, l. c., all the forms referred here to *C. tetragonum* agree with each other in branching and all morphological characters. Referring to KY-LIN's descriptions, I shall here describe the specimens occurring at the North coast of Sealand, all referable, in my opinion, to the variety that J. AGARDH designated by the name of *fruticulosum*.



Fig. 234. Callithamnion tetragonum var. fruticulosa. Part of stem showing cortication and adventitious branches. 50:1.

The plants reach a length of up to 7 cm; in aspect they resemble the typical *C. tetragonum* and have the same brownish red colour. The main branches have a pyramidal outline. The main axes are vigorous, straight and covered with a cortex of decurrent filaments, from which here and there adventitious shoots are given off without any distinct order; young and older shoots may arise intermingled with each

other. The branches of the main axes are spirally disposed with an angle of divergence of about 1/4 or between 1/3 and 1/4. The branches of the second and higher orders are arranged in a spiral as those of the first order, except the first 1—5 which are alternate, biseriate and arranged in a transversal plane. The ultimate short



Fig. 235.

Callithamnion tetragonum var. fruticulosa. A and B, upper ends of growing plants showing the nuclei. C, upper end of branchlet with arresting growth. D, part of stem cell with corticating filaments showing the nuclei. A, B, C 350:1. D 203:1.

axes (fig. 238). In such cases the 4th or 5th cell from the top usually contained more than one nucleus. In the decurrent filaments, the apical cell may contain numerous nuclei (fig. 235 D). The chromatophores are numerous, in the young cells they are rounded or oblong discs, in the older they are longer and irregularly bent.

The tetrasporangia are obovate,  $74-81 \mu$  long,  $46-61 \mu$  broad, placed on the inner face of the pinnæ, in their under part<sup>1</sup>, sometimes only on the undermost cell, in

<sup>1</sup> According to HARVEY, l. c. p. 232, pl. 35 fig. 5, C. Baileyi appears to differ from our plant in

branches bear only biseriate pinnulæ. A sympodial ramification does not occur. The branching designated with this term by Nä-GELI (1861, p. 305—306) is really monopodial, the end of the growing axes being only bent by the developing branches. For further details of the arrangement of the branches reference may be made to my above quoted paper (1920 p. 7).

The pinnulæ are all acuminate when their growth is arrested. Only exceptionally a feebly developed obtuse pinnula may be met with (fig. 234). The lower cells are 3— 5,5 (6) times as long as broad, usually 4—5 times as long. Hairs do not occur.

The older cells contain a great number of nuclei, but also the younger cells are polynucleate and this stage is not unfrequently primitive, the apical cell and the youngest segments containing each two nuclei (fig. 235). But in other cases the uppermost cells are uninucleate; this is particularly the case in the pinnulæ when the growth has arrested, but it is also frequently met with in growing

other cases on two or more consecutive cells. Most of the sporangia are placed on the branched part of the pinnæ, but they may also be placed on the unbranched parts (the pinnulæ). As the pinnæ are pinnate below with transverse branches the sporangia are usually placed beside a branch but at a lower level; but the sporangia may also be opposite to the branches (fig. 236). The sporangia are usually placed singly near the upper end of the cell, but a second, younger sporangium may be produced under the first one or in an oblique direction from it and



Fig. 236. Callithamnion tetragonum var. fruticulosa. Branches with tetrasporangia. A 150: 1. B c. 100: 1.

then sometimes under the branch given off from the same cell. In sporangiferous individuals procarps are frequently found; thus in a such specimen with nume-



Callithamnion tetragonum var. fruticulosa. Part of plant with antheridial clusters. 215 : 1.

rous sporangia a branch was met with bearing a great number of procarps above but sporangia below.

The antheridia are placed in hemispherical cushions, as described by NÄGELI for *C. tetragonum* (l. c. p. 345, fig. 30) and Ky-LIN for *C. fruticulosum* and *C. spiniferum* (l. c. pp. 155—161, figs. 32—33). Comp. our fig. 237. These cushions have the same position as the tetrasporangia; they are placed singly or two in the same cell. The antheridia are usually found on the same individuals as the procarps.

The procarps always arise in a branchbearing cell and in such position that the carpogonium is opposite to the branch, the

two auxiliar-mothercells lateral. The carpogonial branch is composed of 4 cells the two outermost of which are superposed while the first cells of the branch form a horizontal row. Spermatia were repeatedly found attached to the trichogyne, what

the sporangia being placed "near the middle of the ramuli"; in the quoted figure, the undermost cell in the pinnulæ bears no sporangium.

makes it probable that fertilisation really takes place. However, it must be said that trichogynes with attached spermatia but with undeveloped auxiliary mother-cells



Fig. 238.

Callithamnion tetragonum var. fruticulosa. Procarps. To the right in B the auxiliary mother-cell which supports the carpogonial branch. A, B 270:1. C 350:1.



Fig. 239. Callithamnion tetragonum var. fruticulosa. Ripe cystocarps. A 70:1. B 145:1. C 200:1.

though of rather advanced age were in some cases observed. (These observations are communicated here because sporangia frequently occur on the same plants as the

sexual organs). Each of the auxiliary cells produces a glomerulus which is ovoidglobular or a little irregular. Usually a smaller conical lobe is seen at the base of the glomerulus. As shown in fig. 239 *C* the glomerulus is supported by a large sterile cell, the "Centralzelle" of OLTMANNS, while the small lobe is given off from the stalk-cell of the auxiliary cell (the "Basalzelle" of OLTMANNS and KYLIN 1923). The conical body cannot therefore belong to the gonimoblast and it must be concluded that it is unable to produce normal carpospores. A similar smaller lobe developed under the primary glomerulus has first been mentioned by JANCZEWSKI (1877, p. 119) in *Call. tetricum* and later by OLTMANNS in *C. corymbosum* (1898, p. 118) and KYLIN (1907) in *C. fruticulosum, C. spiniferum* and *C. Brodiæi*, comp. above p. 316. In the cases described by JANCZEWSKI and OLTMANNS, however, the smaller lobe arises from the same cell, the central cell, which has produced the glomerulus and is therefore a part of the gonimoblast. — The cystocarp-bearing cells remain shorter than the sterile cells of the filaments.

This variety has been found growing on various Algæ, e. g. *Furcellaria* and *Cladophora rupestris*, in 1 to 8 meters depth, with sexual organs and ripe sporangia in May to September, with cystocarps in July to October.

Localities. Kn:  $6^{1}/_{2}$  miles S.W. by W.  $1/_{2}$  W. of Læsø Trindel light-ship, 8 m (C. A. J.) — Ke: Gilleleje; on the shore at Nakkehoved (?) (Lyngbye). — Su: off Ellekilde; Hellebæk; Blokhus Grund (Henn. Petersen).

### 4. Callithamnion corymbosum (Engl. Bot.) Lyngbye.

Lyngbye, 1819, p. 125, tab. 38 C; J. Agardh, 1851, p. 41; Harvey, Phyc. Brit. III, 1851, pl. 272; Thuret, Ét. phyc., 1878, p. 67, pll. 33—35; Reinke Algenfl. 1889, p. 24; Oltmanns, Bot. Zeit. 1898, p. 114, Taf. VI—VII; Kylin, 1907, p. 165; Kolderup Rosenvinge, 1911, p. 25; 1920, p. 25.

Conferva corymbosa Engl. Bot., pl. 2352, 1812.

Ceramium pedicellatum Lyngbye, Flora Dan. tab. 1596, 2, 1818.<sup>1</sup>

Phlebothamnion corymbosum Kützing, Spec. Alg. 1849, p. 657, Tab. phyc. XII Taf. 9.

Poecilothamnion corymbosum Nägeli, 1861, p. 360.

Callithamnion hiemale Kjellman in Kylin 1907, p. 170, ex parte.

Referring the reader, for the ramification, to the papers of Nägeli, Kylin and myself (1920), I shall only mention that the branches are usually arranged in a spiral with an angle of divergence varying between  $\frac{1}{5}$  and  $\frac{1}{3}$ , the spiral turning with equal

<sup>1</sup> In the herbarium of the Botanical Museum of Copenhagen a number of specimens of this species from Hofmansgave are to be found together with a leaf with drawings of the same species by LYNGBYE with the following remark in LYNGBYE's handwriting: *Ceramium roseum* Var.? Nov. 1815 Hofmansgave, and signed with the letters A—D. The three last of these figures have been reproduced in Fl. Dan. Tab. 1596, 2 (under the name *Ceramium pedicellatum*). Fig. A which represents the habit of the species in feeble magnification and shows the corymbous ramification is in Fl. Dan. replaced by another figure which agrees fairly well with the fig. 38 C 1 of LYNGBYE's Hydr. but does not give a good idea of the ramification of the species. Confusion with another species has perhaps taken place. The fig. C (the undermost, to the left) which shows antheridial bushes has also been rightly interpreted, for LYNGBYE has marked it: "C mas?". Fig. D shows the upper sporangium opened with a split in the original drawing, but that has not been reproduced in the engraving.

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Fig. 240. Callithamnion corymbosum. A, upper end of shoot. B, somewhat older cells. 210:1.

frequency to the right and to the left. The ramification of the branches begins from the very base but the first branches are not as a rule included in the spiral arrangement. Most frequently the first two or three branches are biseriate in a transverse plane. The ramification is often pseudodichomous (camptopodial Nägeli), in particular in the upper part of the plants, the branches reaching the same size as the mother axis and diverging almost equally with this from the original direction of the mother axis, for which reason it is often difficult to decide which of the rays is the main axis and which the branch. When the pseudodichotomous ramification is very pronounced, the greater sections of the frond may get a semicircular outline; when the main axes are more

vigorous than the others, the outline becomes pyramidal. In other cases the outline is more indistinct, the greater complexes of shoots being dissolved in smaller corymbous bunches. Very rarely two branches were found on the same joint; they were



Fig. 242. Callithamnion corymbosum. Lower part of older cell showing the nuclei, 200 : 1.

not opposite but diverging with an obtuse angle from one another (fig. 241).

The young cells contain a single nucleus; later on it divides and as a consequence of continued divisions the older cells contain a great number of nuclei equally distributed over the cell (fig. 242). They are distinctly visible in the figures of THURET (1878, pll. 33-35).

Hyaline hairs normally occur. They have been mentioned and partly figured by Kürzıng, Nägeli, Thuret, Kylin and myself

(1911). They are present in the whole season of vegetative development, but are wanting in winter (December, January). No specimens have been collected in February and March, but all the specimens collected in April to October were provided with hairs. Only in very rare cases were the specimens collected in summer devoid of hairs; thus, some large specimens from Herthas Flak in 20 to 23 meters depth had only very few



Fig. 241. Callithamnion corymbosum. A joint bears two branches (III) at the upper end. 200 : 1.



#### Fig. 243.

Callithamnion corymbosum.A, Upperend of branch with terminal hairs. B, the hairs are pushed aside by the sympodial development of the branch. Two hairs are shed but their basal pits are still visible. A 240 : 1. B 300 : 1. poorly developed hairs and some scars after hairs which had fallen off. Similar specimens were found in the harbour of Skagen in July, but the ends of the branches showed sympodial development and sometimes a pit in the end wall at the point where the hair had been inserted. The hairs are terminal on the branches the development of which is stopped by the formation of the hair, but the hair is often pushed aside by a lateral branch formed under it, and such a sympodial development may repeatedly occur on the same branch (fig. 243, comp. L. K. R. 1911, p. 212). Not rarely two hairs are to be found on the same terminal cell; the one is then terminal, the other lateral (comp. THURET 1878, pl. 33 and 35). The shoots in full



Callithamnion corymbosum. Upper end of shoot of plant collected in December; the young branches are hairless and incurved over the top. 270:1.

Fig. 245.

Callithamnion corymbosum. A, cortical filaments with adventitious shoots, B, part of plant with stoloniform filaments partly ending with hapters. B 50:1.

growth do not terminate with a hair but only the shoots with feebler or ceasing intensity of growth. In autumn the hairs are shed, and in the specimens found in December and January the hairless branches are curved in over the summit of the shoot (fig. 244).

The main axes increase gradually in thickness downwards and are in the lower part provided with a cortex of decurrent filaments. The cells issuing from the bases of the branches and growing in the outer wall of the joint cells of these filaments contain several nuclei. Small adventitious shoots may issue from them (fig. 245 A).

In specimens from the harbour of Kerteminde numerous free filaments were found issuing from the lower end of the cells of the crect filaments and growing out in a direction perpendicular to these filaments; they consisted of long cells and

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might attain a considerable length without branching, but on meeting a solid body they had fixed themselves to it and produced numerous branches partly



Fig. 246. Callithamnion corymbosum. Antheridial cushions. 260:1.

branch. When the production of antheridia is very abundant, they occupy not only the branchlets but also the mother axes. The cushions consist of much branched short branch-systems, the upper cells of which are the antheridia (spermatangia) (fig. 246).

With regard to the position and the development of the procarps and the cystocarps reference may be made to the quoted papers of THURET (1878, pl. 34 and 35), OLTMANNS (1898) and Kylin (1907, p. 166).

As mentioned by earlier observers, the tetrasporangia are seated on the inner side of the upper branchlets, on the lower joint, usually at its upper end. The first branch of the second order having a transversal position, the sporangium then forms a right angle with this branch. The sporangia are single or a younger sporangium appears under the first formed, sometimes in an oblique direction under it or nearly beside it (fig. 247 A). A third sporangium may rarely be found under the second. In rare cases the sporangium is inserted in the middle of the joint

adhering to the same body (fig. 245 B).

The antheridia always occur on particular male specimens. They form small, often hemispherical cushions on the upper branchlets; they are usually seated, in analogy with the sporangia, on the upper side of the lower joint of the branchlets, near its upper end, but, as shown by THURET, two or three cushions are frequently seated under one another and these may be fused together. The joint may thus be occupied in its whole length or nearly so by a long compound antheridial cushion, and the joint is then usually more or less recurved by epinastic growth and bears no vegetative



(fig. 247 B, C); in the case shown in fig. 247 C, a second sporangium is seated over the first formed. - As shown by THURET (1878, plate 35 fig. 14), the sporangia open by a transversal split near the upper end of the sporangium; the upper part of the wall then forms a lid fixed by a hinge. At the discharge, which was once

observed, the two upper spores first escaped almost simultaneously and shortly after a third. During the liberation, the spores changed form when squeezing through the narrow split and afterwards regained the globular form. A liberated spore was seen to move between some filaments of the same species, likewise changing form when squeezing through the narrow interstice between the filaments.

Germination of tetraspores and carpospores is easily realized in cultures, as shown by THURET (1878 p. 71, pl. 35 fig. 15), who obtained, however, only very young stages consisting of few cells. The seedlings in my cultures reached a greater size and began to branch (fig. 248). As mentioned by THURET,

the seedlings resulting from the two kinds of spores are alike. The germinating spore gives off two opposite germinating tubes, the one becoming the primary axis of the plant, the other growing out to a long articulate rhizine. The original spore-cell remains for a long time distinguishable by its greater thickness, at least in the cultures. The branching of the primary axis may begin immediately over it or at a higher level.

Antheridia have been met with in April to September, cystocarps in June to October, tetrasporangia in June to December and in January, but not in the spring. The cystocarp-bearing specimens are often smaller than the tetraspore-bearing ones. Sterile specimens are not rarely found in considerable number between the fertile ones, and they are then often larger than these. In the Smaaland Sea, in the Sound south of Hveen and in the Baltic Sea, thus in the innermost localities, only sterile specimens were found.

The species has been met with at all seasons; that it has not been observed in the months of February and March is certainly due to the fact that only very few collections have been made in these months. It can without doubt continue alive from one season to the next, but it can also accomplish its life-cycle during a short time, being thus ephemerous,



Callithamnion corymbosum. Sporelings from Frederikshavn. A, 3 weeks, B, C, 4 weeks old. 150 : 1.

and perhaps produce more than one generation in the season. The duration of life must at all events be short when it is epiphytical on Algæ or parts of Algæ which die in the autumn. It may be met with in well developed specimens at all seasons; it occurs, however, in the greatest quantity in summer and autumn, when it also attains its greatest development. Most of the specimens certainly die in the autumn. The specimens found in winter are not in growth and without hairs (fig. 244) but may still bear tetrasporangia. *Callithamnion hiemale* Kjellm., Kylin seems at least in part to be such a winter-form of *C. corymbosum*, for a specimen of the named species kindly sent me by dr. KyLIN agreed with my winter specimens of the latter by its structure and its corymbous ramification; the number of the nuclei could not, however, be ascertained in the dried state. A few hairs were still pre-

sent.<sup>1</sup> — The growth of the species apparently begins at the end of the winter. As the germination of the spores takes place immediately after the dissemination of the spores, it is probable, that the species usually passes through the winter as small plants having reached only a small size at the beginning of the winter. — It grows on stones, wood, leaves of *Zostera* and numerous Algæ as f. inst. *Furcellaria fastigiata*, *Ahnfeltia plicata*, *Fucus vesiculosus*, *Polysiphonia* spp., *Phyllophora* spp. and many others.

The species varies in the length of the cells and the different degree of contraction of the branches thereon dependent, apparently owing to the various conditions of the environment; further, as mentioned above, in the relation of the longitudinal growth of the branches to that of the mother axis. When the ramification is decidedly pseudodichotomous the outline of the sections of the frond becomes semicircular or nearly circular. The branches are then often more divaricate than usual, thus in the f. *intricata* Lyngbye (Hydr. p. 125), which occurs in sunny localities in shallow water.

The species is spread from the North Sea to the south end of the Sound and to the western part of the Baltic. In the North Sea it has only been met with in two localities very remote from land at greater depths (24,5-31 m) and further in the harbour of Thyborøn; in the Skagerak it has been collected in several places, mostly at small depths near land, and in the inner waters it is commonly spread from low-water mark to 20 meters depth (in the Limfjord only to 6 m). In the Sound south of Helsingør it does not occur at depths smaller than 9,5 m, and in the Smaaland Sea not at depths smaller than 4,5 m. It usually reaches only a length of 5 cm; it may, however, attain 7,5 cm (f. inst. in one of the innermost localities, south of Langeland at 11,5 meters depth) and specimens up to 9 cm high were found once, in Grenaa harbour.

Localities. NS: aF, Thyborøn beacon S.E. 1/2 E., 19,5 miles, 31 m 🔾 Aug.; ZQ jydske Rev, 24,5 m; harbour of Thyborøn. - Sk: YU, Roshage, Hanstholm, near land, 1-2 m; YM<sup>1</sup>, Bragerne; YN, within Bragerne; ZK, off Lønstrup; Lønstrup, near land, 1 m; Hirshals, mole and boulders near land; N.W. of Hirshals, 15 m; Skiveren, on wreck; north Side of Skagens Gren. - Lf: ZS, Kobberød; Ydre Røn by Lemvig; MC1; south side of Jegindø Tap, 6 m; east of Jegindø; MH, off Skrandrup, Thisted Bredning; Nykøbing (Th. Mortensen); Glyngøre; off Knudshoved, Fur; north coast of Fur; MK, Holmtunge Hage; LQ, Lendrup Røn; Løgstør Kanal; Løgstør; near Marbjerg Tange (Boye Petersen). - Kn: Harbour of Skagen; south of Fyrbakken, 4 m and south of Skagens Gren, 13-15 m; off Hulsig, 7,5 m (B. P.); Herthas Flak, 19 m; TV, Krageskovs Rev; various places around Hirsholmene; Frederikshavn, harbour and various places in the neighbourhood; BP, off Sæby, VT and TK near Nordre Rønner; north end of Nordre Rønner; NH, north of Læsø, 15 m, + in Sept.; Vesterø harbour, Østerø harbour; TP and ZA, Tønneberg Banke, about 16 m;  $6^{1/2}$  miles S.W. by W. 1/2 W. of Læsø Trindel light-ship, 8 m (C. A. J.). - Ke: FD, east of Læsø; VY, Fladen, 18 m, sterile in July; XA, S.E. of Kobbergrundene; east end of Anholt; 141/2 miles S.S.E. of Anholt Knob lightsh., 10 m, + Oct. (C. A. J.); Gilleleje. - Km: 6 miles S.S.W. 1/2 W. of Læsø Rende lightsh., 8 m (C. A. J.); 51/2 miles N. by E. 3/4 E. of Østre Flak lightsh., 9 m. (C. A. J); BO, Stensnæs; Asaa, mole; EZ, south of Læsø; ZC1, Kobbergrundene; BK, Tan-

<sup>1</sup> Dr. KYLIN has later arrived at the opinion that *C. hiemale* is a winter-form of *C. Furcellariæ* (Botan. Notiser 1916, p. 65), as he has found specimens with lobed gonimoblasts. It appears therefore that two species have been confounded under this name.

j,

gen; NC, east of Tangen. - Ks: Pakhusbugt, Anholt, 19 m; Grenaa harbour; NB, Havknudeflak; MZ, north of Hjelm; D, north of Grønne Revle; RL; EH and NL, off Lynæs, Isefjord. - Sa: BF, off Sletterhage; Kalø Rev; Aarhus; PC, between Sejerø and Ordrups Næs; PK, Norsminde Flak; YV, east of Samsø, 15 m (+ and 3 in June); MX, at Tunø Rev; BC, off Hov Røn; BB, Søby Rev; aV, east of Endelave; DK, Bolsaxen; MQ, Paludans Flak; entrance to Korshavn; north coast of Æbelø; Hofmansgave (Lyngbye, Hofman Bang, J. Vahl, C. Rosenberg). - Lb: Horsens Fjord west of Alderø; AX, Bjørnsknude; FZ, Kasser Odde; Fænø Sund; cZ, Knudshoved Grund; Aarøsund (Reinke, !); CD, Helnæshoved Flak; Sønderborg. - Sf: CC, south side of Hornenæs; banks off Nakkebølle Fjord; UX and UV, north of Ærø; CV, Billes Grunde; BX, Svendborgsund; Svendborg. - Sb: South side of Refsnæs; MN, north of Asnæs; GU, S.W. of Asnæs; AG, Romsø; Reersø; GQ, west side of Slettings Grund; Kerteminde; Korsør; GY, west of Gjellegrund; Z, off Skagbo Huse; NS, BS near Nyborg; GZ, north of Egholm; Lohals harbour, near low-water mark; Snøde Rev, west of Langeland, 4 m, st.; T, Staalgrund, 9,5 m, 9; LB, Langelandsbelt, 17 m, Q. - Sm: CK, 9,5 m; CQ, 4,5 m, st. - Su: Hellebæk (Børgesen, !); north of Helsingør; PZ, east of Hveen, 10-19 m, 9; TF<sup>1</sup>, Staffans Flak, 11-13 m, st.; RH, Knollen, 9,5 m, st. - Bw: Flensborg Fjord (Suhr, Hansen): Egernsund, Graasten; cX, off the South end of Kobbel Skov; bZ, south of Sønderborg; DV, south of Marstal 9,5-11 m, st; LC, south of Gulstav, 11,3 m, st; KZ, off Kramnisse, 4,5 m, st.

### 5. Callithamnion roseum Harvey.

Harvey in Hooker, The English Flora, Vol. V, part I. 1833, p. 341; Manual Brit. Alg. 1841, p. 106; Phycol. Brit. pl. 230, 1849; Wyatt, Algæ Danmonienses No. 44. J. Agardh, 1851, p. 36; Bornet in Børgesen, Mar. Alg. Fær. 1902, p. 377; Le Jolis, Alg. mar. de Cherbourg, no. 162; Kolderup Rosenvinge 1920, p. 44.

Phlebothamnion roseum Kützing, Tab. phyc. Vol. XI, tab. 97, 1861. Callithamnion byssoides K. Rosenvinge, 1911, p. 209.

This species grows in certain localities in the harbour of Frederikshavn where it has been met with repeatedly during the last 27 years. Otherwise it is seldom found in the Danish waters. The Danish specimens agree with the species as described by HARVEY and as understood in the above citations. They are up to 10 cm high.

The filaments are branched on all sides, sometimes, however, the branches are alternate biseriate, in particular in the undermost part of the upper branches, and then usually placed in a transversal plane, as pointed out by BORNET (l. c.). The main axes are distinct, scarcely bent in zigzag. When the branching is regular and the plant is in active growth the segments are cut off by inclined walls. The young segments are only a little longer than broad (fig. 249). The branches are never branched from the base. The number of joints below the first branch varies from 2 to many, at least 25; as a rule, it is greatest at the base of the older branches.



#### Fig. 249.

*Callithamnion roseum*. Upper ends of shoots. In that on the left and in the middlemost the branches are arranged in a spiral, in the shoot on the right they are biseriate. 290:1. A number of branches remain unbranched, though consisting of a rather large number of cells; such branches occur frequently at the base of the longer axes but also near the top (fig. 250). When the ramification has begun, it usually continues uninterrupted, each joint bearing a branch. It happens, however, that one or two consecutive branchless articles may occur here and there, in particular in the lowermost part of the main axis and the branches. The branches of the long shoots are always arranged in a spiral, at all events in the upper part of the shoots, and here



Fig. 250. Callithamnion roseum. A, upper end of long shoot. B, shoot with tetrasporangia. 70:1.

the angle of divergence is usually 1/4; the arrangement of the lowermost branches, however, is irregular or alternate biseriate. (Comp. L. K. R. 1920). It very rarely happens that one joint bears two branches. The filaments are  $10,5-14 \mu$  broad right under the apical cell. They are not usually terminated by a hair, such organs may, however, occur sometimes (fig. 251, comp. L. K. R. 1911 p. 209); the hairs are rather short; they are a little thinner than the end of the filament, about 7  $\mu$  thick.

The cells contain one nucleus and numerous irregular lengthened chromatophores; numerous starch grains may occur (fig. 252).

The lower part of the principal filaments is corticated with descending filaments

given off from the lowermost cell of the branches, sometimes also from the second and following cells. They are frequently formed in a number of three from the basal

D Fig. 251.

Callithamnion roseum. A-C, development of the hairs. D, Fully developed hair pushed aside by a branch from the subterminal cell. A-C 700:1. D 300:1.

cell; they grow in the outer membrane of the filaments but become partly free at the base of the principal axis, here forming free, pluricellular, branched filaments which fix the plant to the substratum. The cortical layer may be so much developed that the cells of the filament are scarcely distinguishable. Adventitious shoots do not occur or only exceptionally.

The tetrasporangia are usually placed in a row on the upper (inner) side of the branches of the last order. The tetraspore-bearing branchlets are thus,

as a rule, unbranched, but fertile branchlets more or less branched above not unfrequently occur. The tetrasporangia-bearing branchlets are frequently alternate bi-

seriate. The sporangia usually form a short row of 1-4 or 5 on the lowermost cells, one on each cell (figs. 250 B, 254, comp. HARVEY, Phyc. Brit. l. c. fig. 2-3), but the row is frequently interrupted, by single cells bearing no sporangium. Sometimes, the undermost articles are bare, and the formation of sporangia begins only at a higher level. The sporangia placed at some distance from the base are not always situated on the upper side but frequently on the flanks or even on the outer (under) side of the branch

(fig. 254). The number of sporangia on a branch is often only 1 or 2. Cells bearing more than one sporangium have never been met with. The ripe sporangia are (60-)

Callithamnion roseum. Part of stem with corticating filaments. 50:1.

 $70-80 (-84) \mu$  long,  $45-55 (-70) \mu$  broad. Once I found an unusually large sporangium measuring  $98 \times 74 \mu$ . The sporangia open by a transversal slit above.

D. K. D. Vidensk. Selsk. Skr., 7. Række, naturvidensk. og mathem. Afd. VII. 3.

Fig. 252 Callithannion roseum. Part of cell with chromatophores and Floridean starch.





Callithamnion roseum. A, sporangia-bearing branch. B, sporangia situated on the outer side of the branch. A, 52:1. B, 80:1.

two, one over the other. Sometimes, the undermost cell or cells bear no antheridial clusters, the formation of these beginning only at a higher level, or the row is interrupted by joints bearing no antheridial bush. The branchlets bearing these organs are usually unbranched, but it occurs sometimes that they are branched above and the case may also be met with that a cell of a branchlet bears a branchlet and an antheridial bush as well (fig. 255 C). The main axis of the antheridial cluster consists of five or six cells, which are usually shorter than their breadth. It is slightly curved towards the top of the branch and bears a number of

Fig. 255. Callithamnion roseum. Antheridial clusters. A 205:1. B, C 560:1.

The antheridial clusters have a similar position to that of the sporangia, namely in a row of 1 to 6 on the upper side of the pinnulæ, usually one on each cell, rarely

> Fig. 256. Callithamnion roseum. Procarp before fertilisation. Only one auxiliary mother-cell is present, a<sup>1</sup>, situated behind the carpogonial branch. 350 : 1.

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Fig. 257.

Callithannion roseum. Procarps before and after fertilisation.  $a^1$  and  $a^2$  auxiliary mother-cells, or in D and E auxiliary cells.  $a^1$  that from which the carpogonial branch is given off. 1, 2, 3, c, the cells of the carpogonial branch. In A  $a^2$  is wanting. In C fertilisation has taken place; s sporogenous cell before fusion with the auxiliary cell; under it the rest of the carpogonium. In D and E the auxiliary cells have been cut off, except  $a^2$  in D; b the stalk cells of the auxiliary cells. The three cells under  $a^1$  seem to be the young gonimoblast. B 270:1, the others 350:1.

short branches principally on its convex side, but on the flanks and the upper side too, consisting of one or few cells and producing numerous antheridia which organs may also project directly from the cells of the main axis.

The procarps are nearly opposite to the branch projecting from the same cell.

The auxiliary mother-cell  $(a^1)$  from which the carpogonial branch is produced is situated very near the branch, the other one  $(a^2)$  is somewhat removed from its other side (fig. 257). The carpogonial branch consists of four cells, the second of which is situated obliquely over the first, the carpogonium exactly over the third (fig. 257). The one auxiliary mother-cell  $(a^2)$  may sometimes be wanting (fig. 256). The cystocarps are composed of two ovate gonimoblasts; their outline may be more or less irre-



Fig. 258. Callithamnion roseum. Cystocarps, A young, B almost ripe. A 260 : 1. B 150 : 1.

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gular, but not lobed. A few gonimoblasts on the same specimens were, however, more irregular and lobed, much as in *C. Furcellariæ*. A little special lobe is developed at the base of the gonimoblast, as in other species (fig. 258). In Phyc. Brit. pl. 230 fig. 5 HARVEY figures a cystocarp consisting of a small number of cells; perhaps it represents a young stage. I have not seen anything corresponding to the 'cluster of favellæ' figured in Harvey's fig. 4. The vegetative cells in the neighbourhood of the cystocarps usually produce rudimentary or more developed decurrent filaments



Fig. 259. Callithamnion\_troseum. Sporelings found on a tetraspore-bearing specimen of C. roseum. 204 : 1.

which undoubtedly serve to strengthen the parts of the filaments bearing these heavy organs (fig. 258 B).

On a tetraspore-bearing plant were found a number of sporelings apparently of the same species. Some of them were unbranched, others were branched, the ramification being irregular, alternate or secund.

The species is nearly related to C. Furcellariæ from which it differs in particular by its robuster filaments, by the principal axes being corticated in their lower part, and by the ovate, not lobed gonimoblasts.

The above description is founded on numerous living and preserved specimens from Frederikshavn. Elsewhere the species has only been met with in two other places in a sterile state.

The basal part of the plants is usually enveloped by dense masses of detritus. In one case, the lowermost part of the main axis had no cortex while the next following part had a well developed cortex. The species has been observed with sexual organs and with ripe cystocarps and tetrasporangia in the months of July and

August, the only months in which it has been collected at Frederikshavn. In this locality it has been met with only in the harbour from low-water mark to about one meter's depth. In the Smaaland Sea it has been found in 11,5 meters' depth.

Localities. Lf: Fuur "apportavit Kjølbye", Herb. LYNGBYE, determined by Lyngbye as *C. ro*seum. A specimen from Limfjorden communicated by HORNEMANN to Lyngbye in the same year (1826) probably originates from the same locality. All the specimens are well developed but sterile. — Kn: Frederikshavn, in the harbour for boats at the end of the north mole (1891—1923), on the head of the northern transverse mole and at the harbour of the pilots. Vesterø Havn, Læsø. — Sm: (?) Agersøsund, 11,5 m, sterile.

### 6. Callithamnion Furcellariæ J. Agardh.

J. Agardh, 1851, p. 57; Kylin 1907, p. 167; Kolderup Rosenvinge 1920, p. 49; Kylin 1923, p. 56. Callithamnion byssoides Areschoug, 1850, p. 107, Tab. V, B; Svedelius, Östersj. hafsalgfl., 1901, p. 126. Callithamnion hiemale Kjellm., Kylin, 1907, p. 170, teste Kylin, Botan. Notiser 1916, p. 65, ex parte.<sup>1</sup>

<sup>1</sup> As mentioned above, p. 330, a specimen of *C. hiemale* communicated to me by prof. KYLIN has turned out to be a *C. corymbosum*; but as the said author has found lobed gonimoblasts in other specimens, it seems that two species have been confounded under the name of *C. hiemale* Kjellm.

The Alga here treated has been mentioned for a long time in my annotations under the name of *Call. byssoides*. As, however, it is doubtful whether it is warranted to refer it to the species of ARNOTT and HARVEY and as the limitation of this species in regard to related forms is uncertain, I prefer to give to the species of the Danish waters the name of *C. Furcellariæ*, because it is at all events identical with this species of AGARDH. It must then be left undecided whether it can be identified

with the British species wholly or in part; I must content myself with referring to SCHMITZ's remarks on the synonymy of *C. byssoides* and related forms in his paper: Die Gattung Microthamnion in Ber. d. deut. bot. Ges. 1893 pp. 280 and 283.

The species occurs in all the Danish waters; it usually reaches only a length of 2 cm or a little more, in the inner waters Sf and Sb, however, it becomes 3 cm and at Bornholm up to 4 cm high.

The ramification has been treated at length by KYLIN (1907, p. 167) and by me (1920, p. 49). It is less regular than in the other Danish species. The branches are, however,



Callithamnion Furcellariæ. Upper end of plant from Fænø Sund, with irregularly arranged branches and dispores. 70:1. Fig. 261. Callithamnion Furcellariæ. Upper end of plant from Bornholm, with biseriate branches. 270 : 1.

usually arranged in a spiral, but in several shoots the branches were irregularly arranged or more rarely biseriate (specimens from Bornholm). When the branches are arranged in a spiral, the angle of divergence is more variable than in the other species; the angle of divergence varied in the examined shoots from 67° to 131°. Not rarely did the direction of the spiral change in the same shoot. The branches are usually branched from the base, the first joint normally bearing a branch; but it happens now and then that the first joint is branchless, and in specimens from Bornholm several joints at the base of the branches were branchless. The spiral arrangement as a rule begins at a certain distance from the base, the first branches being irregularly arranged, sometimes, however, partly biseriate in a transverse or oblique plane. In several cases two branches of unequal size were found inserted



Fig. 262.

Callithamnion Furcellariæ. Bases of plants with intramatrical and extramatrical descending filaments. A 45:1. B 95:1.







on the same joint, diverging from one another at an angle of a little over or a little under  $90^{\circ}$ ; the larger one entered into the spiral. For more details see my paper (1920 pp. 49-58).

The principal axes are distinct and straight or only a little bent in zigzag. The ramification is thus distinctly monopodial but sometimes it may be somewhat corymbose, thus reminding of that of C. corymbosum. The length of the cells in proportion to the breadth is rather variable but usually considerable, varying from 4 to 12, rarely up to 17, but in the lower part of the main axis the cells are shorter.

In the lower part of the principal shoot single descending filaments occur, being partly intramatrical, partly extramatrical, but in the first case not forming a continuous cortical layer. The intramatrical ones may be free before reaching the base (fig. 262). Moreover, free horizontal shoots arise from the lowermost part of the principal axes, usually given off from the lower end of the cells. They have the character of rhizomes producing new erect filaments. Fig. 263 shows such much-branched rhizomes growing in a bow towards the sub-

stratum. In the seedlings, too, such horizontal filaments are to be found (fig. 271).

The filaments as a rule terminate without hyaline hairs. This character is so constant that it can be used to distinguish this species from *Call*. corymbosum. It must, however, be admitted that hairs may occur in rare cases in genuine specimens of C. Furcellariæ (YV, Hatterbarn, Sa (Fig. 266); D, Ks and UV, Sf). The hairs were much less numerous and feebler developed than in C. corymbosum, only  $12-140 \mu$  long and  $3,5 \mu$  broad in no. 7380 (YV). The specimens in question were collected in May to June in depths of 11-15 meters.

The cells always contain a single

0 G

Fig. 265. Callithamnion Furcellariæ. Tetrasporangia. A, showing their arrangement, plant from northern Kattegat (TP). B-G showing the varying arrangement of the spores in the sporangium. A 160:1. B-G 220:1.

nucleus and numerous long, narrow, more or less curved chromatophores (fig. 264).

In specimens conserved in alcohol curious fusions between cells in the older parts of the plants were observed (fig. 264). The transverse wall was dissolved to a greater extent in the periphery and the two cells thus connected by a broad bridge of protoplasma, much broader than the central pit connecting the two cells. This fusion is not followed by any formation of pit-membrane and may be compared with the cell-fusions by the *Corallinaceæ* and *Squamariaceæ*, but they take place between cells which were before-hand connected by a pit. The process is not accompanied by a migration of nuclei; the two cells fusing with each other contain each one central nucleus like the other cells.

The sporangia are borne on the inner side of the branches of the last or penultimate order. They are 4-parted or 2-parted, most frequently the first, but there is



Callithamnion Furcellariæ. Part of plant with disporangia. From YV. 200 : 1.

always one sort of sporangia only on the same plant. They form a short row on the inner side of the branches, frequently in a number of 3 or 4, but sometimes there is only one, on the first joint. When the number is greater, they are not always all placed on the inner side but some of them on the flanks of the branches (fig. 265). There is usually one sporangium only on each joint but a young sporangium may sometimes be found under the normal one, more rarely over it. Such small, incompletely developed sporangia were met with in plants with four-parted and with two-parted sporangia as well, most frequently in the latter. The sporangiabearing branches may be simple but are frequently branched and the branches then issue over the sporangiabearing part (fig. 266). It is very rare to find a cell bearing at the same time a sporangium and a branch (fig. 273).

The sporangia are ovate or obovate or broadly ellipsoid. The tetrasporangia are tetrahedrically divided, but the spores are sometimes so arranged that the sporangia seem to have been cruciately divided (fig. 265), a fact to which HAUCK has already paid attention in the species

mentioned by him under the name of *C. byssoides* (Österr. bot. Zeitschr. 1878 p. 288, Taf. 3 Fig. 9). The tetrasporangia are (44-) 53-79  $\mu$  long, 33-51  $\mu$  broad. When the specimens from the waters within Skagen only are taken into account, the size is a little smaller, viz. (44-) 53-65  $(-67) \mu$  long, 33-42  $\mu$  broad, which quite agrees with the dimensions stated by KYLIN. The specimens from the Skagerak, some of which were not with certainty referable to this species, had larger sporangia, 66-79  $\mu$  long, (38-) 42-53  $\mu$  broad.

The disporangia are of the same size as the tetrasporangia, or, when only the specimens within Skagen are taken into account, generally larger than the tetrasporangia, viz.  $56-78\mu$  long,  $43-65\mu$  broad. The size was rather variable in specimens from different localities. Thus in specimens from Fænø Sund gathered in June the disporangia were 56-60  $\mu$  long, 43-47  $\mu$  broad, while in specimens from a locality north of Ærø gathered in May, they were  $67-78\,\mu$ long, 53–63  $\mu$  broad. The disporangia were formerly mentioned by KYLIN (1907, p. 169) who raises the question whether they might possibly be young stages of tetrasporangia. He arrives at the conclusion that they are fully developed, partly on account of the



Fig. 267. Callithanmion Furcellariæ. Disporangia. A young, B ripe, C emptied. A, B 270:1. C 195:1.

fact that he found some of them emptied, which conclusion I can fully confirm. The disporangia-bearing specimens in all other respects fully agree with the



Fig. 268. Callithamnion Furcellariæ, A, antheridial clusters. B, cystocarps. From Tønneberg Banke. A 270:1. B 195:1.

D. K. D. Vidensk. Selsk. Skr., 7. Række, naturvidensk. og mathem. Afd. VII. 3.

tetrasporangia-bearing ones so there seems to be no sufficient reason to consider them as a special variety. They occur more rarely than the others; in Fænø Sund both kinds of individuals have been met with. The disporangia are divided by a horizontal wall on each side of which a large nucleus is situated. A finer cytological investigation of the disporangia is much needed.

Both kinds of 44



Fig. 269.

all sides of the cluster and by being "very elongated". — According to KÜTZING (Tab. phyc. Vol. 12 pl. 8), the antheridial clusters of *C. byssoides* are, at any rate in great part, axillary. The species of KÜTZING seems, however, to be very different not only from our species but also from HARvEY's by its much corticated

main axes. - The antheri-

dial clusters of C. byssoides

Börgs. from the Danish

Callithamnion Furcellariæ. Procarps. In A  $a^1$  and  $a^a$  the two auxiliary mother-cells; 1, 2, 3, c, the cells of the carpogonial filament. The lowermost trichogyne was very long. B-D, the auxiliary mother-cells  $a^a$  is wanting. A 350:1. B 270:1.

sporangia open by a transversal slit in the upper part of the sporangium. The disporangia have been met with in May to July, the tetrasporangia in June to October.

The antheridial clusters have been described and figured by KYLIN (1907, p. 169, fig. 35 b). They are usually arranged in a row on the upper side of the upper pinnulæ, often on the lowermost 4-6 joints, but they may also be borne on branches of penultimate order. On each joint one to three clusters are to be found. Even when seated very densely they are never fused together as in certain other species. The clusters consist in a usually somewhat curved axis composed of 3 or 4 cells which are almost isodiametrical and bear each a number of antheridia mostly on the convex side turning downwards. The antheridia are 7-7,5  $\mu$  long, 4,5-5  $\mu$  broad. They were met with in July and September.

Buffham has described and figured the antheridial clusters in *Call. byssoideum* (1884, p. 341, pl. X figs. 4, 5); they agree with those of *C. Furcellariæ* by the position and the structure of the axes, but they seem to differ, according to BATTERS, by the antheridia being developed equally on

Fig. 270.

Callithamnion Furcellariæ. Ripe cystocarps. From Hirsholm. 200:1.

West Indies (F. BØBGESEN, Mar. Alg. Dan. W. Ind. 1917 (Dansk Bot. Ark. III, p. 218, Fig. 207) are also different, being cushions consisting "of a system of short (branched) branchlets in which the uppermost cells are the antheridia". They may some-

times occupy nearly the whole upper side of the cell of the branch. — The quoted differences in the structure of the antheridial clusters of the various plants referred to C. by solides suggest that different species have been confounded under this name.

The carpogonial filaments are borne on the upper end of joints bearing a branch on the opposite side. They are, as in the other species, composed of four cells arranged in a zigzag line. There are usually two auxiliary mother cells, but sometimes

there is only one,  $a_1$ , from which the carpogonial branch is given off, while  $a_2$ is wanting (fig. 269). The growth of the procarp-bearing cell is arrested during the development of the cystocarp and this cell is therefore much shorter than the other cells in the filament, when the cystocarp reaches its definite size, but it has often more protoplasmic contents. The fertilisation and the development of the gonimoblast has quite recently been described by Kylin (1923 p. 56) and found to be as in C. corymbosum as described by OLTMANNS. The gonimoblasts are lobed; the lobes are at first cylindrical, then conical (fig. 268), and finally rounded, ovate (fig. 270). At maturity there is usually a longer end-lobe and a shorter side-lobe, both issuing from a large cell, and sometimes furthermore a small supplementary lobe derived, as shown by KYLIN, from the auxiliary cell. In some cases the lateral lobe is not developed, and the gonimoblast is then much like that of *C. roseum*. The procarps were met with in June to September, the cystocarps in July to October.



Callithamnion Farcellariæ. Two sporelings from sown tetraspores, 4 weeks old. 47:1.

Tetraspores sown in July at Frederikshavn immediately germinated. 4 days later the sporelings were partly unbranched, about 10- to 13-celled, partly more or less branched. After four weeks they had grown much longer and variously branched but sterile (fig. 271). Filaments having the character of rhizomes were frequently given off from the basiscopic end of the cells, and these rhizomes produced erect filaments. In fig. 271 to the right one rhizome is given off from the basiscopic end, another from the acroscopic end of the same cell, but this cell is perhaps the original spore cell.

C. Furcellariæ has been met with in the months of May to October. The spores produced in summer and autumn are able to germinate immediately and give rise

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to plants which in part probably only reach a small size before winter. It must be supposed that the plants die in autumn or winter, entirely or with the exception of



Fig. 272. Callithamnion Furcellariæ. From YV, June. Part of plant with disporangia. Above a procarp. 70:1.

the basal portion which may survive the winter. New erect shoots may then grow out in spring from the basal remains of the erect shoots from the foregoing year (fig. 263 *B*). The species occurs in all the Danish waters except the North Sea where hitherto it has not been met with, and it has been found in depths from 7,5 to 24,5 meters, rarely in slighter depths. It grows on various Algæ e. g. *Furcellaria* and *Polysiphonia elongata*, further on *Zostera*, *Flustra foliacea* etc. The three kinds of organs of reproduction occur in different individuals. Once only a disporangium-bearing individual was found bearing at the same time some few procarps (fig. 272). A general difference in size of the three kinds of individuals as that stated by ARESCHOUG (1850, p. 107), could not be ascertained. As a rule the plants are less branched in the inner Danish waters with feebler salinity, which

is in accordance with the observations of KYLIN at the west coast of Sweden. But, with decreasing salinity the size of the plants rather increases, for while in the Skagerak and Kattegat it reaches only a little over 2 cm, it is up to 3 and 4 cm in Store Belt and the Baltic Sea, greatest near Bornholm. Specimens with procarps and cystocarps were frequently met with in the Kattegat together

with sporangia-bearing ones, but in the inner waters south of the Samsø area sex organs were not found, while sporangia were frequently present. The sporangia were in most cases four-parted; disporangia have only been recorded from three localities in Sa, Lb and Sf.

Some specimens from Skagerak are dubious. That is particularly the case with a specimen from Hirshals (no. 7077, Hirshals lighthouse in S.E.,  $2^{1/2}$  miles), differing by the cells not quite young containing more than one nucleus; in other respects it agrees with *C. Furcellariæ*, but fully developed cystocarps were





not present. The plant might possibly be of hybrid origin. The number of nuclei in the cells is otherwise, according to my experience, a very constant character. Other specimens were, as mentioned above, different in having bigger sporangia, up to  $79 \mu \log$ , so

in specimens from SY, north of Løkken. These specimens were more vigorous than the typical *C. Furcellariæ* and partly showed another arrangement of the tetrasporangia, these being partly terminal on short branchlets (fig. 273). It might further be mentioned that a small specimen with unripe round, not lobed gonimoblasts but otherwise agreeing with *C. Furcellariæ* was found on Herthas Flak in the Northern Kattegat. Typical specimens of the same species have repeatedly been found in the same place.

Localities. Sk: SY, north of Løkken, 1 mile  $(+ \bigcirc 8)^1$  (aberrant); ZK<sup>12</sup> off Lønstrup, 8,5 m (+8); Hirshals light-house in S.E.  $2^{1/2}$  miles 13 m (+98), aberrant); XO, Møllegrund off Hirshals 11-15 m (+ 8). - Lf: Oddesund, 6,5 m. - Kn: FG and XJ, Herthas Flak, 19-22,5 m ( $3 \bigcirc +7$ ); ibid. F. Børgesen (+ 9); fE, Krageskovs Rev; Nordostrev at Hirsholm, 7,5-9,5 m ( $3^{\circ}$   $\bigcirc$  + 7); harbour of Frederikshavn  $(+\bigcirc 7)$ : TP and TO, Tønneberg Banke, 16–18 m  $(5\bigcirc +9)$ : fG, 3 miles W. of Læsø Trindel light-ship, 15 m (O + 10); TR, near Trindelen, 23,5 m (+ 9). - Ke: VZ, Groves Flak, 24,5 m; Groves Flak, F. Børgs.  $(\bigcirc +9)$ ; ZF, near Fladens light-ship, 22,5 m (+7); 1 mile W. by N. of Fladens light-ship, 17 m (+ · 10). - Km: VN, near the entrance to Randers Fjord. - Ks: RL, near Ostindiefarer Grund, 15 m ( $3^{\circ} \bigcirc + 7$ ); D, near Grønne Revle, 11,3 m ( $\bigcirc 7$ ); aU, Lumbsaas church in S. 32° W., 2 miles (O, sporg. 8). - Sa: YV, near Hatterbarn, 15 m (9 2s 6); AO, Endelaves Sydostflak; GC, north of Fyn, 13 m. - Lb: Fænø Sund (2s + 6); CF, west of Lyø, 15 m; DX, Vodrups Flak, 13 m (sporg. 5). - Sf: CZ, south side of Hornenæs, 9,5-15 m (+ 5); UX, at the North end of Ærø, 9,5 m; UV north of Ærø, 13 m (2s 5). - Sb: cN, S.W. of Musholm, 18 m (2s 6); AF, Møllegrund, 7,5 m; DN, Vengeance Grund, 12 m (sporg. 5); LH, off Bøstrup, Langeland. - Su: HK off the N.W. end of Hveen, 9,5-21 m; QC, east side of Saltholms Flak. - Bw: bV, N.E. of Kobbel Skov (sp. 6); Middelgrund south of Als, 13 m (2s 6); bY, off Sønderskov, Als; cG, Trindelen, West side of Kegnæs; cF, south of Kegnæs light-house; LE, North Side of Vejsnæs Flak, 9,5 m. - Bm: ON, off Køge Søhuse, 6,5 m; QS, north of Møens Klint, 20,7 m (+7); VG, north of Møens Klint, 17 m; 7 miles N.E. 1/2 W. of Hestehoved light-house, south of Møen, 11-13 m (st. 6) (C. A. J.). - Bb: 8 miles S. <sup>1</sup>/<sub>2</sub> E. of Rønne, 11-19 m, (st. 6) (C. A. J.); SL, off Allinge, 5,5-11,3 m (+ 8); 3 miles S.S.E. of Nexø, 21 m (st. 6) (C. A. J.); YD, near Salthammer Rev 19 m; YC near Salthammer Rev 24,5 m (+7); 7 miles S.E. <sup>3</sup>/<sub>4</sub> S. of Adler Grund light-ship, 20 m (st. 6) (C. A. J.).

# 7. Callithamnion sp.

In October 1922 I found a small specimen of a *Callithamnion* growing on *Desmarestia aculeata* dredged in a depth of 30 meters at Fladen in the eastern Kattegat. As this specimen, which is only 3 mm high, cannot be referred with certainty to any known species, it is described here in the hope that it may later be identified. The branching is strictly alternate, biseriate or pectinate, all the branches falling in the same plane. The branches of the main axis (stem) are regularly distichous from the base, and the ramification of the main branches is the same, with the exception that the two or three first branches of the second order are seriate on the upper side of the branch, and in the lowermost main branches the first 1 to 4 joints bear no branches at all. In the branches on the upper part of the plant the secund branching of the branches is very manifest, in particular in the branches with limited growth in which the number of pinnulæ arranged in a row on the upper side of the pinnulæ gives the

<sup>1</sup> + designates tetrasporangia, 2s disporangia, sp young sporangia,  $\mathcal{D}$  procarps,  $\bigcirc$  cystocarps, the number at last the number of the month.

plant a peculiar appearance reminding one of the Antithamnia. The main axis is distinct, increasing gradually in thickness downwards. A little above the base it is over 100  $\mu$  thick and consists there of cells about twice as long as broad, while the cells in the upper part of the plant are 3-4 times as long as broad. The lower-most two or three joints of the stem are provided with cortical filaments which



Callithamnion sp. A 80:1. B 150:1.

continue their way into the basal disc. All the cells contain one nucleus and numerous elongated chromatophores. The upper end of the branches are  $12 \mu$  thick; they are rounded, never terminating in a hair or in a point. The plant bears a few sporangia situated in the place of a pinnula. They are tetrahedrically divided,  $60 \mu$ long,  $46 \mu$  broad.

A pectinate ramification like that described above seems to be rare within the genus *Callithamnion*. According to J. AGARDH it occurs in *C. scopulorum* Ag. the pinnæ of which are "rarius interiore latere pinellis brevissimis secundis quarum inferiores

longiores instructæ« (Sp. g. o. II p. 47). In the existing figures of this species, however, the pectinate branching is only shown in one pinna in Børgesen's fig. 56 b (Mar. Alg. Fær.), and it is evidently a rare occurrence, as also stated by J. Agardh, while in our specimen it is to be found on all the branches. This may possibly be due to the young age of the plant.

A similar seriate branching occurs in *Phlebothamnion spinosum* Kütz. (Tab. phyc. 11 tab. 98), but only dispores are shown in KÜTZING's figure, there is not so great a number of seriate pinnulæ, and the primary axis is corticated (comp. Sp. Alg. p. 653). *Call. spinosum* is, by the way, recorded by J. AGARDH under *species inquirendæ*. In *Phlebothamnion Gailloni* Kütz. (Tab. phyc. 11 tab. 98 II) two seriate pinnulæ on the upper side of the pinnæ are shown in two pinnæ in the quoted figure, but this species seems to differ more by its fasciculate-corymbose branching.

As only a very small specimen is present it remains undecided, whether the main axis is corticated and whether the described branching is characteristic also of the adult plants.

Locality. Ke: fJ 3<sup>1</sup>/<sub>2</sub> miles W. by N. of Fladens light-ship. 30 meters, Oct.

# Seirospora Harvey.

#### 1. Seirospora Griffithsiana Harv.

Harvey, Phyc. Brit. Vol. I plate 21, 1846; Kützing, Tab. phyc. Bd. 12, Taf. 17, 1862; Schmitz, Die Gattung Microthamnion J. Ag. (= Seirospora Harv.), Ber. deut. bot. Ges. Bd. 11, 1893, p. 277; Jos.

Schiller, 1913, p. 207; Oltmanns, Morph. I, 1904, p. 667; L. Kolderup Rosenvinge, 1920, p. 32. Callithamnion versicolor  $\beta$ , seirospermum Harv. in Hooker's Journ. of Botany Vol. I, 1834, p. 302. Callithamnion seirospermum Griffiths, Harvey Manual 1841, p. 113; Areschoug, 1850, p. 108, Tab. IV G;

J. Agardh, 1851, p. 42; Bornet et Thuret, Notes algol. fasc. I, 1876, p. XIV; Thuret et Bornet, Etudes phyc., 1878, p. 70.

Pæcilothamnion seirospermum Nägeli, 1861, p. 364, Fig. 13.

The ramification of this species which somewhat reminds one of *Callithamnion* corymbosum to which it has also been referred, has been described by NägeL1 in 1861 and recently treated at large in my paper (1920) to which the reader may here be referred for more details. The main axes are vigorous, in their lower part covered by a well developed cortex composed of downward growing filaments produced in a number of three from the basal cell of each branch. The branches are almost always arranged in a spiral with a divergence varying between 1/5 and 1/3, most frequently between 1/4 and 1/3. The spiral arrangement, however, does not begin at the very base of the branches, but the first branches are usually biseriate and arranged in a transversal plane, and the first joint (or 1 to 3 joints) is as a rule branchless. In all the specimens examined from Frederikshavn and Tønneberg Banke the spiral turned to the left. On the other hand, in a specimen from Herthas Flak only 4 of 16 examined shoots had a spiral turning to the left; in 9 it turned to the right, one



Fig. 275. Seirospora Gri/fithsiana. Upper end of shoot, from Frederikshavn (6361). 300 : 1. had a spiral with changing direction and 2 had irregularly arranged branches. The ramification is often pseudodichotomous in the upper parts of the shoots, the branches being of the same dimensions as the mother shoot and the latter changing direction by each branch (fig. 276 A). In a specimen from Tønneberg Banke I once found two vegetative branches of equal size on the same joint, diverging from each other at a right angle (fig. 276 B), and in the disporangia-bearing region of a specimen from the same locality I repeatedly found two branches on the same joint arranged now side by side, now one under the other or obliquely under the other (fig. 279). Even three branches were found on the same joint, one of which, however, was probably a young sporangium. The two branches were never opposite.

Hyaline hairs do not usually occur. Only in specimens from the harbour of Frederikshavn thin hyaline



Seirospora Griffithsiana. A-C from Tønneberg Banke; A, upper end of shoot with spirally arranged branches. B, two branches are borne on the same joint. C, lower part of stem with cortication. D, hyaline hair. A, B 200:1. C 70:1. D 350:1. hairs were not rarely met with at the end of the branches (fig. 276 D).

As shown by SCHMITZ (1893, p. 277), all the cells contain a single nucleus. The usual thallus cells contain numerous chromatophores which may be rather long (fig. 279 *B*).

Plants with sexual organs haye not been met with in the Danish waters. For these organs see the quoted papers by BORNET et THURET and SCHMITZ. On the other hand, disporangia, tetrasporangia and paraspores were found. The specimens from Herthas Flak were sterile, those from the Samsø area bore only paraspores. The specimens from Frederikshavn, which were fairly numerous, bore many paraspores, but some of them at the same time disporangia and tetrasporangia, though in rather small quantity and partly anomalous. Two specimens were found at

Trindelen one of which bore only paraspores, the other only disporangia, and specimens recently collected at Trindelen in October bore only tetrasporangia.

The tetrasporangia are borne on the inner side, more rarely on the flanks of the upper branches; they are sessile or are sometimes borne on a unicellular stalk, very rarely on a twocelled one (fig. 278 A). The sporangium-bearing joints often bear two or even three sporangia in a longitudinal row, the youngest lowermost, sometimes a sterile branch too. The tetra-



Seirospora Griffithsiana. Tetrasporangia. A, B young, still uninucleated. C, with four nuclei. D division accomplished. 350:1.

sporangia are  $60-77 \mu$  long,  $42-53 \mu$  broad. The outer wall has two layers, each consisting of a firmer outer layer and a soft, gelatinous inner layer. These two layers are not present from the first; the inner one appears only shortly before the division



of the sporangium. The division some in was cases regular, tetrahedrical (fig. 277 D), in others it was irregular, and sometimes more than 4 spores were present (fig. 278). According to SCHMITZ (1893, p. 277) the sporangia in Seirospora are "paarig getheilt (mit zwei gekreuzten

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Paaren von Sporen) oder zweitheilig (mit gerader oder sattelförmig verbogener Theilungsfläche) oder tetraëdrisch getheilt". The most regularly divided tetrasporangium observed by me was evidently tetrahedrically divided (fig. 277 B). Regularly cruciately divided tetrasporangia were not met with.

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The disporangia have the same position as the tetrasporangia, but in the specimen in question, two or even three lateral organs were often borne on the same



Fig. 279. Seirospora Griffithsiana. Disporangia. A, two very young sporangia on the same joint. B, sporangia besides or under a branch. A, B 190: 1. C 200: 1. D 350: 1.

cells in the tufts is thick and at first homogeneous, but later on it is often composed of two or three layers each of which has a firmer outer membrane. In the middle of the dense dark-red contents a large nucleus is visible after staining. A transitional stage between the terminal and the lateral para-

joint. As a rule one of the lateral organs was a sterile branch, the other a sporangium, but two sporangia might also occur on the same joint, the youngest under the eldest. A sporangium may be placed under the branch, but more frequently beside it (fig. 279 *B*). The disporangia which are usually sessile, but sometimes borne on a one-celled stalk are 56—70  $\mu$  long, 35—40  $\mu$  broad. They have always a double outer wall, just like the tetrasporangia.

The tufts of paraspores are, as well known, terminal on the long shoots, and I usually found them so, but lateral tufts, sessile or borne on a unicellular or bicellular stalk are sometimes met with on the upper branches, thus with a similar position to that of the sporangia. The usual terminal tufts of paraspores

are sharply delimited downwards, all the cells of the axis above a certain level and its branches being transformed into paraspores, their form becoming rounded, their contents much condensed and the wall thicker. The branches of the tufts are crowded, and frequently two branches are borne on the same joint. The outer wall of the



Seirospora Griffithsiana. Typical tuft of paraspores. 215 : 1.

spore-tufts is shown in fig. 281, the lowermost one or two cells in the upper branches being sterile. In other cases similar lateral tufts of paraspores are found at a greater distance from the apex, borne on a two-celled or one-celled stalk or even sessile (figs. 281, 282). They may then have a similar position to that of the sporangia. There is, however, no reason to consider them as transformed sporangia, (comp. SCHILLER 1913, p. 12), as

> it is only exceptionally that they have the same place as the sporangia.

At maturity the paraspore escapes from the thick envelope and takes a spherical

shape. I have not ascertained

whether the paraspore is naked or provided with a thin membrane as asserted by SCHILLER (1913 p. 2<sup>1</sup>). According to this author the germination takes place without formation of a rhizoid; but that is not in accordance with my observations. In my cultures the spherical paraspores had after two days given rise to a rhizoid, and some of these were

divided by a transversal wall perpendicular to the rhizoid. At the opposite pole a shoot arose during the following days which soon began to branch in the usual way (fig. 283). In the same culture were found short shoots detached from the plant from which the paraspores were given off; these shoots had also germinated, long rhizoids having arisen from their basal end.

<sup>1</sup> "Doch wird der natürlich schon mit einem zarten Häutchen umgebene Inhalt nicht von der Hülle zur Gänze frei".



Fig. 281. Seirospora Griffithsiana. A, lateral tuft of paraspores. B, the lowermost cells in the lateral branches of the tuft are sterile. 200:1.



Fig. 283. Seirospora Griffithsiana. Sporelings arising from paraspores. A, two days old, the others some days older. 120:1.

Fig. 282. Seirospora Griffithsiana. Branch with tuft of paraspores and disporangium. 200:1. The species has been found growing on stony bottom in 15-22 meters depth in the northern Kattegat and in the Samsø Water and further in the little boat harbour at the end of the northern mole in the harbour of Frederikshavn near low-water mark. In Herthas Flak it reached a length of 17 cm but was sterile. In the harbour of Frederikshavn it attained a length of 10 cm and bore abundant paraspores, more sparingly tetraspores and dispores. In the other localities the specimens were only 1 cm high but fructiferous. The species has only been met with in July, September and October.

Localities. Kn: Herthas Flak<sup>1</sup> (FG, XJ) 20 to 22 m; Frederikshavn (only found in 1896 and 1919); TO, Tønneberg Banke 18 m; fG, 3 miles W. of Læsø Trindel light-ship, 15 m (+ 10). — Sa: MS, near Endelave, 15 m, with paraspores.

# Plumaria Stackhouse, emend. Schmitz. Euptilota Cramer.

# 1. Plumaria elegans (Bonnem.) Schmitz.

Fr. Schmitz, Systemat. Uebersicht, Flora 1889, reprint p. 16; Phillips 1897, p. 361, pl. 18 fig. 17; Kolderup Rosenvinge 1911 p. 210; Kylin 1923, p. 57.

Ptilota elegans Bonnemaison, Hydrophytes loculées ou articulées. Paris 1828. (Not seen). J. Agardh 1851, p. 94; Kützing, Tab. phyc. 12. Bd. 1862, Taf. 56; Pringsheim 1862, p. 32, Taf. 8 Figs. 2—7; Bornet et Thuret, Notes algol. Fasc. I 1876 p. XV; Farlow, Mar. Alg. New Engl. 1881 p. 133; Buffham 1884 p. 342, 1891 p. 247, 1893 p. 303; Wille, Physiol. Gewebesyst. 1887 p. 72 Tab. IV Figs. 42, 43, Tab. VII Figs. 40, 41.

*Ptilota plumosa γ tenuissima* C. Agardh 1822 p. 386; Nägeli 1847 p. 206, Tab. VI figs. 38-42; Areschoug 1850 p. 97.

Ptilota sericea (Gmel.) Harvey Phyc. Brit. Vol. II 1849 Plate 191.

Ptilota plumosa Cramer 1864 p. 6, 108, Taf. I Figs. 4-5 Tab. II Figs. 1-5, Tab. III Figs. 1-3.

The structure and development of the frond has been carefully described by NÄGELI (1847) and CRAMER (1864) whose papers may here be referred to.<sup>2</sup> The longer primary shoots are alternating, being usually separated by two joints. There is no distinct limit between the pinnæ with persisting growth and the pinnulæ with limited growth. The ramification of the feebler pinnæ is less regular than that of the vigorous ones. The young branches are more or less curved inwards, in particular in the most vigorous shoots. Most of the branches become short plumose pinnulæ persisting in the older parts of the frond. The frond is sometimes not plane but vaulted, all the tips of the frond being directed to the same side. The convex side seems then to be directed towards the incident light.

<sup>1</sup> In my paper 1911, p. 205, a sterile specimen of *Seirospora Griffithsiana* has erroneously been recorded as *Griffithsia setacea*.

<sup>2</sup> OLTMANNS has not noticed the puzzling synonymy of this species caused by CRAMER's unlucky denomination; he has therefore been misled into confounding the genera *Ptilota* and *Plumaria* and has in Morph. u. Biol. d. Algen I Fig. 364 under the name of *Ptilota plumosa* reproduced figures both of this species (figs. 1, 4) and of *Plumaria elegans* (figs. 2–3). Comp. Kylin 1923, p. 57.

All the cells contain one nucleus and numerous small discshaped chromatophores. The colour is brownish-red. By treating old parts of the plant with concentrated sulphuric acid the cell-walls were stained blue, which must be due to the presence of iodine in the plant.

The upper pinnulæ not rarely end in a hyaline hair, as first mentioned by PRINGSHEIM (1861 Pl. VIII fig. 2) and later by myself (1911 p. 210). As shown by me, the young hairs contain a number of feebly coloured chromatophores, but these are later reduced, and in the full-grown hairs they are only visible as very small colourless grains (fig. 284). These hairs often cause sympodial ramification, the cell on which the hair is borne growing out about in the direction of the branch and pushing aside the hair. Such hairs were found frequently but not always in the specimens collected in April to September; in April and partly in May the hairs were short, but in autumn and winter (October, November, January) no hairs were met with.

The pinnulæ were sometimes found growing out into articulated, long-celled filaments the cells of which when lengthening take a feebler colour. They might perhaps be considered as ab-



Plumaria elegans. A, form with divaricate pinnulæ. B, pinnulæ transformed into rhizoid-like filaments. A 150 ; 1, B 80 ; 1.

normally developed rhizoids. As they are hair-like but different from the normal unicellular hairs they might be named *trichoids*. They were most strongly developed in a loose spe-

Fig. 284. Plumaria elegans. Hairs with numerous small reduced chromatophores and deformed nuclei. 240 : 1.

cimen found in the Baltic where it must have been introduced by the currents. The same specimen was remarkable by its divaricate, acuminate pinnules (Fig. 285).

As shown by Nägeli (1847, p. 207, see also CRAMER 1864), the cortex early covering the primary filaments is built up of hypha-like filaments fusing together into a dense tissue. In a later stage the cortex shows a pronounced differentiation, as shown by WILLE



seen from the face. 200 : 1.

(1887, p. 72), the innermost layer surrounding the axial cell-row becoming a conducting tissue, the intermediate layer a tissue serving for storage, and the outermost, smallcelled layer having an assimilatory function. The cells of the central axis gradually increase considerably in size and the pits connecting them increase too. The border of the two callus plates which cover the thin pit-membrane is sometimes bent back and continues their way on the surface of the thick transverse membrane, a phenomenon which is perhaps connected with the peripheral growth of the pit (Fig. 286, above). In older shoots the surface of the cortex is often covered by a felt of adventitious shoots of unbranched cell-rows issuing from the superficial cells (Fig. 286). CRAMER (1864 p. 10 and pp. 109-110) has mentioned them and even established three forms of the species according to their frequency:  $\alpha$ , subglabra;  $\beta$ , pilosa and  $\gamma$ , tomentosa.

The sexual organs have never been met with at the Danish coasts. The antheridia according to BUFFHAM form "yellowish bunches near the extremities of the pinnules"<sup>1</sup> (1891, p. 247 Pl. XVI figs. 6–7).

The structure of the procarps has been described by PHILLIPS (1897 p. 362). The ripe cystocarps are usually said to be naked or provided with involucral branches. But as the sori of paraspores have really often been confounded with cystocarps it may be supposed that the latter are always provided with involucral branches. BUFF-HAM asserts, too, that he has never seen the true cystocarps naked (1893 p. 303).

Tetrasporangia have only been met with once and extremely sparsely. In a paraspore-bearing specimen from Busserev gathered in July 1918 I found a ripe and an unripe tetrasporangium (Fig. 287). They had a dense, dark-



Fig. 287. Plumaria elegans. Tetrasporangia before and after division. 390:1.

red content and a thick, two-layered membrane. Within the thin firm cuticle two

<sup>1</sup> The organs which BUFFHAM in a foregoing paper (1884, p. 342, Plate XII Fig. 1) took for antheridia are of dubious nature, possibly foreign sporelings. distinct layers were present, separated in the young sporangium by a boundary line, in ripe ones by a less refringent intermediary layer. The walls separating the spores were in continuity with the innermost layer of the sporangium. The division was tetrahedrical. The ripe sporangium was 53  $\mu$  long, 44  $\mu$  broad.

The heaps of paraspores have, as mentioned above, often been confounded with the cystocarps and described as naked favellæ, but they have nothing to do with the female sexual organs. According to SCHMITZ and HAUPTFLEISCH (ENGL. u. PRANTL p. 493) they occur only in the tetraspore-bearing specimens; the only tetra-

sporiferous specimen I have found bore paraspores at the same time. The heaps of paraspores have further a similar position to that of the tetraspores, namely on the end of the pinnulæ, and it has therefore been supposed that they were modified tetrasporangia (comp. OLTMANNS Morph. p. 667). This interpretation is, however, in my opinion unjustified. While the tetrasporangia are from the first dark-red, darker than the vegetative cells, the young heaps of paraspores are lighter, as emphasized by BUFFHAM (1893 p. 303) and as it is visible in PRINGS-HEIM's figures (1862, figs. 3-5), and as shown in my fig. 288. Further, the outer wall has another constitution. It is to begin with similar to that of the vegetative cells, grows gradually thicker and may sometimes be indistinctly lamellate, but it is often homogeneous and is in continuity with the separating walls be-







tween the cells of the heap. An end-cell that will develop into a heap of paraspores is distinguishable by its feebler colour and by indistinct chromatophores, while the nucleus appears very distinct. The cell is usually divided by an oblique wall and the daughter-cells are further divided. In the four-celled stage the cells are still rather feebly coloured. During the further divisions the paraspore-heap grows out to a roundish, more or less irregular ovate or obovate or obcordate body and the chromatophores become gradually more distinct and take a deeper red colour. 8-celled and 16-celled heaps are comparatively often met with, but other numbers too occur, f. inst. 5, 6, 12. According to BUFFHAM the number of spores at maturity is 16, and it is certainly frequently so, but I have found at least 18 spores, and in other cases maturity seems to arrive when the number of cells is much lower, as in the four-celled heap represented in fig. 288 *F*. The spores when discharged are globular and naked<sup>1</sup>, but are soon surrounded with a thin membrane. The cell-wall was sometimes found thickened on one side, undoubtedly where the first rhizoid would later appear. The cell is then divided by an eccentric wall in a smaller cell which gives rise to the rhizoid, and a larger cell which divides by walls parallel to the first and gives rise to the primary axis.



The rhizoid is separated from the small cell by a transversal wall. My pictures (fig. 289) agree with PRINGSHEIM'S figs. 7 b, d which represent spores germinating within the membrane of the heap.

The species is perennial and has been met with in all seasons. It attains a length of up to 8 cm. In winter it is generally smaller, some of the shoots being shed, but new shoots are produced from the remaining parts. The older shoots are often overgrown with *Membranipora*. It grows partly on stones, partly on various Algæ, as f. inst. *Fur*-

cellaria, Chondrus, Ahnfeltia, Fucus serratus, from low-water mark to 9 meters depth. When occurring near low-water mark it always grows in shadow f. inst. under Ascophyllum nodosum. The paraspores have been met with at all seasons except in spring, in the greatest quantity in summer.

Localities. Kn: TV, Krageskovs Rev; Hirsholm, at various places (Hornemann 1815, !); Busserev, Brune Rev, Laurs Rev and Marens Rev by Frederikshavn; harbour of Frederikshavn; TL, west of Nordre Rønners light-house, 9-14 m. - Su: Gnetare Grund (Swedish coast, Boye Petersen). - Bm: SD, N.E. of Møen, 23,5 m, loose, with other loose Algæ, a small specimen with divaricate acuminate pinnules, sterile (see above).

# Ptilota C. Agardh.

# 1. Ptilota plumosa (L.) Ag.

C. Agardh, Synops. Alg. Scand. 1817, p. 39; Lyngbye 1819, p. 38 Tab. 9A; Kützing, Phyc. gen. 1843, p. 378, Taf. 46; Harvey, Phyc. Brit. I, 1846, Pl. 80; Kützing, Tab. phyc. Vol. 12, 1862, Taf. 54; B. M. Davis, Developm. of the procarp and cystocarp in the genus Ptilota, Botan. Gazette Vol. 22, 1896; Buffham 1896 p. 189; R. W. Phillips 1897, p. 362 Pl. 18 Figs. 16, 18; Kylin 1913, p. 58.

*Fucus plumosus* Linné, Mantissa pl. alt. 1767, p. 134; Fl. Dan. Tab. 350, 1767. *Pterota plumosa* Cramer 1863 p. 25 Taf. III Figs. 4, 5, IV Figs. 1-7, V Figs. 1-5, VI Figs. 1-5.

The development of the frond has been carefully described by CRAMER whose paper (1863) may here be referred to. Transversal and longitudinal sections of a younger frond have been figured by KÜTZING (1843, Plate 46). In both is shown a small-celled outer cortex and an inner layer composed of larger cells and surrounding the axile cell-row. In the longitudinal section it is rightly shown that the opposite pinnulæ only issue from every other joint, but the connection between the pinnulæ and the axial cells of the long shoots is not represented. As shown in my

<sup>1</sup> According to BUFFHAM (1893, p. 303) the paraspores are "possessing a cell wall even before discharge". If this must be understood to mean that the spores are also provided with a cell wall when discharged, it is not in accordance with my observations.
fig. 290 the central axes of the pinnulæ traverse the cortex of the stem and are connected with the central axis of the latter through large pits. The greater part of the

cortex consists of large rounded cells which have principally the character of storage cells; they contain numerous starch grains and narrow, branched chromatophores. The outermost cells are small and constitute a one- or twolayered assimilatory tissue. The cells of the central axes going out to the pinnulæ are also rich in starch, but the central axes of the stems do not contain starch; the granular plasma of their cells is concentrated in the upper half of the cell while the lower half has only a thin layer surrounding the vacuole. In the somewhat older stems a number of thin rhizines arise from the



Fig. 291. Ptilota plumosa. Pinna with tetrasporangia. 230 : 1.

inner cortical cells, forming a layer surrounding the central axis and increasing in



Fig. 290. Ptilota plumosa. Longitudinal section of frond in the plane of ramification. 110:1.

thickness. This production of rhizines later advances outwards, so that the cortical cells in older shoots are partly separated by thick bundles of rhizines, and transverse sections of old stems may in great part be composed of rhizines. All the cells contain one nucleus.

Hyaline hairs have not been met with except those which occur near the procarps and which will be mentioned below.

The tetrasporangia are terminal on short monosiphonous filaments borne on the margins of the pinnulæ and terminal on the pinnæ; they are tetrahedrically divided (fig. 291, comp. KYLIN 1923 p. 59, fig. 39).

The antheridia have been shortly mentioned by Phil-LIPS (1897, p. 365) who says that they "cover the tips of the branches, and correspond closely in appearance to

the similar structures in *Plumaria*, which have been figured by BUFFHAM ('90)". I have found antheridia in a dried specimen dredged in the Kattegat in May. They were

D. K. D. Vidensk. Selsk. Skr., 7. Række, naturvidensk. og mathem. Afd. VII. 3.

borne principally on the edge but also on the flat side of the pinnulæ. They were cut off in a number of 2 or 3 by inclined walls from the low stalk cells (Sperma-



Ptilota plumosa. A, pinna with antheridia. B, pinnula with antheridta and two spermatia. 350:1.

tangien-mutterzellen Svedelius) which seem to contain chromatophores (Fig. 292).

The cystocarps develop terminally on short pinnulæ and are surrounded by a whorl of sterile branches. The procarps have been described by DAVIS and PHILLIPS, but the interpretations of these authors are diverging. Upon the end of the fertile pinnæ arises a group of short cell-filaments each ending in a hvaline hair. According to DAVIS (1896) these are groups of procarps the number of which is variable, though typically 5. DAVIS interpreted all the hvaline hairs as trichogynes, but as he has never found spermatia adhering to them and as he has not observed antheridia he supposed that the cystocarp develops apogamously. PHILLIPS (1897) arrived at another interpretation, the 4-celled external short-celled branch being the only true carpogonial branch while the others are only vegetative structures. KYLIN who has recently (1923) carefully studied the development of the pro-

carps arrived at the same conclusion. He observed the fertilisation

and the transmission of a small sporogenous cell to the auxiliary cell which is cut off from the basal cell immediately after fertilisation. In one specimen dredged in the Sound north of Helsingør in June I found procarps before fertilisation. The trichogyne was usually thicker than the sterile hairs and frequently swollen at the top. It is strange that these vegetative hairs are normally present while vegetative hairs are otherwise wanting in this species.

The gonimoblast according to DAVIS consists of 2-5 nearly globular lobi which are quite separated from one another but are all attached to the central cell. The lobes are as a rule in widely different stages of maturity. According to KYLIN (p. 61) the basal cell ("Tragzelle") fuses more or less

involucral branches varies up to at least 8.



Fig. 293. Ptilota plumosa. Carpogonial branch (to the right) and surrounding sterile filaments ending in hyaline hairs. 390 : 1.

with the auxiliary cell and the first cell of the gonimoblast. The number of the

The three kinds of organs of reproduction (antheridia, procarps and tetrasporangia) normally occur on distinct individuals. BUFFHAM, however, (1896, p. 189) found tetrasporangia on female plants. In one case "the involucre of an old cystocarp (or possibly of an unfecundated procarp) became branched near the tips and developed tetrasporangia".

The species occurs in the Skagerak, where it has been collected at 11—15 meters depth, in the eastern and southern Kattegat in the under-current with high salinity, in about 20—30 meters depth and in the northern part of the Sound in the same current. It most frequently grows on the stipes of Laminaria hyperborea and L. digitata. It is perennial but has only been collected in the months May to October. It reaches a size of 15 cm. In specimens gathered in June the new shoots had a more clear red colour than the older parts of the frond which were more brown-red. The new shoots in great part formed a continuation of the old ones, but adventitious shoots also occurred, arising from the base of the pinnulæ, as described and figured by CRAMER (l. c.). In August the vegetative growth has ceased. Antheridia were met with in May, unfertilized carpogonia in June, and ripe cystocarps and tetrasporangia in June to September.

Localities. Sk: Off Hirshals, 12 m (Børgesen); XO, Møllegrund off Hirshals, 11–15 m. – Ke: IQ, ZF and fH, Fladen, 17–30 m;  $4^{1/2}$  miles S.W.  $^{3}/_{4}$  W. of Fladens light-ship, 30 m (C. A. J.). – Ks: Lysegrund, June 1832 (Lyngbye); Nordvestrev by Hesselø, July 1832 (Lyngbye). – Su: Gnetare Grund and Grolle Grund at the shore of Sweden (Boye Petersen); off Hellebæk, soft bottom with shells (id.); north of Helsingør (Liebman, Ørsted).

#### Antithamnion Nägeli.

### 1. Antithamnion cruciatum (Agardh) Nägeli.

- C. Nägeli, 1847, p. 200, id., 1861, p. 378; J. Reinke, Lehrbuch d. allgem. Botanik, 1880, p. 171 Fig. 121;
  G. Berthold, 1882, pp. 573, 605, Pl. 19 Figs. 1—10, Pl. 20 Figs. 3—4; P. Kuckuck, Bemerk. z. mar. Algveg. Helgoland, Wiss. Meeresunt. Abt. Helgoland N. F. Bd. 1, 1894, p. 254 Fig. 22; Nestler 1899, p. 5, Taf. I Figs. 11—19; B. Schussnig, 1914 p. 2.
- Callithamnion cruciatum C. Agardh, Flora 1827 II, p. 637; Harvey, Phyc. Brit. II 1849, p. 164; J. Agardh, 1851, p. 27; Kützing, Tab. phyc. Vol. 11, 1861 Taf, 87 I; J. Agardh, Florideernes Morfologi, 1879 (K. Sv. Vet. Akad. Handl. Bd. 15 No. 6), p. 103 Pl. I Fig. 20 (Cystocarp).

 $\alpha$ , genuina.

β, radicans J. Agardh, Symbolae, Linnaea, 1841, p. 44.

This species is easily distinguishable from the two following species. Each joint in the long shoots bears two opposite or four verticillate pinnæ. In the Danish specimens I found them only opposite; they were decussate, and thus arranged in four rows. The angle of divergence often diverged from 90° and was variable, and the arrangement in longitudinal rows therefore not distinct. As shown by BERTHOLD (1882, p. 605), the position of the pinnæ is dependent on the light, the pinnæ being inclined to place themselves in a plane perpendicular to the incident light. According to NÄGELI (1861, p. 379) the pinnæ in the whorls do not arise simultaneously and the first pinnæ of the successive whorls are arranged in a spiral with the divergence

46\*



270:1.

of 1/4. The primary long shoots arise in the place of a pinna; the joint on which it is borne usually bears no other branch (fig. 294, 4th joint). The primary long shoots have no or only a slight influence on the direction of the mother axis. Besides the primary long shoots, adventitious shoots frequently arise from the basal cell of the pinnæ (Nägeli l. c.). They may be given off from the upper side (REINKE l. c.), from the under side (fig. 297) or from the flanks of this joint which remains short and usually produces no pinnulæ.

The pinnæ are variously branched. The lower ones, in particular on the creeping parts of the long shoots, are often entirely unbranched (fig. 295) while those on the upper part of the plant bear alternate, secund or opposite pinnulæ. As shown by Nägeli in 1847, the pinnæ are usually branched in a

transversal plane. The plane of ramification is, however, also dependent on the light (BERTHOLD 1882, p. 605). With regard to the gland cells occurring on the pinnulæ

reference may be made to NEST-LER'S and SCHUSSNIG'S papers quoted above; they rest on three cells of the pinnula in contradistinction to those of A. Plumula.

Pluricellular rhizoids arise from the basal cell of the pinnæ in the lower part of the plant; they are particularly well developed in the specimens found in the harbour of Frederikshavn and referred to f. radicans. The long shoots were here creeping in their whole length or almost so, and bore rhizoids issuing from all the basal cells facing the substratum. These rhizoidal



Fig. 295.

Antithamnion cruciatum f. radicans. A, the pinnæ unbranched, the rhizoids with free ends. B, the outer cells of the rhizoids thrown off. 150:1.

filaments had usually free ends; they penetrated a layer of detritus bound to-

gether by animal secretion, in which the plants grew without fixing themselves on the algae covered by the layer of detritus (fig. 295 A, comp. KUCKUCK 1894 fig. 22). The outer cells in these filaments lengthen, become gradually poor in contents and are finally thrown off, but the innermost cell often remains for a long time and every trace of the decaying of the outermost cells is then effaced, the wall of the upper end of the cell being rounded (fig. 295 B). In Fig. 296 the scar is still visible (\*). In other cases, the rhizoids fix themselves on the substratum forming an adhesion disc composed of a number of radiating cell-filaments. According to BERTHOLD (1882, p. 607) the cells of the rhizoids afterwards shorten, the cells becoming barrelshaped and the cell-wall incrassated. Such rhizoids sometimes arise at a certain distance from the substratum, as shown in fig. 296, where the rhizoid has fixed itself to the mother axis of the pinna and formed an adhesion disc embracing it.

The tetrasporangia are placed laterally on the pinnæ, borne on a one- or two-celled stalk. They are larger than



Antithamnion cruciatum. A, a shoot is produced from the basal joint of a pinna. B, tetrasporangium. 200:1.



Fig. 296. Antithamnion cruciatum. Lower part of plant; a rhizoid has fixed itself to the stem. 110:1.

July. Sexual organs were not observed. They generally seem to be rather rare; HAR-VEY (Phyc. Brit.) did not know them and HAUCK too did not mention them (Meeresalgen, p. 71). On the other hand, the cystocarps are mentioned and figured by J. AGARDH (1879) as consisting of several lobes.

those of A. Plumula,

73-102 µ long, 51

 $-68 \mu$  broad. They

were met with in

The species has been found only in a few places in the Limfjord and in Kattegat. It has been gathered in June to November, growing on stones and wood (piers) and on other Algæ. In the harbour of Frederikshavn it usually occurs in the creeping form *radicans* which may probably under favourable conditions grow out as the typical erect form.

Localities. Ns: 13<sup>1</sup>/2 miles N.E.<sup>1</sup>/2 E. of Hanstholm light-house, 23 m, C. A. J., very small specimen Oct. 1922. - Lf: Off Hanklit, Thisted Bredning, on Fucus; MK, Holmtunge Hage, c. 2 meters' depth. - Kn: Harbour of Skagen (November 1911, Kramp); harbour of Frederikshavn, berths on the end of the moles and in other places on piers. - Ks: aU off Lumbsaas, 13 met.

### 2. Antithamnion Plumula (Ellis) Thuret.

Thuret in Le Jolis, Algues mar. de Cherbourg, 1864 p. 112; R. W. Phillips 1897 p. 356, Pl. 18 Figs. 11—12; A. Nestler 1899, p. 1, Taf. I Figs. 1—10; Killian, Über die Entwickl. einiger Florideen. Zeitschr. f. Bot. 6. 1914, p. 215; B. Schussnig 1914 p. 1; Kylin, 1915 p. 11; id., Über die Keimung der Florideenspren. Arkiv f. Botanik Bd. 14, No. 22, 1915, p. 15; id. 1923 p. 61.

Conferva Plumula Ellis, Philos. Transact. Vol. 57 I, 1768 p. 424 Tab. 18.

Callithamnion Plumula Lyngbye, 1819, p. 127; J. Agardh, 1851 p. 29; Harvey, Phyc. Brit. III 1851, Pl. 242; Kützing, Tab. phyc. Bd. 11, 1861, Taf. 83 I.

Pterothamnion Plumula Nägeli in Nägeli u. Cramer, Pflanzenphys. Unters. 1. Heft 1855 p. 54, Taf. VI, Figs. 11-13, Taf. VII; Berthold 1882, p. 614, Taf. XX Figs. 1-2, Taf. XIX Fig. 11-17; id., Vertheil. d. Alg. im Golf von Neapel; Mittheil. a. d. zool. Stat. zu Neapel 1882, Heft. III; Schmitz, Unters. üb. die Befrucht. d. Florid., Sitzber. d. k. Akad. d. Wiss. zu Berlin, 1883, p. 236, Fig. 35.

In the Danish waters this species reaches a height of 9 cm, but usually it does not exceed 5 cm. The fixation of the primary shoot is strengthened by free

Fig. 298. Antithamnion Plumula. See text. 70:1.

rhizoids springing from the lower end of the cells of the main axes and the lower part of the lateral axes, while intramatrical rhizoids do not occur. It happens, however, that several of the downward growing filaments do not reach the substratum. Some of them may take the character of runners which give rise to upright shoots; they then consist of shorter, thicker cells. Intermediate stages between assimilative shoots and root-like filaments, showing unstable polarity, may occur too. The long shoot to the right in the fig. 298, for instance, is essentially an assimilatory shoot; the filament issuing from its second joint is, however, a branched rhizine though it has been produced at the upper (distal) end of the cell. The 8th cell of the same shoot has also produced at its upper end a filament having if anything the character of a rhizine though it is directed upwards, but from the lower part of the same cell a typical assimilative shoot is given off.

The ramification has been carefully described by NÄGELI and BERTHOLD, The frond is usually flat, the long shoots being contained in one plane, issuing alternately to the right and to the left, and the two ranks of opposed pinnæ are given



Fig. 299. Antithamnion Plumula. Shoots with tetrasporangia, from Herthas Flak. A, a normal pinna. B, pinnæ mostly unbranched. 95:1.

off in the same plane. Each joint usually bears a pair of pinnæ, but the long shoots take the place of a pinna, and the joint which bears a long shoot usually bears no pinna on the opposite side, and in the following joint (or joints) the pinnæ are often wanting over the long shoot (Fig. 299 *B*). On the other hand, the joint which bears a long shoot often produces two unbranched pinnulæ issuing in a plane perpendicular to the plane of the frond (Fig. 299 *B*). Similar pinnulæ sometimes occur on other joints than those situated immediately under the branchings, thus in several

specimens from the Kattegat. Such specimens form a transition to others which have normally 3 or 4 ranks of pinnæ, as most of the specimens found in the Skagerak. 3 ranks were most frequently met with. When the number of pinnæ in the whorls is constant, they are usually superposed, though not regularly. In these specimens the long shoots are not contained in one plane but issue in different directions. According to BERTHOLD (1882 p. 614), the ramification is dependent on the light, so that plants growing in unilateral light branch in one plane, while plants illuminated



Antithamnion Plumula. Tetraspore-bearing shoot with unusually numerous gland cells, from Lille Belt. August. Reduced pinnæ. 380:1.

equally from all sides bear branches on all sides. This, however, cannot be the sole determining factor, for in all the specimens examined by me from eight localities in the North Sea and the Skagerak the pinnæ were arranged in 3 or 4 rows, while the specimens from all the localities within Skagen were branched in one plane and at most bore unbranched pinnulæ on the face of the frond at the angle of the branches, or rarely on a few adjacent joints too. Only in specimens from the south side of Skagens Gren and in one specimen from Groves Flak (Ke, 26 m) the pinnæ were arranged in 3 or 4 rows. These specimens were all growing in water of comparatively high salinity. In the latter specimen the pinnæ were arranged in 4 rows, those on the flat side were, however, feebler than the others, and in many cases no pinnæ occurred on the flat side.

The pinnæ only bear pinnulæ on the upper side, and these may be un-

branched or they bear pinnulæ of the second order on their upper side. More rarely the pinnæ are unbranched or very little branched, as in some specimens from Herthas Flak in more than 20 meters depth (fig. 299 *B*), which, however, bore typical branched pinnæ in the lower part of the plants. The pinnæ are at first directed upwards, later usually divaricate, or some of them may even be recurved. Only in specimens from Skagerak off Lønstrup (8 m) a great number of the pinnæ were recurved. The pinnæ and pinnulæ are finally pointed, the ultimate cell ending in a thin point consisting only of the cell-wall. This pointing takes place at the end of the period of growth; in the later part of July and in August acuminate pinnæ may occur, even near the growing point, while in the first part of July specimens without acuminate pinnæ may be met with.

The cells contain one nucleus and numerous ribbon-shaped or irregular chromatophores (Fig. 301 B, comp. NESTLER fig. 1). For the nuclei see SCHILLER (1911). The gland cells are borne on the inner (upper) side of the pinnæ, resting on a single cell. Their number is rather variable, owing to unknown causes. They are normally present; in single cases, however, I have sought them in vain. In the Skagerak they were never missing, and they were met with, partly even abundantly, in specimens growing near the southern limit of the species (fig. 300); they further occurred in numbers in slight and in great depths (e.g. Groves Flak, 32 m). The function of the gland cells is unknown. NEST-LER is inclined to suppose them to be absorbing organs; SCHUSSNIG supposes that they function in the same manner as air-bladders.



Fig. 301. Antithamnion Plumula. Antheridial bushes. 390:1.

The tetrasporangia are borne on the upper side of the pinnæ usually in small clusters. Often a single sporangium is found terminal on a short stalk-cell, but this



Fig. 302. Antithamnion Plumula. Procarps. In A the carpogonial branches are shaded. A 300:1. B 390:1. D. K. D. Vidensk, Selsk, Skr., 7. Række, naturvidensk, og mathem. Afd. VII, 3.

cell usually bears further one or two or three younger sporangia or rudiments of sporangia, and the stalk may sometimes consist of two or three cells (figs. 299, 300). Besides the sporangia borne in clusters sessile sporangia may occur too, principally on the outer part of the pinnulæ. Sporangial clusters opposed to a pinna may sometimes be met with; they represent a pinna reduced to a cluster of sporangia (figs. 299, 300). At the end of the period of growth the sporangia may even become terminal on the long shoots, when their growth is ceasing (fig. 300). The ripe sporangia were 42-45,5 µ long,  $29-40 \mu$  broad in specimens from the Skagerak; in a specimen from the Little Belt they were only  $35-38 \mu$  long,  $27-30 \mu$ broad. They open by a slit.

The antheridia (fig. 301) have a similar position to the tetrasporangia. They are Ard. VII. 3. 47 borne on small bushes, seriate on the upper side of the pinnæ, reminding one of those in *Callithamnion Furcellariæ*, but often a little bigger. These bushes may also occur on the long shoots, taking the place of a pinna. The antheridial clusters may be sessile but are usually provided with a one- or two-celled stalk, their shape is irregularly roundish or more or less lobed, ovate, or more or less elongated with a



Fig. 303.

Antithamnion Plumula. A and B young cystocarps showing the first gonimolobe on the upper face of the auxiliary cell; in B the carpogonial branch is shown behind the filament. C, nearly ripe cystocarp seen from below; the carpogonial branch is still visible. D, cystocarp seen from above. E, sporeling found on a cystocarp-bearing plant. 350: 1.

distinct 4- or 5-celled main axis, and the antheridia may then be most numerous on the acroscopic side.

The carpogonial branches are, as described by SCHMITZ and PHILLIPS, and recently by KYLIN, 4-celled and borne laterally on the undermost cell of the pinnulæ and connected with it. The content of the basal cell and of the next cell of the pinnula is different from that of the vegetative cells and resembles that of the cells of the carpogonial filament. The nucleus of the three undermost cells of the carpogonial branch often divide in two before the fertilisation. After fertilisation an auxiliary cell is cut off upwards from the basal cell, and it fuses shortly afterwards with a little sporogenous cell from

the fertilised carpogonium (comp. PHILLIPS 1897 fig. 12; KYLIN 1923 fig. 40 h); it then divides, according to KYLIN in a smaller lower and a greater upper cell, the first gonimoblast cell which successively produces the gonimolobes. There are at least four gonimolobes. During this development, according to PHILLIPS (l. c. p. 357), the cells immediately above and below the auxiliary cell become fused with it. The first gonimolobe is given off from the upper side, others downwards in an oblique direction (fig. 303). The particular gonimolobes are borne on an unicellular stalk and are globular or reniform. Their size is very different, the first formed being fully developed while the youngest one only consists of a small number of cells and perhaps never reaches full development. Stalk-cells without fertile cells may occur too. The trichogyne decays quickly while the rest of the carpogonium may be kept for a longer time (fig. 303).

Antheridia, carpogonia and tetrasporangia as a rule occur on distinct individuals; in two cases, however, tetrasporangia were found on cystocarp-bearing plants.

Paraspores in Anthithamnion Plumula have been found in the Mediterranean by SCHMITZ and SCHILLER (1913 p. 3, Plate V). Such organs have never been met with in the Danish specimens.

The germination begins, as in *Callithamnion*, by the division of the spore-cell by a transversal wall into two cells, one of which gives rise to the first rhizoid, the other to the primary axis (comp. KILLIAN and KYLIN 1915). Young seedlings were met with on the surface of and in the neighbourhood of the cystocarps (fig. 303).

The species has been met with in several localities in the Danish waters with salinity of 2 p. c. or higher, but it does not occur in the Limfjord or in other fjords. The best developed specimens were found at Skagen, south of Grenen, where it reached a length of over 8 cm, and where it was found as the predominating species in 13 to 15 meters depth in a locality with clayey sand with molluscs. In the Kattegat it otherwise reaches a length of 6 cm, and at Hellebæk in the northern part of the Sound 3 cm; but in the Samsø water and the Little Belt it was only 1,5 cm high at most.

The relation of this species to *A. boreale* will be dealt with under the last named species. Only specimens from one locality in the Little Belt (EE) could be said to approach *A. boreale* by having longer cells in the lower part of the main axis and by the pinnæ bearing, though rarely, pinnulæ on the under side.

The species has been met with in depths of 9 to 32 meters, and furthermore slightly below the surface on vertical granitic walls in the harbour of Frederikshavn. It grows principally on mollusc shells and therefore often occurs on soft bottom, further on the tubes of *Tubularia* and on various Algæ, e. g. *Rhodomela, Furcellaria, Phyllophora*. It has only been gathered in the months April to October. The tetrasporangia have been met with in July to October, the sexual organs in July and August and ripe cystocarps in July to October; the latter, however, more rarely than the sporangia.

Localities. Ns: aF, off Thyborøn, 31 m. — Sk: eX, north of Bragerne, 16 m; SY, north of Løkken, 13 m; ZK, off Lønstrup, c. 8 m; YL, XO and other localities off Hirshals, 11—15 m (Børgesen, !). — Kn: Skagen, south side of Grenen, c. 5—15 m; FG and XJ, Herthas Flak, c. 20 m; YS<sup>2</sup>, north of Hirsholmene, 15 m; YX, east of Nordostrev, Hirsholm, 23—28 m; on shells of Ostrea, Frederikshavn (Ørsted 1840); off Frederikshavn, east of Marens Rev, c. 20 m (!, Ostenfeld), 11 m (Kramp); harbour of Frederikshavn; TP, Tønneberg Banke, 16 m; near Læsø Trindel, 11—26 m; 3 miles W. of Læsø Trindel light-ship 15 m. — Ke: FC, east of Læsø, 17 m; fH and fl, 1 and 3 miles W. by N. of Fladen light-ship, <sup>\*</sup> 17 and 30 m; ZH, ZI, Groves Flak, 32 and 26 m, soft bottom; EQ, east of Anholt;  $14^{1/2}$  miles S.S.E. of Anholt Knob light-ship, 10 m (C. A. J.). — Sa: MS, west of Endelave, 15 m. — Lb: North side of Fænø; EE, west of Fænø, 15 m; Fænø Sund, 10—15 m. — Su: Hellebæk (Schmidt 1873).

#### 3. Antithamnion boreale (Gobi) Kjellman.

Kjellman, Norra Ish. algfl. 1883 p. 226, Pl. 16 figs. 2—3 (Alg. Artc. Sea p. 180); Reinke, Algenfl. westl. Ostsee 1889, p. 23 (f. baltica), Atlas deutsch. Meeresalg. I 1889 Taf. 22; Kylin 1907, p. 173.
Antithamnion Plumula var. boreale Gobi, Algenfl. des weissen Meeres. St. Pétersbourg 1878, p. 47.

While in a former paper (Grønlands Havalger, 1893, p. 787; Ann. sc. nat. 7<sup>e</sup> sér. t. 19, 1894, p. 64) I have regarded this species as a variety of *A. Plumula*, in ac-

cordance with GOBI, my later investigations of the Danish specimens have led me to agree with KJELLMAN'S view that it must be considered as a distinct species. Ac-



Antithamnion boreale. Lower part of plant. 100 : 1.

cording to KJELLMAN and other authors it differs from A. Plumula by being more slender, by longer cells in the long shoots, by the pinnæ in great part bearing pinnulæ on two sides and then opposed or alternate, while the pinnæ of A. Plumula bear only pinnulæ on the upper side, and by the sporangia being always sessile. Kylinladds the character that A. boreale is sporangia-bearing early in June while

in A. Plumula the sporangia appear only in July. I can confirm these statements and add a little more.

The base of the plant resembles that of *A. Plumula*, as shown in fig. 304 where free descending filaments are given off from the cells of the main axis and the proximal part of the pinnæ. Fig. 305 shows the lower part of a plant gathered in April. The lowermost part which is short-celled and had a darker colour had undoubtedly been formed in the foregoing year while the upper, brighter and more long-celled part of the shoot had grown out in spring. The first pinnæ are unbranched and the next following ones bear only one or two pinnulæ on the upper side.

The shoots usually bear two rows of pinnæ; how-

Fig. 305. Antithamnion boreale. Specimens gathered in April. The lowermost part (shaded) is a survival from the foregoing year. 95: 1,

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ever, a certain number of joints occur which bear only one pinna. On the other hand, joints which bear three pinnæ may also occur, though rarely. The pinnæ

Fig. 306. Antithamnion boreale. Tetraspore- and antheridia-bearing specimen from the Baltic Sea (UL), May. 70:1.

bear not only pinnulæ along their upper face but also on the under face or on the flanks; in the first case the pinnulæ are very often opposite. The pinnæ are more slender and often longer than in *A. Plumula*. Gland-cells (fig. 307) similar to those of *A. Plumula* may be present or wanting. They were present in all the examined specimens from the eastern Kattegat and further in some of the specimens from the Samsø waters, though in some cases only in small number, while they were wanting in other specimens, and they were also wanting in all the examined specimens from the Øresund and from the Baltic Sea. The latter specimens can be referred to f. *baltica* Reinke (l. c.) which is chiefly distinct by this character. The specimen represented by KUCKUCK in Atlas deutsch. Meeresalg. Taf. 22 has in great part unbranched



Antithamnion boreale. Pinnulæ bearing antheridia at the top, and sporangia, s. g gland cells. In A the chromatophores are shown. A-C 390 : 1. D 230 : 1.

pinnulæ, which occurs more rarely in the specimens from the Danish waters.

The tetrasporangia are sessile on the upper face of the pinnulæ or on their flanks, usually singly on the joints but sometimes in pairs and the second being inserted at a lower level but at the same time beside the first. The sporangia are bigger than in *A. Plumula*, usually 60– $85 \mu \log, 35-50 \mu$  broad. In the specimens from Fænø Sund, however, I found them a little smaller, only 46–49  $\mu \log, 35 \mu$  broad, thus almost of the same size as those in *A. Plumula*.

In some specimens from the Little Belt and the Baltic Sea antheridia were met with. They were borne on the upper end of short pinnulæ which in several cases bore sporangia too (figs. 306, 307). These pinnulæ usually consist of 3—6 cells the

uppermost one or two of which bear a small number of closely placed nearly globular antheridia. The pinnula may sometimes bear a small branch which likewise bears antheridia at its top (fig. 306 above), but antheridial clusters like those in A. *Plumula* never occur.

Female sexual organs and cystocarps have never been observed in this species.

The presence of antheridia-bearing pinnulæ in tetraspore-bearing specimens and the different shape of these branchlets corroborate the view that *A. boreale* is specifically distinct from *A. Plumula*. As stated by previous authors, *A. boreale* is nearly related to *A. americanum* (*Callithamnion americanum* Harvey, Nereis bor. amer. II, 1853 p. 238 pl. 36 A). In a specimen of this communicated in Phykotheka univers. No. 501 I found gland-cells and sporangia 56–60  $\mu$  long, 35–37  $\mu$  broad.

A. boreale occurs in the Danish waters almost exclusively south of Anholt, in 7 to 40 meters depths, most frequently in 13 to 30 meters depths. The innermost localities known are Davids Banke north of Bornholm and a place east of Bornholm where only very small specimens were met with which were much reduced, many of the joints bearing only one branchlet. The specimens from the Kattegat were up to 5 cm high while those from the southern waters reached only a length of 2,5 cm. It usually grows on other Algæ e. g. *Delesseria sinuosa, Furcellaria fastigiata* and *Corallina offinalis* and on Hydroids. It has been met with in the months April to August and bore sporangia in the same months. Antheridia were met with in May and June. — In the western part of the Baltic Sea it has been found by REINKE in four localities, at the west coast of Sweden it has not been found north of Laholms Bugt (KYLIN).

Localities. Kn: Harbour of Frederikshavn. — Ke: ER, Fyrbanken, east of Anholt, 28 meters. — Ks: EO, north of Lysegrund, 26 m. — Sa: PJ, Ebeltoft Vig, 13 m; PL, Wulffs Flak; DK, Bolsaxen, 14 m. — Lb: Fænø Sund, 15 m; dQ, bank south of Lyø, 22 m; dH<sup>1</sup>, east of Hesteskoen, 18—19 m. — Sb: DL, south of Refsnæs, 7 m; cN, south-west of Musholm, 18 m; cL, north-east of Sprogø, 25—27 m; Z, off Skagbo Huse, 19 m; UH and UT, Langelandsbelt, 19—22 m; US, Langelandsbelt, c. 40 m; US<sup>1</sup>, near the former, 20 m. — Su: Off Aalsgaarde, shelly bottom (Boye Petersen); north of Lappegrund, 19—26 m (Henn. Petersen); bM, south of Hveen, 23 m. — Bw: Trindelen, west side of Kegnæs, Als; UL, Øjet, 20 m. — Bb: SN, Davids Banke, 15—17 m; 3 miles S.S.E. of Nexø, 21 m (C. A. J.).

MAGNUS (Bot. Erg. Nordseefahrt p. 67) has reported *Callithamnion Plumula* Lyngb. from "N.W. von Roesnäs 28 Faden" and "N.W. von Fænö 16—10 Faden". Without examining the specimens in question it is impossible to decide whether they must be referred to *A. Plumula* or *A. boreale*.

# Ceramium (Roth) Lyngbye.

In 1908 Dr. HENNING PETERSEN published a monograph on the Danish species of the genus *Ceramium*, based principally on the material contained in my collections, and in a later paper (1911) he has again mentioned some of the species. Since the publication of these papers I have made further collections of *Ceramia* in the Danish waters, and Dr. PETERSEN has then readily complied with my request to examine these new collections together with his own later gatherings, and he has at the same time made a revision of his earlier determinations. These investigations have in several cases led Dr. PETERSEN to another limitation of the species, and as the new collections have brought species to light which were formerly not known from the Danish coasts, the number of Danish species has been increased from 10 to 18. Dr. PETERSEN has communicated to me descriptions and remarks on several of the species, which are given below, partly with Dr. PETERSEN's own words, further some drawings and a new key to the species, while I contribute the account of the occurrence and fructification of the species and give some drawings and a few general remarks on the morphology.

The vegetative morphology and development has been treated by CRAMER (1863).

The germination has been repeatedly studied by various authors, (comp. KYLIN 1917, where further literature is quoted). I have examined the germination of the tetraspores of *C. rubrum* and of the paraspores of *C. strictum* which take place in essentially the same manner, but I have nothing to add to the earlier descriptions. In more developed plantlets several multicellular rhizoids are developed from the corticating bands near the base of the plant, giving rise to adhesive discs (holdfasts)



Fig. 308. Ceramium diaphanum. Base of plant with downward growing branches producing finally terminal hapters. 48:1.

ment (1908 p. 50); they were recorded in several Danish species, as a rule in particular male plants, in C. fruticulosum in the same plants as the carpogonia.

The development of the cystocarps was described by JANCZEWSKI (1876), PHILLIPS (1897) and KYLIN (1923). In the species examined by the two first-named authors two carpogonial branches were found, one on each side of the auxiliary mother-cell, while KYLIN found only one in *C. rubrum*. In *C. fruticulosum* I found two (fig. 309). In the same species I found numerous spermatia loosely adhering to sterile hairs in the neighbourhood of the procarps (fig. 309 *B*).

The division of the tetrasporangia in the

at their tip. In fig, 308 is represented a long rhizoid showing narrow cortical bands at the nodes like the upright fronds.

The hyaline hairs have been mentioned by HENN. PE-TERSEN (1908) and by me (1911). They have been met with in almost all the species and may perhaps occur in all of them. However, in one species they have not been observed, namely in *C. cimbricum*, which has only been found in the Limfjord in rather deep water of slight transparency. These hairs may be very numerous and vigorous (K. R. 1911, fig. 3) and remain alive long; in other cases they reach only an inconsiderable size and decay early (fig. 314). They appear early in the plantlets a few days after the beginning of the germination. According to PETERSEN the hairs are wanting in winter.

Gland cells occur in *C. tenuissimum* and *C. Areschougii*, as shown by PETER-SEN (1908 and 1911).

The antheridia were briefly described and pictured by BUFFHAM (1884 p. 342 pl. XII

figs. 2-5, 1888 p. 260,

pl. XX fig. 4), and

HENN. PETERSEN de-

scribed their develop-

#### Fig. 309.

Ceramium fruticulosum. A, young carpogonial branches, partly still tricellular. B, carpogonial branch with still infertilised trichogyne; numerous spermatia adhere loosely by a sterile hair. C, fertilised carpogonium. A, B 625: 1, C 390: 1. genus Ceramium is said in the systematical works (KÜT-ZING, J. AGARDH, HAUCK) to be tetrahedral (triangular) and most of the pictures of KÜTZING and HARVEY are in accordance with this statement. In Kützing's figure of C. rubrum (Tab. phyc. XIII pl. 4), however, the oblong sporangia are shown divided by a transversal and a vertical wall. HENN. PETERSEN does not mention the mode of division, but his picture of C. strictum (1908 fig. IV, 1) shows very clearly a similar rectangular division, while

the mode of division is not quite clear in his fig. III, 2 of



Fig. 310. Ceramium vertebrale. An isolated tetrasporangium seen from three sides. 230 : 1.



Fig. 311. Ceramium diaphanum. Tetraspore mother-cells, dividing. Only two, resp. three nuclei were present in the sections. In A tetrahedrical division. 390 : 1. C. tenuissimum. COLLINS and HERVEY<sup>1</sup> describe a new species C. cruciatum in 1917, the sporangia of which are "cruciate, sometimes regularly, sometimes decussately". And recently Mrs. WEBER-VAN BOSSE<sup>2</sup> describes another new species C. cingulatum with a similar division of the sporangia. As I have myself found sporangia with rectangular division in C. vertebrale (figs. 310, 322), C. septentrionale a. o. species but on the other hand have also ascertained the occurrence of tetrahedral division in Danish species (e. gr. C. tenuissi-



Fig. 312.

Ceramium rubrum. Tetrasporangia in division. A-C after the division of the nuclei but before the division of the cell. F two sections of the same sporangium. 340:1.

<sup>1</sup> The Algae of Bermuda. Proceed. Amer. Acad. Vol. LIII No. 1. Cambridge 1917, p. 144.

<sup>2</sup> Liste des Algues du Siboga. III Rhodophyceae. 2<sup>e</sup> partie. Leiden 1923, p. 332. D. K. D. Vidensk. Selsk. Skr., 7. Række, naturvidensk, og mathem. Afd. VII. 3.

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mum, fig. 314) I judged it convenient to examine the division process itself in imbedded proofs of *C. diaphanum* and *C. rubrum*, and in both species tetrahedral and rectangular division was ascertained in different sporangia of the same plant. In every case the division of the nuclei was accomplished before the division began (fig. 312 A - C). The division of the cell takes place by walls growing gradually from the periphery towards the centre of the cell, but the orientation of the walls is variable. In figs. 311 A and 312 E are represented typical tetrahedral divisions. In



Fig. 313. Ceramium diaphanum. Young heap of paraspores. 390 : 1. other cases a transversal wall is first formed as an annular list while two other walls, perpendicular to the first are formed a little later but before the first wall is finished (figs. 311 B, 312 D, F, H). The division seems thus in all cases to be a division in four of one cell and not a bipartition of the spore-mothercell into two cells which afterwards divide into two.

Paraspores occur in *C. diaphanum*, *C. strictum* (comp. HENN. PETERSEN 1908 pp. 51, 85) and *C. Deslongchampsii*, and I have found a couple of sori of paraspores in a specimen of *C. vertebrale* which bore at the same time tetrasporangia (fig. 323). These paraspores were remarkable by peculiar pseudopodia from the protoplast to

the membrane. The paraspores, as shown by HENN. PETERSEN, develop from a superficial cortical cell (fig. 313), often from a marginal cell of a cortical band. They never occur in the sexual plants but often in tetrasporiferous plants.

HENN. PETERSEN states briefly that he has met with a sort of monospores in C. diaphanum (1908 p. 14).<sup>1</sup>

### Key to the Danish species of Ceramium.

### (By HENNING E. PETERSEN).

- 1. Cortication only at the nodes; distinct cortical bands.
  - 2. Gland cells present, outer edge of apex dentate ..... 1. C. tenuissimum.
  - 2\*. Gland cells wanting, outer edge of apex usually even.
    - 3. Cortical bands usually over 100  $\mu$  high, lower border-cells irregularly shaped; frond not creeping.
      - 4. Apices always curved inward.

5\*. The named cells usually  $17-20\,\mu$  in transversal diameter .... 3. C. strictum.

- 4\*. Apices always straight.
  - 5. Bands of about equal height and breadth ........... 5. C. Deslongchampsii. 5\*. Bands usually broader than high; often up to 30-40 axial
    - cells between the bifurcations; only in the inner waters ... 6. C. vertebrale.

<sup>1</sup> Dr. PETERSEN refers to GOBI's fig. 8 in Die Rothtange des Finn. Meerbusens. Mém. Acad. St. Pétersb. XXV No. 7, 1877; but the bodies alluded to in this figure according to the author represent tetrasporangia ("Tetrasporen") the division of which is not shown.

$3^*$ . Bands very narrow, usually c. 50 $\mu$ , rarely over 100 $\mu$ high, con-
sisting of 1-3 (usually 2) transversal rows of cells; cells in the
lower edge of the bands often with parallel upper and lower sides;
frond sometimes creeping 4. C. cimbricum.
1 <sup>*</sup> . Cortication partly or entirely continuous.
2. Cortication with distinct bands in the upper part or in a greater
part of the frond.
3. The outer cortical cells very small, 7–10 $\mu$ in diameter, usually
longitudinally elongated
3*. Not so.
4. Bands with sharply limited lower border occur; bands at least
thrice higher than the diameter.
5. Ramification biseriate alternate or dichotomous; in the
latter case the apices are incurved 16. C. fruticulosum.
5*. Branches not biseriate, apices straight, at least in older
specimens.
6. Bands often over 2 mm high, usually distinct below,
though often approaching each other 17. C. septentrionale.
6 <sup>*</sup> . Bands not 10 high. Cortication usually continuous
below; apices thin 15. C. Areschougii.
4*. Bands with sharply limited lower border do not occur; bands
not so high, increasing downwards in various degree.
5. Cells of the bands, in particular of the upper ones, are
arranged in distinct longitudinal rows; distinct bands only
in the upper parts of the frond 13. C. scandinavicum.
5*. Cells not in distinct longitudinal rows; distinct bands in
the upper parts or in greater parts of the frond.
6. Bands slightly increasing downwards, cells in the lower
border often broad 14. C. abyssate.
6 <sup>*</sup> . Bands much increasing downwards; altogether slight
difference between upper and lower border of the band.
7. Cortication usually continuous over more than two
thirds of the length.
6. Apices very thin, often capitary, inten branched.
branchas
0* Pamification usually pronouncedly dichotom
ous secondary branches not much developed 8 C rubriforme
8* Anices vigorous slightly branched near the top
9 Colour dark often much developed main
stems and secondary branches: cortication
continuous over the greater part of the frond 11 <i>C. atlanticum</i>
9*. Colour light: vigorous main stems without
secondary branches 10. C. Rosenvingij
7*. Bands distinct in the upper third of the frond:
light colour. 7. C. danicum
2* Cortication continuous over the whole frond 18. C. rubrum.

\*

# 1. Ceramium tenuissimum (Lyngb.) J. Agardh.

J. Agardh, 1851, p. 120; Henn. Petersen 1908, pp. 54, 49 pl. I Fig. 1, 190, p. 97; idem 1911, p. 97. *C. diaphanum* var. *tenuissima* Lyngbye Tent. p. 120.

As shown by HENN. PETERSEN, the species is easily distinguished by the denticulate outline of the young incurved branches, by the presence of gland cells and by the extruding tetrasporangia usually single in the cortical zones. It reaches a length of 8—10 cm; in the Little Belt and the South Fyn Waters, however, specimens higher than 3 cm were not met with. It occurs in all seasons; in winter,



Fig. 314. Ceramtum tenuissimum. A. upper end of filament with hairs, partly decayed. B, band with tetrasporangium. A 390 : 1. B 230 : 1.

however, it is only 1—2 cm high. It is spread in all the Danish waters from the Skagerak to the south Fyn waters, but has not been met with in the Great Belt, the Sound and the Baltic Sea; it thrives well in the fjords (Limfjord, Isefjord, Odensefjord). It occurs from a little under low-water mark downwards; in the eastern Kattegat it has been met with in 22,5 m depth. It has been found with tetrasporangia in July and August, with cystocarps in July and September. Antheridia were met with in July 1923; they covered the surfaces of the joints in longer stretches of the frond. Epiphytic on various Algæ and on Zostera.

Localities. Sk: YN<sup>2</sup>, E. of Bragerne; SY, N. of Løkken, 13 m; XO off Hirshals; Hirshals mole (Børgesen) and near land. — Lf: Nissum Bredning; ZS, ZY; Thisted Bredning: MH; Sallingsund: Nykøbing; Løgstør Bredning:

LS, 7 m, bT; off Feggeklit, 4 m. — Kn: Off Hulsig, 8 m (B. Petersen); N.E. of Hirsholm (Ostenfeld); TP, Tønneberg Banke, 16 m; Brune Rev by Frederikshavn (H. E. P.); ZP, UC, N. of Nordre Rønner. — Ke: Fladen: ZG, ZF, VY, 18—22,5 m; Gilleleje (Lyngbye). — Km: Læsø Rende: Dana St. 2919 (C. A. J.); BO off Stensnæs; ZC<sup>1</sup> within Kobbergrund; VL south of Tangen; BH off Gjerrild Klint. — Ks: Isefjord: EH off Lynæs, near Rørvig (Joh. Lange), Lammefjord. — Sa: Reef by Kalø; BB, Søby Rev; Korshavn, reef; Odensefjord, Hofmansgave (Lyngbye, C. Rosenberg). — Lb: Helnæs Hoved Flak; CC, Hornenæs. — Sf: Shoals off Nakkebølle Fjord.

## 2. Ceramium diaphanum Harv. et J. Agardh.

Henn. Petersen 1908 pp. 56, 87 figs. I,1, II and IV,1, 4, pl. I figs. 2—5, pl. II figs. 3—4, 1911 p. 98, fig. I,1, 4, pl. I fig. 2.

This species is common in the inner Danish waters where it usually grows near the low-water mark on piers in harbours and in stony reefs in about one meter's depth, more rarely descending to 4—5 meters depth or even to 13 m. It grows on stones and wood, *Chorda Filum, Zostera, Fucus vesiculosus* a. o. Algæ. It reaches a length of 8 cm. It has been met with from April to November but is most developed in the summer months. The most frequent fructifications are tetraspores and paraspores, often occurring in one individual. Tetraspores have been met with in May to Sept., paraspores in July to Sept., anther-

idia and cystocarps each once in September.

Dr. PETERSEN has in 1908 distinguished 5 forms to which he has now added the f. *umbellifera* here described.

1. F. typica.

2. F. strictoides,

subf.  $\alpha$ ,

subf. β, corticatula Kylin (Cer. corticatum Kylin 1907 p. 176).

3. F. modificata.

4. F. radiculosa.

5. F. zostericola.

6. F. *umbellifera* H. Prtsn. n. f. — Much branched towards the apex, with short internodes and somewhat divaricate branches. Form from protected water, analogous to *C. rubrum* f. *radians* and *C. strictum* f. *stricto-tenuissima*. Related to f. *strictoides*. (Henn. Petersen).

Fig. 315.

Ceramium diaphanum. Young pseudodichotomy. In both branches the last segment is on the point of branching. t, apical cell; s, new branches, c, central cell. 390:1.

Localities. F. typica. Ks: Harbours of Anholt and Lynæs. — Sa: Harbours of Koldby Kaas and Horsens. — Lb: Harbour of Rosenvold. — Sf:

Svendborg. — Sa: Hofmansgave (Hofm. Bg.). — Sf: Svendborg. — Su: Harbour of Sletten. — Bw: Harbour of Gedser. — Bm: Rødvig; Faxe Ladeplads.

F. strictoides. Ks: 3 localities in Isefjord. — Sa: Hofmansgave (Hofm. Bg.). — Sf: UV, 13 m. — Sb: 3 loc.; Nakskov Fjord (Th. Mortensen). — Sm: Venegrund. — Su: 5 loc.; harb. of Helsingør; Kalvebod Strand (M. L. Mortensen). — Bm: 1 loc.

F. modificata. Ke: Gilleleje (Lyngbye). — Ks: Harbour of Grenaa; near Rørvig. — Sa: 4 local. — Lb: 3 loc. — Sf: Svendborg Sund (E. Rostrup). — Sb: 4 loc. — Sm: 6 loc. — Su: 6 loc. — Bw: Near Sønderborg. — Bm: Stevns, Rødvig, harbour of Hesnæs. — Bb: 6 loc. around Bornholm, Christiansø, That.

F. radiculosa. Bb: Allinge, Gudhjem, Christiansø.

F. zostericola. Lf: LR, E. of Livø. — Sb: GY, 5,5 m. — Sm: HI; Stubbekøbing; Guldborgsund. — Su: Knollen.

F. umbellifera. Ke: Gilleleje, E. of the harbour. - Su; Bay of Hornbæk.

#### 3. Ceramium strictum Greville et Harvey.

Harvey, Phyc. Brit. III Plate 334. Henn. Petersen 1908 pp. 61, 89, Figs. IV,2, 3. Tab. I Figs. 6, 7, Tab. II Fig. 1; idem 1911, p. 98, Fig. I,2, 3.

With regard to the relation of *Ceramium strictum* to *C. diaphanum* reference may be made to the quoted papers by Dr. PETERSEN. *C. strictum* in the Danish waters reaches a length of 10 cm. Paraspores are the most frequent organs of reproduction; they were met with in almost all the waters where the species occurs, in May to September. The tetrasporangia are much less common (once in Sm and some places in **Bb**, July and September); they occur partly in paraspore-bearing specimens,

Sexual reproduction seems to take place much more rarely than the asexual. Antheridia have been met with only in a few places (Su, Bw and Bb, July, August);



Fig. 316. Ceramium strictum, from Bornholm. A, upper end of shoot with hairs. B, upper end of shoot of female plant. pc procarpial branch. 390 : 1. they covered completely globular joints. Cystocarps have only been observed in one place (**Bb**, August); they were subtended by up to six involucral ramuli. A specimen collected by dr. O. PAULSEN in Kriegers Flak (**Bm**) in 15 meters depth, showed witches' broom-like bushes of dark-red, much branched, short straight branches with short articles and with monopodial, lateral branching. The species has only been met

with in April to October. Ceramium strictum occurs in all the Danish

waters within Skagen, most frequently in the inner waters, from low-water mark to c. 10 meters depth, more rarely deeper; it has been met with in the greatest depth at Bornholm (29 m).

Dr. Petersen distinguishes forma *vera* and f. *stricto-tenuissima*, characterised by more divaricate branches and more elegant habit.

### F. vera H. Ptrsn.

Localities. Lf: 5 localities. Oddesund, S. side of Jegindø Tap. — Kn: FF, Læsø Trindel, 15 m (?). — Ke: East end of Anholt; IC, Store Middelgrund, 10,5 m; about same place (Dana St. 2925 C. A. J.); Gilleleje, 1—5 m. — Ks: EH, West of Lynæs; GG, Sjællands Rev. — Sa: GE near Sejerø; PG, west of Hatter Rev; Begtrup Vig, stony reef. — Lb: Off Ivernæs; Aarøsund; DB, Lillegrund. — Sf: CU; CV. — Sb: LK, Elefantgrund; Kerteminde; Nyborg; UF, N. of Langeland; Snøde Rev; Smørstakken; Nakskov Fjord (Th. Mortensen). — Sm: CL, Raagø Sund (+); CO; Holsteinborg Nor; Karebæk Fjord (Warming); Petersværft; Grønsund, 4 m. — Su: Off Aalsgaarde (3, Aug.) (H. E. P.); N. of Julebækshusene; the point at Hvidøre; Copenhagen; SA, SB, Flinterenden. — Bw: bV, N.E. of Kobbel Skov; bZ and dO, S. of Als; DU, off Dimes Odde; KY, Femerbelt, 12,5 m; KZ, off Kramnisse; Gedser Rev, 8,5 m, (3, July). — Bm: KS, E. of Falster; VH, S. of Møen; Præstø Fjord; Faxe Ladeplads; off Mandehoved, Stevns; QF, S. of Saltholm; QH, Falsterbo Rev; bP, Kriegers



Fig. 317. Ceramium strictum, from Bornholm. The dotted part of the wall of the internodial cell was more deeply stained by hæmatoxylin than the lowermost part; the latter was probably younger. 230:1.

Flak (O. Paulsen). — **Bb:** N.W. of Sandvig on rock; Allinge  $(\stackrel{\circ}{\supset} \bigcirc)$ ; Davids Banke, 15—29 m; YF, within Arnager Rev; YE, off Øleaa; near Salthammer Rev (+, p).

#### F. stricto-tenuissima H. Ptrsn.

New localities. Sa: Hofmansgave (Hofm. Bang). - Sb: DN, Vengeance Grund, 12 m.

### 4. Ceramium cimbricum Henn. Petersen n. sp.

C. interdum repens, subdichotome ramosum, apicibus rectis, longis, sæpe inæqualibus; zonis semper distantibus, marginibus non crescentibus, e cellulis paucis



Fig. 318. Ceramium cimbricum. A, young pseudodichotomy. B-D, adult cortical bands. Henn, E. Petersen del. 330 : 1.

compositis, plerumque 2—3 cellulis altis, maximis 60  $\mu$  altis, 100  $\mu$  latis, aliis 1—2 cellulis altis, c. 25  $\mu$  altis, 50  $\mu$  latis, cellulis inferioribus sæpe usque ad 32  $\mu$  latis; internodiis maximis zonis 5—7-plo

longioribus. — Color rubro-violaceus. — Pili, tetrasporangia et organa sexualia non observata (figs. 318, 319).

Habitat in Limfjorden.

Affine *C. stricto* sed differt zonis angustissimis et ramificatione. Apices juveniles sæpe curvatura characteristica supra nodos instructi sunt (fig. 318*A*). (Henn. Petersen).

This small *Ceramium*, which has only been met with in two localities in the Limfjord, was first referred to *C. strictum*. However, as it differs by the habit, the branches of the pseudodichotomies being often of unequal size, and by the very narrow cortical bands, Dr. PETERSEN has distinguished it later as a distinct species and given me the diagnosis above. *C. cimbricum* 



Fig. 319. Ceramium cimbricum. A, end of shoot. B, branching. C, D, bands and internodial cells. 345 : 1.

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Fig. 320. Ceramium Deslongchampsii. Part of frond with two bands. Henn. Petersen det. 270:1.

Fig. 322. Ceramium vertebrale. Part of frond with tetrasporangia. 230:1.

is found growing on *Laomedea* and on various algæ, partly creeping with rhizoids, reaching a length of 1-3 cm. It has only been found sterile.

Localities. Lf: near Jegindø Tap, 5,5 m; IT, West of Ejerslev Røn, 7 m.

# 5. Ceramium Deslongchampsii Chauvin.

J. Agardh, 1851 p. 122; Henn. Petersen 1908 p. 83 (89).

This species which is principally characterized by the cortical bands being of almost equal height and breadth,

and by the straight ends of the branches, has only been recorded with certainty from one locality, viz. the harbour of Frederikshavn, where it occurs constantly at the ends of the northern outer mole and of the northern transverse mole. It grows at low-water mark and reaches a length of 4 cm. All the specimens collected were sterile till July 1923 when

specimens up to 6 cm high were met with, partly with tetrasporangia or paraspores. The sporangia were vert-



Fig. 321. Ceramium Deslongchampsii. Heap of paraspores. 200:1.

icillate, the fertile joints much swollen. The heaps of paraspores are solitary or several on the same joint (fig. 321, comp. HARVEY Phyc. Brit. pl. 219).

Localities. Lf: Nykøbing Mors (Børgesen), referred with doubt to this species. — Kn: Harbour of Frederikshavn (April—August).

#### 6. Ceramium vertebrale Henn. Petersen.

Henning Petersen, 1908 p. 63, 90 Fig. V, Tab. II Fig. 2.

As shown by Dr. PETERSEN, this species is on the one hand related to *C. diaphanum* and *C. strictum*, on the other hand to *C. Deslongchampsii*. It is distinguished in particular by the last branches becoming straight, by the great number of articles in the internodes and by the thick cell-membranes. It reaches a length of 4 to 6 cm.

Dr. PETERSEN did not find hairs in this species. I observed these organs in specimens gathered in August; the rare occurrence of hairs probably depends on the fact that the species has only been recorded in July and August. Tetrasporangia were observed in specimens collected in August at Bornholm; I found them cruciately divided (or better perpendicularly divided). The tetrasporangiferous bands which contain one or a small number of sporangia are considerably swollen (figs. 322). In a tetrasporangiferous specimen a few sori of paraspores were observed, developed from superficial cortical cells (fig. 323). *C. vertebrale* occurs in 5,5 to 15 meters' depth. It has only been recorded from localities around Bornholm and from one locality at the boundary between the Sound and the Baltic Sea.

Localities. **Bm:** RH, at Knollen west of Saltholm. — **Bb:** SN, Davids Grund, 15—17 m; SL, off Allinge; SO, off Gudhjem; SK, Højbratterne; SH, South of Broens Rev; YF, within Arnager Rev; SF, Adler Grund. — (The locality Nyborg Havn recorded by



Fig. 323. Ceramium vertebrale. Zone with a heap of paraspores. From a dried specimen. Delicate pseudopodia radiate from the protoplasts towards the outer wall.

Dr. Petersen (1908 p. 64) must be omitted, the specimens being now referred by Dr. Petersen to C. strictum f. radiculosa).

# 7. Ceramium danicum Henn. Petersen n. sp.

C. Rosenvingii H. Petersen f. tenuis et f. intermedia H. Petersen 1908, pp. 66, 90, pl. II figs. 5, 6.

Frons dichotoma, apicibus incurvatis teretibus, in partibus superioribus et intermediis zonis discretis, in partibus inferioribus cortice continuo instructa. Zonæ juveniles marginibus non crescentibus, adultiores ab utroque margine crescunt ut in *C. Rosenvingii*. Interstitia pellucida interdum zonis 5—7-plo longiora. — Cysto-carpia in ramis primariis. — Color subruber. — Individua minus corticata habitum *Cer. stricti* offerunt.

*Ceramium Rosenvingii* as described by me in 1908, comprises partly forms with feebly developed cortex, with the habit of *C. diaphanum* and *C. strictum*, partly forms with somewhat more developed cortex and finally forms approaching to *C. rubrum*. As such a variation must be considered too great, even when taking the species in a wide sense, I have found it correct to divide the species into two. It would perhaps be most correct to distinguish three species corresponding to the three forms which were described in 1908; however, I am not satisfied whether there is so distinct a limit between f. *tenuis* and f. *intermedia* that they ought to be regarded as distinct species. On the other hand f. *transgrediens* is so distinct from the two just named forms that it seems warranted to draw a specific limit between them. I describe therefore a new species comprising the forms *tenuis* and *intermedia*, while the name *C. Rosenvingii* is retained for the f. *transgrediens*.

*C. danicum* comprises forms with continuous cortex at the base or reaching a little over the middle of the frond and with the habit of *C. diaphanum* or *C. strictum* in the upper parts of the frond, while *C. Rosenvingii* comprises more robust forms with continuous cortex reaching to the apex or near the apex, with rubroid branches and without any habit of *C. strictum*. HENN. PETERSEN.

D, K. D, Vidensk. Selsk. Skr., 7. Række, naturvidensk. og mathem. Afd. VII. 3.

C. danicum has been met with in May to July, in 4-13 meters' depth. It reaches a length of 15 cm and has been found with antheridia in May, with cystocarps and tetraspores in July.

Localities. Sa: GC, north of Fyn. — Lb: DF, E. of Bogø; DC, Aakrog Bugt; DB, Lillegrund; DX, Vodrups Flak. — Si: UX, Skjoldnæs; CV, Billes Grunde. — Sb: UE, Vresens Puller; UU, Snøde Rev. — Bw: DU, off Dimes Odde. — Bm: KT, Gedser Rev; at Stevns Klint (Joh. Lange).

#### 8. Ceramium rubriforme Kylin.

#### Kylin 1907 p. 183, pl. 7 fig. 7.

After having examined recently original speeimens of *C. rubriforme* Kylin Dr. PETERSEN refers to this species two specimens from one locality in the northern Kattegat and with doubt one from the South Fyn Waters, formerly referred to *C. Rosenvingii* f. *intermedia*. The former are 15 cm long and bear ripe tetrasporangia (May).

Localities. Kn: Krageskovs Rev, 4-5 m. - Sf: (?) CU, at the N. end of Flæskholms Flak, 5,5 m.

#### 9. Ceramium arborescens J. Agardh.

J. Agardh 1894 p. 33; Henn. Petersen 1908 p. 67 and 91, pl. III figs. 1-2; 1911 pl. II fig. 6.

The species is rather extensively spread in the Danish waters from the North Sea to the Baltic Sea around Møen. It seems to be only little influenced by the salinity of the water, for the maximal length, 17—18 cm, is reached in the North Sea and the Baltic Sea as well. It occurs mostly near low-water mark, but has been met with in depths down to 12 meters. It is most frequent in spring (May) but has been observed in the months of April to September, with cystocarps and tetrasporangia in May to July.

Localities NS: Thyborøn, pier. — Sk: Hirshals, E. side of mole and stony reef near land. — Lf: Glyngøre. — Kn: Frederikshavn, harbour; boulder at Jegens Odde. — Ke: GI, Ostindiefarer Grund. — Ks: OP, Lysegrund. — Sa: KL, Bjarkes Grund; Kalø reef; Korshavn, reef; Hofmansgave (Hofm. Bang); Odense Fjord (C. Rosenberg). — Lb: Knudshoved, S. of Anslet Hage. — Sf: Svendborg. — Sb: Korsør (Hornemann); DN, Vengeance Grund, 12 m; UF, near Hov Sand; DQ, off Nakskov Fjord; UR, S. of Albuen. — Su: Dragør. — Bw: UQ, off Tillitse; UP, off Kramnisse Gab. — Bm: Stevns Klint, washed ashore (Joh. Lange); Rødvig, reef E. of the harbour; Klintholm harbour.

### 10. Ceramium Rosenvingii Henn. Petersen emend. auct.

C. Rosenvingii Henn. Petersen f. transgrediens Henn. Petersen 1908, pp. 66, 91, figs. VI,2, VII,1, pl. II fig. 7.

Frons dichotoma, apicibus rectis vel curvatis. Corticatio confluens, exceptis apicibus ramisque superioribus. Zonæ corticales discretæ ab utroque margine crescentes. Tetrasporangia verticillata non erumpentia. Color subruber. HENN. PETERSEN.

With regard to the present circumscription of the species comp. above p. 381. It has been collected in April to July, most frequently in May, in 1 to 9,5 meters' depth.

The frond reaches a length of up to 14 cm. Tetrasporangia have been met with repeatedly in May to July, antheridia once in May, cystocarps only once in a dubious specimen from the southern Kattegat, gathered in July. The tetrasporangia were at any rate often cruciately divided.

Localities. Kn: Skagen, south side of Grenen. — Ks: (?) EJ, Lysegrund; OT, Hastens Grund. — Sa: PG, W. of Hatterrev; Hofmansgave (Lyngbye). — Lb: FZ, Kasserodde; Baaring, harbour; Dyreborg. — Sf: CV, Billes Grunde; DZ, Egholms Flak. — Sb: UU, Snøde Rev.

### 11. Ceramium atlanticum Henn. Petersen.

Henning Petersen 1911 p. 112.

Dr. Petersen refers to this species a specimen collected in April 1906 in the harbour of Skagen then unfinished. It has formerly (1908) been referred to *C. fruticulosum* f. *rubroides*. It was 13 cm high, but still sterile. *C. atlanticum* has till now been recorded from Iceland and the Færöes.

Locality: Kn: Harbour of Skagen.

#### 12. Ceramium Boergesenii Henn. Petersen.

Henning Petersen 1911, p. 108, fig. I, pl. II fig. 8. C. fruticulosum f. rubroides Henn. Petersen 1908 pp. 73, 93 ex parte, pl. IV fig. 1.

Dr. PETERSEN has found that some specimens from the Limfjord, formerly referred to *C. fruticulosum* f. *rubroides*, must be referred to *C. Boergesenii* which was described on the basis of specimens from the Færöes, and which is easily recognisable by the characteristic small-celled cortication. The species was met with near low-water mark in July and September, in all the places with tetrasporangia, in one place with cystocarps in July. The collected specimens are 7-9 cm long.

Localities. Lf: Thisted; Nykøbing; Hals. — Kn: Two specimens from Nordre Rønner must probably, according to Dr. Petersen, be referred to this species though the cortication is not quite typical.

### 13. Ceramium scandinavicum Henn. Petersen. n. sp

C. fronde regulariter dichotoma  $\pm$  corymbosa fastigiata apicibus incurvatis, in partibus basalibus et intermediis cortice continuo, in partibus superioribus interstitiis pellucidis semper brevibus instructa. Zonæ superiores ab initio adproximatæ, marginibus vix crescentibus, deinde ab utroque margine inprimis a superiori crescentes. Cellulæ marginis inferioris semper latæ in seriebus longitudinalibus ordinatæ. Cystocarpia in ramis principalibus; antheridia in soris; tetrasporangia verticillata in partibus nodalibus parum erumpentia. — Color in individuis danicis subruber, in individuis ex regionibus borealibus fusco-rubiginosus. (Fig. 324).



Fig. 324. Ceramium scandinavicum. Cortical band. H. Ptrsn. del. 330:1.

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This species comes near to *C. atlanticum*, *C. Rosenvingii* and *C. rubriforme*, from which it differs by cortical bands more resembling those in *C. Areschougii*, with cells arranged in characteristic rows in the lower part of the zones. In contradistinction to *C. atlanticum* the ramification is distinctly dichotomo-corymbose with slight formation of secondary shoots. The specimens from the Baltic Sea have formerly been referred to *C. Rosenvingii* f. transgrediens. (HENNING PETERSEN).

In the Northern Kattegat it has been found with antheridia, cystocarps and tetrasporangia in June. The Danish specimens reach a length of 8,5 cm.

Localities. Kn: Several places in the neighbourhood of Frederikshavn, e. g. Degets Nordøstrev. — Bw: KU, Schönheyders Pulle. 11 m. – Bm: VH, Böchers Banke.

# 14. Ceramium abyssale Henn. Petersen n. sp.

#### C. rubrum f. decurrentoides Henn. Petersen 1908, pp. 82, 96.

C. fronde dichotoma vel subdichotoma, apicibus excl. juvenilibus  $\pm$  rectis, cortice continuo vel zonis juxappositis difficile distinguendis instructa. Zonæ discretæ solomodo in basibus ramorum occurrunt, typo C. fruticulosi vel C. Areschougii, in marginibus superioribus magis quam in inferioribus crescentes. Cystocarpia in ramis principalibus vel secundariis. Tetrasporangia verticillata vel sparsa parum erumpentia. Color subruber. Hab. in regione abyssale.

On closer examination of the specimens which in 1908 were referred to *C. rubrum* f. *decurrentoides* I have found that these specimens, owing to the structure of the cortication, must rather be considered as related to *C. fruticulosum* than as a form of *C. rubrum*. It differs from *C. fruticulosum* in particular by the presence of distinct bands at the base of the branches. HENNING PETERSEN.

C. abyssale has only been met with in considerable depths, (8,5-31 m) in water of high salinity. It has been collected only in summer (July, August), with cystocarps and tetraspores; it reaches a length of 11,5 cm.

Localities. Ns: aF, Jydske Rev, 31 m. — Sk:  $ZK^{12}$ , off Lønstrup, 8,5 m; off Hirshals, 15 m. — Kn: FG, Herthas Flak, 21 m. — Ke: VY, Fladen, 18 m.

### 15. Ceramium Areschougii Kylin.

Kylin 1907, p. 179, Taf. 7 Fig. 6; Henn. Petersen 1908 p. 69, Figs. VI, 1 and VII, 2, 1911 p. 100 Fig. II.

The species has only been met with in summer, May to August, most frequently in June and July. It seems to thrive best in the inner western waters where it reaches a length of 15—16 cm. It has been found with tetraspores in May to August, with cystocarps in June and July, and both modes of fructification occur in all the waters where the species has been met with. It grows in all the waters in various depths from 1/2 m to 15 m; in the Little Belt it has once been found in a depth of 19 m or deeper. Localities. **Kn**: Various localities at Frederikshavn and Hirsholmene (C. M. Poulsen, H. E. P., K. R.); VT, VU, ZL, North of Læsø; FE, FF, Læsø Trindel, 10—15 m. — **Ke**: EU, Lille Middelgrund. — **Km**: FA and XC south of Læsø. — **Ks**: D, off the entrance to Isefjord. — **Sa**: FT, north of Samsø; hay of Nexelø (Th. Mortensen); BD, north of Tunø; AH<sup>1</sup>, Lillegrund at Fyns Hoved. — **Lb**: W. side of Æbelø; cV, off Røgle church; Snoghøj; Fænø Sund; Linderum; Aarøsund; Augustenborg Fjord. — **Sf**: UV, north of Ærø, 13 m; Nakke Odde, Avernak Ø. — **Bw**: Several places south of Als (bV, bY, bZ, cE, cG, near land at Kegnæs light-house, dK, Pøls Rev); LE, Vejsnæs Flak; LC, south of Gulstav.

# 16. Ceramium fruticulosum (Kützing) J. Agardh.

J. Agardh 1894 p. 31; Henning Petersen 1908 p. 70, 1911 p. 101.

Hormoceras fruticulosum Kützing, Linnæa 1841 p. 734, Spec. Algar. 1849, p. 676, Tab. phyc. 12 1862, pl. 73.

Dr. PETERSEN distinguishes the following forms:

 $\alpha$ , dichotoma H. Ptrsn. 1911 p. 71, H. Ptrsn. 1908, Tab. IV Fig. 2). Branches dichotomous or main stems may be developed.

 $\beta$ , penicillata (Aresch.) H. Ptrsn. 1908 Tab. IV Fig. 3; 1911 Plate I Fig. 4. (Hormoceras fruticulosum Kütz. sensu stricto et Ceramium penicillatum Aresch.; C. penicillatum f. fasciculata Kylin 1907 p. 177).

Very distinct main axes with lateral distichous shorter bushels.

The third form described in 1908, f. *rubroides* H. Ptrsn., has been withdrawn by Dr. PETERSEN as, on closer examination, it turned out to comprise two distinct species, most of the specimens belonging to *C. Boergesenii*, one to *C. atlanticum*.

C. fruticulosum occurs in the Northern Danish waters with comparatively high salinity. It has been met with in all seasons but most frequently in summer. It reaches a length of 9 to 13 cm. It was found sterile in winter (December), and spring (April), with tetrasporangia in May to October, with cystocarps in June to August; antheridia were met with in July. Antheridia may occur in the same individuals as the cystocarps; they cover completely the joints of the upper part of the branches. In female plants spermatia may be found adhering in great number to sterile hairs in their whole extent (fig. 309). Sexual specimens are at least just as common as tetrasporiferous ones. The species occurs always near the low-water mark where it may be rather abundant, in particular in exposed localities, in the Skagerak often in company with *Polysiphonia Brodiæi*.

The two varieties have much the same distribution (Skagerak, northern Kattegat) and occur often in the same locality connected with intermediate forms.

Localities. Ns: Thyborøn harbour, outside of W. mole  $(\beta)$ . — Sk: Hanstholm, 2 m  $(\beta)$ ; Bragerne, 2 m  $(\beta)$ ; Lønstrup  $(\beta)$ ; Hirshals, mole and stones  $(\alpha, \beta)$ : Højen  $(\alpha)$ . — Kn: Harbour of Skagen  $(\alpha, \beta)$ ; harbour of Hirsholm  $(\alpha)$ ; Deget  $(\alpha)$  (Boye Petersen); Rønnerne N. of Frederikshavn; Busserev, in Ascophyllum nodosum  $(\beta)$ ; harbour of Frederikshavn  $(\alpha, \beta,$  outside of S. mole); off Frederikshavn  $(\alpha)$ (A. Otterstrøm); Østerby harbour, Læsø  $(\alpha)$ ; harbour of Sæby  $(\alpha)$ . 17. Ceramium septentrionale Henn. Petersen.

Henn. Petersen 1911 p. 110, figs. II-IV.<sup>1</sup>

C. circinnatum Kützing f. borealis Foslie, The norweg. forms of Ceramium. D. kgl. norske Vidensk. Selsk. Skrifter 1893, Trondhjem 1894 p. 9.

Having examined FOSLIE's original specimens of the above named form I must consider this form as belonging to *C. septentrionale* described by me in 1911. It differs much from *C. circinnatum* which is characterised by downward growing zones. *C. septentrionale* is characterised by very high cortical bands, often reaching a height of 1-2 mm. (HENN. PETERSEN).

The Danish specimens referred to this species are all older specimens reaching a length of 13 cm, collected in July and August, with tetrasporangia and cystocarps. The tetrasporangia are cruciately divided. A specimen still in growth, with cystocarps, collected by A. OTTERSTRØM off Frederikshavn in Aug. 1902, formerly referred to *C. fruticulosum f. dichotoma* and represented under this name in Ceram. Stud. 1911 pl. I fig. 1 is now referred with some doubt by Dr. PETERSEN to *C. rescissum* Kylin.

Localities. Kn: Near Hjellen 6-7 m (H. E. P.), Københavner Rev (Boye Petersen) and Borrebjergs Rev (H. E. P.) near Frederikshavn.

### 18. Ceramium rubrum (Huds.) Agardh.

Henning Petersen 1908 pp. 73 and 93, Plate IV Figs. 5, 6, Plates V-VII; id. 1911 p. 113, Plates III, IV, V Figs. 25, 27-30.

Whereas in 1908 I referred certain forms with partly separate cortical bands to this species, I now judge it better to exclude such forms. Distinct bands have been met with in certain forms from deeper water, which in 1908 were named f. *decurrentoides*, and further in f. *irregularis* subf. *subcorticata*. As to the latter I am at present in doubt but I hope to contribute later to the question of its systematical position. On the other hand I do not doubt that f. *decurrentoides* cannot be referred to C. *rubrum*, and I have therefore described it as a new species, C. *abyssale* (p. 384).

As a new form is distinguished f. *furcata* which seems to be a f. *irregularis* developed from f. *prolifera*; it has a similar occurrence to this. It is characterised by robust branches and often straight apices with long forcipes. In certain cases it resembles *C. rubrum* f. *linearis* H. Ptrsn. 1911, p. 116 fig. VI, pl. IV fig. 21.

Another form new in the Danish flora is f. *fasciculata*. HENN. PETERSEN. The numerous forms occurring in the Danish waters of this widely spread species have been treated at length by Dr. PETERSEN (1908 pp. 73 et seq.). All the forms now distinguished by this author are named below.

The forms *prolifera*, *secundata* and *pedicellata* (*virgata*) have only been met with from Ns and Sk except f. *prolifera*, which has also been found in the Limfjord (N. side of Fur).

<sup>1</sup> In Cer. Stud. 1911, the pl. V fig. 26 is given as representing *C. septentrionale*, but this is erroneous; the figure in question represents either a new species or a particular form of *C. rubrum* (H. Ptrsn.)

Forma fasciculata H. Ptrsn. 1911 pp. 114, 116, pl. IV fig. 23. Habit of C. fruticulosum f. penicillata.

Localities. Ns: Thyborøn, groin. - Kn: Østerby harbour, Læsø.

Forma modificata H. Ptrsn.

Localities. Sk: Hirshals. — Lf: Common. — Kn: Common along the east coast of Jutland from Skagen to Sæby; Læsø Trindel. — Km: Asaa.

Forma *subtypica* H. Ptrsn.

New localities. Sk: Off Højen. – Ke: Gilleleje. – Km. – Ks. – Sa. – Lb: Bogense, harbour. – Sf. – Sb: Lundeborg, harbour. – Sm: Nykøbing F. – Su: SB, Flinterenden, 8,5 m.

Forma *furcata* H. Ptrsn. n. f., a vigorous f. *irregularis* with long straight ends of branches. The plant represented 1908 pl. 7 fig. 3 approaches to this form. (Henn. Petersen).

Localities. Sk: Off Hirshals, 14 m. – Lf: Nykøbing Mors. – Kn: Hirsholm, E. side of Tyskerens Rev (18 cm long).

#### Forma irregularis H. Ptrsn.

Localities. Lf: MD, off Doverodde. — Kn S. of Hirsholm. — Ke: Off Gilleleje. — Ks: RL, Isefjord. — Sa: Kyholm, Korshavn, Hofmansgave. — Lb: Off Stenderup; CC, Hornenæs. — Sf: Birkholm. — Sb: MN, N. of Asnæs; Lerchenborg (O. Smith), Kerteminde. — Sm: Guldborgsund; Petersværft. — Su: Hellebæk (Joh. Lange); RH, Knollen; SB, Flinterenden. — Bw: S. side of Als; CE, S. of Als, 13 m; UP, off Kramnisse Gab; Gedser. — Bm: Hesnæs; QZ, off Møens light-house; Stevns; QF, S. of Saltholm; RG.

Forma irregularis subcorticata H. Ptrsn.

Localities. Km: Boels Rev off Randers Fjord. — Su: BQ, off Ellekilde; PS, off Charlottenlund. — Bm: QG, off Bredegrund; QP, Kalkgrund; QR, Gyldenløves Flak; RB, within Hollænder Grund. — Bb: SQ, S. of Broens Rev, 9 m.

### Forma baltica H. Ptrsn.

Localities. Bw: UL, Øjet, 20 m. – Bm: QY, Bjelkes Flak; RC, within Danneskiold; QG, off Bredgrund. – Bb: Rønne; SH, Rønne Banke; SK, Højbratterne, 11 m; YG, Arnager Rev; SQ, S. of Broens Rev, 9 m; off Allinge, off Gudhjem; Christiansø; That.

### Forma radians H. Ptrsn.

New localities. Lf. — Sa: Hofmansgave. — Lb: E. side of Aarøsund. — Sf. — Bw: bV, N.E. of Kobbel Skov.

#### Forma divaricata H. Ptrsn.

New localities. Lb: Near Fænø Kalv; Augustenborg Fjord.<sup>1</sup>

<sup>1</sup> 19. C. rescissum Kylin. The above (p. 386) named specimen collected by Mr. A. OTTERSTRØM at Frederikshavn, earlier referred by me to C. fruticulosum f. dichotoma (1911 Tab. I fig. 1) must probably be referred to C. rescissum Kylin (1907, p. 182). This species is in my opinion nearly allied to C. septentrionale H. Ptrsn., but the latter differs from it by another habit, caused in particular by the straight or little branched apices. HENNING PETERSEN.

(Note added during printing).

# Rhodochorton Nägeli.

The systematical position of the genus *Rhodochorton* is undecided owing to the fact that cystocarps are unknown, and it is even uncertain whether its place is rightly within the *Ceramiaceæ*. There is much resemblance to certain species of *Acrochætium (Chantransia*<sup>1</sup>) of the family *Helminthocladiaceæ*, and transfers have in reality taken place between the two genera. Thus, *Rhodochorton chantransioides* has been transferred to the genus *Chantransia* by KYLIN in 1906, I have judged it necessary to transfer *Rh. seiriolanum* Gibs. to the same genus (see below, p. 390), and I think that it may be necessary also with *Rh. endophyticum* Kylin (1907, p. 188) which has only monosporangia, no tetrasporangia.

The cell structure usually gives good distinctive characters between the two genera, most of the species of *Acrochætium* having one chromatophore with a pyrenoid, while *Rhodochorton* has several band-like chromatophores. However, as shown by KUCKUCK (1897, p. 21), *Rh. floridulum* has several stellate chromatophores containing a central pyrenoid, which organ is otherwise only known within the *Helminthocladiaceæ*. On the other hand, the species of *Acrochætium* subg. *Grania* have several ribbon-shaped, more or less spiral-shaped chromatophores without pyrenoids in each cell.

Antheridia have hitherto not been observed in the genus *Rhodochorton*. As mentioned below, they have now been detected in *Rh. penicilliforme*; these organs give no indication of the systematic position of the genus as they are in accordance with the antheridia of other *Ceramiaceæ* and of *Acrochætium* as well. The discovery of the antheridia raises the hope that cystocarps may also be found.

The sporangia are always first divided by a transversal wall and afterwards by two vertical ones. The same mode of division occurs in *Acrochætium* and in *Antithamnion* as well.

#### 1. Rhodochorton penicilliforme (Kjellm.) K. Rosenv.

L. Kolderup Rosenvinge, Les Algues marines du Groenland. Ann. d. sc. nat. Bot. 7<sup>e</sup> série tome 19, 1894, p. 66; id., Deuxième Mém. Alg. mar. Groenl. 1898, p. 23; F. Børgesen, Mar. Alg. Fær. 1902, p. 389.

Thamnidium mesocarpum f. penicilliformis Kjellman, Spetsb. Thallof. I, Bih. K. Sv. Vet. Akad. Handl. Bd. 3 No. 7, 1875, p. 30.

Rhodochorton mesocarpum f. penicilliformis Kjellman, N. Isl. Algfl., 1883, p. 235 (Alg. Arct. Sea p. 187), tab. 16 figs. 6—7; Kolderup Rosenvinge, Grønlands Havalger, 1893, p. 792.

The species is easily recognisable by its basal system composed of regularly radiating connate filaments; it has been figured by myself (1893, fig. 9 A) and BØRGESEN (l. c.). Transverse fusions between cells belonging to different rows were repeatedly observed (fig. 325). The free filaments project in dense tufts or more scattered. In several cases they were unbranched and sterile; they are 9-12 (-14)  $\mu$ 

<sup>1</sup> Though I do not see the necessity of exchanging the old name *Chantransia*, which has been autorized by long spending, with the later Acrochætium, I here follow the modern authors in using the latter name.

thick. The cells are usually  $1^{1/2}$ —3 times as long as broad; they contain one nucleus and several more or less elongated disc-shaped or ribbon-shaped chromatophores (fig. 326).

The sporangia are usually, as figured by KJELLMAN (N. I. Algfl. 1883, fig. 6—7), terminal on short lateral branches mostly given off from the upper part of the otherwise unbranched erect filaments. But they may also be terminal on these filaments or, more rarely, terminal on longer lateral branches. The sporangiferous branchlets may be branched; KJELLMAN has figured such a case (l. c. fig. 7). In specimens from the Little Belt near Fænø Kalv (no. 1365) I found several cases of branched



Fig. 325. Rhodochorton penicilliforme. Basal layer showing cellfusions. 300 : 1.

branchlets, the branchlets of the second order terminating also with a sporangium (fig. 327). The sporangia are first divided by a transversal wall and afterwards by two vertical ones which are never in the same plain. The sporangia are (25-)



Fig. 326. Rhodochorton penicilliforme. Young sporangium growing out within the wall of an emptied sporangium. 625 : 1.

29–32 (-35)  $\mu$ long, (21–) 23– 25 (-27) $\mu$  broad. After evacuation of the spores a new sporangium may arise within the empty sporangial wall by budding from the next cell (fig.<sup>1</sup>326).

In the named specimens from the Little Belt (no. 1365), growing on *Phyllophora membranifolia* gathered in 13 meters' depth in June 1891, antheridia were found besides

tetrasporangia. They occurred in small clusters in the same specimens which bore tetrasporangia and in the neighbourhood of these, sometimes even on the same lateral branch. The antheridial clusters are usually lateral, more rarely terminal on the



Fig. 327.



D. K. D. Vidensk. Selsk. Skr., 7. Række, naturvidensk, og mathem. Afd. VII. 3.

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erect filaments (fig. 327) or on lateral branches. The lateral branches bearing antheridial clusters are short-celled. The antheridial clusters consist of short, recurved filaments composed of short, rounded cells and bearing on their convex side a small number of one- or two-celled short branches bearing together with the main axis of the cluster a number of antheridia on the upper side and giving to the cluster a corymbose appearance. The antheridia are ovate,  $6-7 \mu \log$ ,  $4-5,5 \mu$  broad; they contain a rather large nucleus. As these organs have only been observed in specimens conserved in alcohol, their colour could not be ascertained, but they seem to contain no chromatophores.

Female sex organs have not been observed.

The species has been found growing on *Phyllophora membranifolia*, *Ph. Brodiæi* and *Ph. rubens*, further on the chitinous membranes of *Tubularia* sp. and *Abietaria* abietina, in 5 to 25 meters' depth.

A membrane agreeing exactly with the basal layer of this species, but without erect filaments, was found growing on a specimen of *Cladophora rupestris* gathered near Kerteminde. — The species was found with sporangia in May, June, September (unripe) and November.

Localities. Kn: Near Hirsholm, 11 met.; Nordøstrev by Hirsholm. — Ke: IT and EV, Groves Flak, 23—25 met.; IQ, Fladen. — Ks: Nakkehoved, 22. Nov. 1827, (Lyngbye). — Sa: MS, south of Klophagen, 15 m. — Lb: North of Fænø Kalv, 13 m; off Stenderup; dQ, bank south of Lyø, 22 m. — Sb: LL, off Brolykke by Kerteminde, on Cladophora rupestris, without free filaments; determination uncertain; UH, east of Langeland. — Bw: cE, Middelgrund south of Als, 13—15 m.

*Rhodochorton seiriolanum* Gibs., described in 1890 by HARVEY GIBSON (Journ. Linn. Soc. Bot. Vol. 28, p. 204) has a monostromatical layer resembling that of *Rh. penicilliforme*. In a specimen of the same species from the Færöes kindly communicated to me by Dr. F. Børgesen I found that the cells contain one single chromatophore with a thick central portion including a pyrenoid. The species must certainly be referred to the genus *Chantransia (Acrochætium)*.

#### 2. Rhodochorton Rothii (Turton) Nägeli.

Nägeli, 1861, p. 356, Taf. I Figs. 1, 3; Reinke, Algenfl. westl. Ostsee, 1889, p. 22; H. Gibson, Developm. of the sporang. in Rhodochorton Rothii. Journ. Linn. Soc. Bot. Vol. 28, 1891, p. 201; Kuckuck, 1897, p. 20, fig. 5 (cell contents); Børgesen, Mar. Alg. Færöes, 1902, p. 390.

Conferva Rothii Turton, System of Nature VI, p. 1806 (teste Dillwyn); Dillwyn, Brit. Conf., 1809, plate 73. Callithamnion Rothii Lyngbye, Tent., p. 129, Tab. 41 A; Hornemann, Flor. Dan. tab. 2261, 2-3; Harvey,

Phyc. Brit. Vol. I, 1846, Plate 120 B; J. Agardh, 1851, p. 17; Kützing, Tab. phyc. Vol. XI, 1861, pl. 62 I.

Thamnidium Rothii Thuret, in Le Jolis, Alg. mar. de Cherbourg, 1861, p. 111, Pl. V.

This species occurs frequently in the littoral zone where it forms purple velvety patches e. g. under the *Fucus* bushes. These patches consist of creeping filaments from which arise erect filaments which are usually without branches below. The creeping filaments may be composed of short inflated cells (fig. 328) or they may be thinner, composed of rather long cells (fig. 330). The erect filaments are usually given off from the middlemost part of the cells of the creeping filaments. Descending filaments are sometimes given off from the lower part of the erect filaments; they

have the same appearance as the creeping ones and usually issue from the lower end of the cells while the erect branches are produced at their upper end. Exceptions from this rule and transitional forms between the erect and the descending or creeping filaments may sometimes occur. Thus, creeping filaments may arise from the upper end of a cell, and erect filaments may change into a creeping one (fig. 330 A).

The erect filaments are usually  $10-15 \mu$  thick (6-17  $\mu$ ), and the thickness is essentially the same in all the Danish waters; at Bornholm, however, the thickness is on an average a little smaller, 6-12  $\mu$ . The cells contain a single nucleus and a number of small parietal chromatophores without pyrenoid (KUCKUCK, l. c.). In the



Fig. 329. Rhodochorton Rothii. Plant probably arisen by regeneration of an isolated part of the frond. 200 : 1.

older transversal walls a refringent ring like that described by me in *Rhodochorton islandicum* K. Rosenv.<sup>1</sup> may sometimes appear.

A vegetative propagation is sometimes realised by fragments of the thallus consisting of a branched filament loosening from the mother plant and producing at the surface of fracture a downward growing filament (figs. 329, 330 E), becoming thus "cuttings" such as those described by me in *Rhodochorton islandicum*, l. c. p. 67. The middlemost cell in fig. 330 D is perhaps preparing the formation of



Fig. 328. Rhodochorton Rothii, from Bornholm. Creeping filament giving off two erect filaments. The latter have been regenerated after the apical part has died. 270 : 1.

such a cutting, giving rise to a small rhizoid penetrating into the subjacent cell. These cuttings were principally found in specimens collected at Copenhagen (Frederiksholms Kanal) in September.<sup>2</sup>

The sporangia are usually clustered at the ends of the erect filaments, as admirably represented in LE JOLIS Liste, pl. V, but they may also be more scattered in the upper end of these filaments. They

<sup>1</sup> Note sur une Floridée aérienne. Bot. Tidsskr. Vol. 23, 1900, p. 67.

<sup>2</sup> SVEDELIUS (Östersj. Algflora, 1901, p. 129) mentions the "cuttings" described by me in *Rh. is*landicum as stolons; they are, however, no stolons, but fragments of ordinary filaments loosening by splitting of a transversal wall, and germinating by giving rise to creeping filaments.

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are usually 25–28  $\mu$  long, 14–19  $\mu$  broad. The longest sporangium which was met with (Middelfart, April) measured 36  $\mu$  in length. The sporangium is first divided



Rhodochorton Rothii. Parts of upright filaments with upright and descending or creeping branches. In *E* regeneration of loosened filament by formation of descending filaments. 270 : 1.

by a transversal wall, afterwards by two longitudinal ones. The sporangia are probably produced in autumn; they were found ripe in the months January to May, empty in June. In specimens collected at Bornholm as late as August a few sporangia were still present, while the greater part had emptied and were fallen off. And specimens found by LYNGBYE near Hesselø in the southern Kattegat in July 1832, growing on Phyllophora Brodiai, still bore ripe sporangia. During and after the fructification new long erect branches may be produced from the sporangial cluster, between and under the sporangia, growing out to a bundle of long filaments.

The erect filaments attain only a length of 6 mm. Mr. Bove PE-TERSEN has, however, given me a specimen gathered at Middelfart in the beginning of July, measuring 17 mm. It reminds one very much of *Rh.intermedium* KJELLMAN (Spetsb. mar. klorof. Thallof. I, 1875, p. 28, Nor. Ish. Algfl. 1883, p. 231 pl. 15 fig. 8), which possibly is not specifically distinct from *Rh. Rothii*. As the specimen in question is sterile, a closer comparison with KJELL-MAN's plant cannot be made.

*R. Rothii* is perennial. It occurs principally in the littoral zone between middle and low-water mark,

but it has also been found in the sublittoral zone to a depth of 36 m; in this zone, however, it does not occur so abundantly as in the littoral zone. In exposed places on the rocky coast of Bornholm and the neighbouring Christiansø it may ascend 2 or 3 meters above the sea level, usually associated with *Verrucaria maura* and
Hildenbrandia prototypus. Here it forms velvety patches of the usual aspect, but the erect filaments are short, about 1 mm, simple or little branched, thin, usually 7-10 µ broad, the cells being about twice as long as broad (fig. 328). The lower part of the filaments are sometimes moniliform, consisting of short inflated cells scarcely longer than broad. These supralittoral specimens thus show no resemblance to Rhodochorton islandicum. — The species is usually found growing on rocks and stones, further on wood (in harbours), more rarely on Mutilus and the hapters and stipe of Laminaria hyperborea and L. digitata, further on Phyllophora Brodicei, partly on a Bryozoan on this. - In three localities in the North Sea, W. of the Limfjord, very small specimens of a Rhodochorton were found growing on Flustra foliacea, forming small tufts reaching only a height of  $180 \mu$ . They were supposed to be much reduced specimens of Rh. Rothii. The creeping filaments were often more or less densely united into a pseudoparenchymatic layer reminding one somewhat of that in Rh. membranaceum, but they were creeping on the surface of the skeleton of the Bryozoan, not penetrating it as in the last-named species, and the free, erect filaments were thicker  $(6-9 \mu, \text{ most frequently } 7-8 \mu)$ . Sporangia were not present, only stipes of shed scattered sporangia (Sept.—Oct.). — The species has been met with in almost all the Danish waters and is probably widely spread except in the Limfjord (and other fjords).

Localities. Ns: eE, 12 miles N.W. by N. of Bovbjerg light-house, 16 m; dZ, 17 miles W.  $^{3}/_{4}$  N. of Lodbjerg light-house, 36 m; eQ, 8 miles NW. by W.  $^{1}/_{2}$  W. of Lodbjerg light-house, 27 m, in all localities on Flustra foliacea. — Sk: Hirshals, reef, under Fucus. — Kn: Tyskerens reef and N.E. reef by Hirsholm, Frederikshavn, moles; Busserev; off Laurs Rev, c. 10 m, on Laminaria digitata; Østerby harbour, Læsø; fG, Tønneberg Banke, 15 m. — Ks: Grenaa, harbour; Nordvest-Renden by Hesselø, on Phylloph. Brodiæi (Lyngbye). — Sa: PG, west of Hatterrev, c. 8 m; north side of Refsnæs, 19 m, on Mytilus (C. H. Ostenfeld). — Lb: Baaring, harbour; Bogense, harbour; Fredericia (Hofm. Bang); Middelfart, harbour; Kongebro; Snoghøj, harbour; dH<sup>1</sup>, east of Hesteskoen, 18—19 m, on Phyllophora. — Sb: Kjerteminde, harbour; near Sprogø, 10—28 m (C. H. Ostenfeld); near Vresen, on Mytilus, 8—9 m (C. H. Ostenfeld); US<sup>1</sup>, Langelandsbelt, 20 m. — Su: København, Frederiksholms Kanal. — Bm: Køge, harbour. — Bb: Davids Banke, 29 m; near Hammershus, up to 2 m above the sea level; Rø, "den vaade Ovn", at the entrance to "den sorte Gryde" up to 3 m, Helligdomsklipperne (Liebman, J. Hartz, !); Græsholm at Christiansø, up to 2 m above sea level.

### 3. Rhodochorton membranaceum Magnus.

Callithamnion (Rhodochorton) membranaceum Magnus, Die botan. Ergebnisse der Nordseefahrt 1872.
II. Jahresber. d. Komm. z. Unters. d. deutsch. Meere in Kiel. Berlin 1874, p. 67, Taf. II figs. 7-15;
Collins, Notes on New England Marine Algæ II, 1883, p. 56 (Bull. Torr. Bot. Club, Vol. X); Strömfelt, Botaniska Notiser 1887, p. 109; Kolderup Rosenvinge, Grønlands Havalger 1893. Meddel. om Grønland III. 3, p. 794; Kuckuck, Beitr. 1897, p. 13.

As shown by COLLINS, STRÖMFELT and KUCKUCK (ll. cc.), the vegetative filaments live in the chitinous walls of various Hydroids. In the Danish waters the species is most frequently found in *Sertularia pumila*, further in *Abietaria abietina* (North Sea, Skagerak and Kattegat), *Tubularia, Hydrallmania falcata* (North Sea), Laomedea, Thujaria Thuja. When growing in Sertularia, the filaments to a great extent fuse together into the membranes first described by MAGNUS. In the tubes of



Fig. 331. Rhodochorton membranaceum. Growing in the tube-wall of Tubularia. 310:1.

Tubularia they may for long stretches remain separate, consisting of long cylindrical cells and giving rise to numerous, often opposite, divaricate branches (fig. 331). Specimens growing in the test of Laomedea never fused into membranes; the filaments growing in the soft substance between the outer and the inner membrane of the wall were curled and consisting of long narrow cells, while the filaments situated near the surface were usually composed of broader and shorter cells (fig. 332). In these specimens foldings of the membrane were not observed probably owing to the soft consistence of the medium, while they are frequently met with in the filaments growing in the firmer tubes of Sertularia and Tubularia. MAGNUS (l. c. p. 67) explains these foldings as caused by the surrounding cells of the same species hindering the extension of the membranes in the places where the filaments are densely crowded. The

foldings are, however, also produced when the filaments are growing separately, as

f. inst. in the tubes of Tubularia (fig. 331), in which case the foldings must be caused by the resistance of the chitinous membrane in which they grow. As emphasised by KUCKUCK (l. c. p. 23), the penetration of the filaments into the membrane of the Hydroid must take place by means of an enzyme dissolving the chitine, but this enzyme is probably only secreted by the young cells, and the older cells are therefore only able to realise their growth by folding their walls when imbedded in chitine on all sides. As shown by KUCKUCK (1897) the cells contain several ribbon-shaped chromatophores (comp. fig. 333).

The free fertile filaments are always short in the specimens growing in *Sertularia pumila*,  $7-8\mu$ 



Fig. 332.

Rhodochorton membranaceum, growing in the test of Laomedea at Hirsholm. On the right a tuft of sporangiferous filaments. 310:1. Fig. 333. Rhodochorton membranaceum. Living cell showing chromatophores and nucleus (n). 675 : 1.

thick, frequently extremely short and unbranched, consisting of one or a small number of short cells and terminating with a sporangium. Or they may be branched, but the

Fig. 334. Rhodochorton membranaceum. From the North Sea, aF, growing in Abietaria abietina. A, portion of basal layer with a fertile branch. B, seetion of the wall of Abietaria showing the intramatrical growth of the Rhodochorton. 390:1.

B

Fig. 335. Rhodochorton membranaceum, growing in Abietaria abietina off Refsnæs. A, free filament with sporangia. B and C, cells showing chromatophores. A 230 : 1. B, C 625 : 1.

A

R

primary filament then always bears a terminal sporangium, and the branches also end with a sporangium (fig. 334, comp. KUCKUCK, l. c. p. 16—17, fig. 2). The free filaments may behave in the same manner when the species is growing in other Hydroids; but in the plants infesting *Abietaria abietina*, the free filaments are sometimes much longer, ending in a long sterile apical cell, while the sporangia are terminal on short lateral branches or sometimes also on branches of the second order. KUCKUCK has described such specimens found growing in the same Hydroid (l. c. p. 17—19, fig. 3); he concludes, in accordance with me, that they must be referred to *Rhodochorton membranaceum*, not to a special form of it. Having found similar specimens in an *Abietaria abietina* dredged at PF off Refsnæs (Sa)  $_{+}^{1,*}$  (fig. 335), I have recently been in doubt. The sum of characters found in

<sup>1</sup> Similar specimens have been recently found in cL, N.E. of Sprogø.

these specimens, the free filaments emerging singly, not in bunches, the cells of these filaments being longer, the chromatophores of the long cells being sometimes partly spiral, the sporangia never being terminal on the principal filaments, give these specimens an appearance so different from those growing in Sertularia pumila that one is tempted to regard them as a distinct form. On the other hand, it must be admitted that the said Abietaria abietina covered with numerous free filaments of the described appearance bore also shorter and very short filaments with terminal sporangia, agreeing perfectly with those typical of the species. It must therefore be assumed that the species under particularly favourable conditions, which are sometimes realised when it is growing in Abietaria abietina, produces longer fertile filaments with longer cells and without terminal sporangia. These filaments remind one rather of Rhodochorton chantransioides Rke. which, as shown by KYLIN (Z. Kenntnis ein. schwed. Chantransia-Arten, Botan. Stud. tilägn. Kjellman, Upsala 1906, p. 118) must be regarded as the asexual form of *Chantransia efflorescens*, an opinion which I have supported in 1909 (Mar. Alg. D. I, p. 137). Monosporangia were, however, not found in the form growing in Abietaria abietina, and the free filaments of this plant differed otherwise by greater thickness  $(6,5-8 \mu)$ , by the shape of the chromatophores being only exceptionally and partly spiral and by the tetrasporangia being larger, 25-30 µ long, 12-17 µ broad.

The sporangia in the specimens growing in Sertularia pumila were  $17-21 (25) \mu$ long, (11) 13-15,5  $\mu$  broad; in those growing in Sertularia pumila and Tubularia they were  $17-30 (31) \mu$  long,  $12-19 (20) \mu$  broad. The fact that the size of the sporangia is rather variable in the same specimen suggests that the sporangia increase in size after division.

KUCKUCK found as a rare case a hyaline hair, like those common in Acrochætium (l. c. p. 17, fig. 2E). I never observed these organs.

The great resemblance with Acrochætium efflorescens suggests that the species might perhaps be referred to the genus Acrochætium.

A sponge dredged in Skagerak off Hirshals (possibly *Chalina oculata*) showed some purple spots, the largest abt.  $1^{1/2}$  cm long. These spots are due to an alga growing in the chitinous skeleton in a similar manner to *Rhodochorton* in the hydroids, and probably identical with this species. They consist of branched filaments, mostly running immediately under the surface, but also deeper, partly distinct, partly fusing together in parenchymatous plates. Some cells showed foldings of the walls. Free filaments were not found, only numerous short round protuberances, probably checked rudiments of free filaments. For want of fructification a conclusive determination is not possible.

The species has been found in all the Danish waters with the exception of the inner parts of the Baltic, from low-water mark to 38 meters' depth. It has been found with sporangia in all depths and in all seasons: in the specimens growing in *Abietaria* collected in September and October in the North Sea and Skagerak, the spor-

angia were, however, thrown off. In small depth it occurs only in shaded places, particularly in *Sertularia* growing on the older parts of *Fucus* (*serratus*).

Lo calities. Ns: aF, off Thyborøn  $14^{1/2}$  miles, 31 met. in Abietaria abietina<sup>1</sup>; aG, off Thyborøn  $19^{1/2}$  miles, 38 met., in Hydrallmania falcata; dZ, 17 miles W. <sup>3</sup>/<sub>4</sub> N. of Lodbjerg light-house, 36 m; eQ, 27 m; eO, 23 m, in Abietaria abiet. and Hydrallmania falc.; aD, off Lodbjerg, 23,5 m; XR, off Ørhage. — Sk: eV, 6 miles N. by E. of Hanstholm light-house, 22 m, in Thujaria Thuja; off Hirshals in Abiet. ab. (Børgesen, !). — Lf: ZS, off Kobberød; XU, W. of Oddesund. — Kn: Various places near Hirsholm, partly in Laomedea; KC, Krageskovs Rev; Frederikshavn; Marens Rev. — Ke: IQ, Fladen, in Abiet. ab.; EV, Groves Flak; ER, Fyrbanken, east of Anholt, 28 m; HY, store Middelgrund. — Km: XF, Læsø Rende; bK, N.W. of Anholt, 15 m, in Tubularia; BK, Tangen; BH, off Gjerrild Klint, in Tubularia. — Ks: OU, Schultz's Grund; GF, Sjællands Rev; D, grønne Revle; EI, entrance to Isefjord: Lammefjord. — Sa: Bjarkes Grund; PC, between Sejerø and Ordrups Næs; PF, off Refsnæs, 18—21 m, on Abiet. abiet. (long free filaments); MP, Falske Bolsax. — Lb: Bjørnsknude by Vejlefjord; near Damgaard, 13 m, in Tubularia; Linderum, dG, Hesteskoen, N.E. of Als. — Sb: GS, Lysegrundene; LK, Elefantgrund; Kjerteminde; between Korsør and Sprogø, "22—32 fathoms" (Magnus 1872); cL, N.E, of Sprogø, 25—27 m, in Abietaria abietina; DN, Vengeance Grund; UF, Hov Sand; Lohals; Spodsbjerg. — Su: BQ, off Ellekilde; SB, Flinterenden. — Bw: LE and UY, Vejsnæs Flak.

## General remarks on the Ceramiaceæ.

Referring the reader to the quoted works of SCHMITZ and HAUPTFLEISCH and OLTMANNS for the general morphology and biology of the Ceramiaceæ, I shall here only advance some remarks on some special subjects, based upon observations of the Danish species.

1. Number of nuclei. The cells in the majority of the species contain a single nucleus. In *Callithamnion corymbosum* the young cells contain a single nucleus, but at a certain distance from the top the nuclei divide without a subsequent cell-division, and by continued divisions of the nuclei the old cells become multinucleate, the nuclei being uniformly distributed over the cell. The same takes place in Callithamnion tetragonum, but the said division of the nuclei begins earlier and may occur already in the apical cell, which often contains two nuclei in a resting stage before any sign of cell-division is to be seen. In both species the downward growing cortical filaments consist from the first of multinucleate cells. In Spermothamnion repens all the cells contain several nuclei, also the apical cells and the mother-cells of the branches. On the other hand the reproductive cells contain from the first one nucleus only. As far as I have ascertained, this is not realized by degeneration of nuclei in an originally multinucleate cell but so that the divisions of the nuclei do not keep pace with the cell-divisions at the transition from the vegetative to the fertile phase, in consequence of which the number of nuclei in the cells diminishes and is finally one in the young fertile cells.

<sup>1</sup> When no host is indicated the plant was found in *Sertularia pumila*. D. K. D. Vidensk, Selsk, Skr., 7. Bække, naturvidensk, og mathem. Afd. VII, 3. 2. Cell-fusions. Secondary pits in the cell-walls have not been observed in any of the Danish species of Ceramiaceæ. Cell-fusions like those occurring in many Cryptonemiales (comp. part II p. 279) have only been met with in *Rhodochorton penicilliforme*, where they take place between cells belonging to different rows in the basal disc. I have further in a single specimen of *Callithamnion Furcellariæ* met with a few cases of fusion between two contiguous cells of the same filament, consequently between cells which were before connected by a central pit in the transversal wall (fig. 264). As this sort of fusion was only observed in one specimen, it must certainly be regarded as an abnormal process.

3. Hyaline unicellular hairs (comp. K. R. 1911) occur normally in almost all the species of *Ceramium*, in *Callithamnion Brodiæi* and *C. corymbosum*; they are only wanting in winter when the growth has ceased. They occur often in *Plumaria elegans*, sometimes in *Spermothamnion repens* and *Callithamnion Furcellariæ*, rarely in *C. roseum* and *Seirospora Griffithsiana*, never in *Trailliella intricata*, *Callithamnion Hookeri* and *C. tetragonum*, further in the species of *Antithamnion* and *Rhodochorton*.<sup>1</sup> In *Ptilota plumosa* they occur only at the ends of the branches which surround the procarps.

4. The number of the auxiliary cells is usually constant. In *Callithamnion* there are normally two, one on each side of the carpogonial branch. In *C. Furcellariæ* and *C. roseum*, however, there is often only one auxiliary mother-cell, namely that which gives rise to the carpogonial branch.

5. The sporangia are lateral, sessile, or terminal on short branchlets. In C. Hookeri only have I as a rare exception found intercalary sporangia. In Trailliella intricata the sporangia are cut off by longitudinal division of the ordinary cells, a mode of formation which is not known in any other filamentous Ceramiaceæ; it is, however, doubtful, whether Trailliella belongs really to this family. The sporangia are usually 4-parted. 2-parted sporangia occur in Callithamnion Furcellariæ and Seirospora Griffithsiana besides 4-parted, but in different plants. In the last-named species, however, a small number of tetrasporangia were met with on a plant with disporangia.

The division of the tetrasporangia is either rectangular or tetrahedrical ("triangular"). In Antithamnion, Rhodochorton and Trailliella the sporangium is first divided by a transversal wall in two cells which afterwards are divided by vertical walls, perpendicular to the first wall. In the greater part of the Danish Ceramiaceæ (Spermothamnion, Callithamnion, Seirospora, Plumaria, Ptilota) the division is tetrahedrical, the sporangium after the quadripartition of the nucleus being divided by six walls meeting in the centre of the sporangium. In Ceramium the division is variable, now triangular, now rectangular, and the two modes of division may occur in one and the same species; but, as shown above, the division of the cell begins only after the accomplishment of the nuclear division, and the rectangular division in Ceramium is thus a true quadripartition, while that in the three first-named genera is established by two consecutive bipartitions.

<sup>1</sup> KUCKUCK once met with a hyaline hair in Rhodochorton membranaceum (1897, p. 17).

Sporangia containing more than four spores were met with as rare exceptions in Spermothamnion repens and Seirospora Griffithsiana.

6. **Paraspores** have been met with in the following species occurring in the Danish waters: Callithamnion Hookeri, Plumaria elegans, Seirospora Griffithsiana, Ceramium diaphanum, C. strictum, C. Deslongchampsii, C. vertebrale. According to SCHMITZ and SCHILLER (1913) they occur in the Mediterranean also in Antithamnion Plumula.

Paraspores are never produced in sexual plants. The paraspore-bearing plants often bear only these organs, but in all the species in question tetrasporangia are sometimes produced by the same plants, most frequently in the Ceramium-species. In Antithamnion Plumula SCHILLER found at Triest paraspores in numerous plants which all bore tetrasporangia too. This author tries to show that the paraspores in the *Ceramiaceæ* must be interpreted as modified tetrasporangia, relying on the fact that they always occur on tetrasporiferous plants and that they often have the same position as the tetrasporangia. This interpretation is certainly warranted for the polysporangia in *Pleonosporium* which wants typical tetrasporangia, but it cannot be accepted for the true paraspores here in question. The paraspores are at their first appearance decidedly different from tetrasporangia. Whereas the latter have an especial form and early show a firm two-layered cell-wall, the shape of the young heap of paraspores is more indefinite, they have a homogeneous more soft wall and the content in an early stage is not more coloured than the vegetative cells, in Plumaria even decidedly less coloured, while the young sporangia are deeper coloured than the vegetative cells. Further, the position of the paraspores is not always the same as that of the tetrasporangia, in particular in *Ceramium* which is also admitted by SCHILLER (1913 p. 149). According to this author two sorts of "paraspores" occur in Ceramium 1º polyspores and 2º true paraspores. The first named organs are produced in the cortical bands, e.g. in C. strictum and C. Deslongchampsii and according to SCHILLER arise from "eine mit einer Tetrasporangienmutterzelle identische Zelle" l. c. p. 11). I have not observed these organs that seem to be similar to the polyspores in Pleonosporium. The second sort of paraspores develop in a quite different manner. In C. strictum<sup>1</sup> described by SCHILLER they arise at the tips of the branches, all the young cells, even the central cells, being transformed into paraspores. In C. diaphanum and C. strictum from the Danish waters the paraspores arise, as shown by HENN. PETERSEN, only from the peripheral cells in the cortical bands, most frequently near the upper edge of the bands, often from the marginal cells (HENN. PETERSEN 1908 p. 52, 57, figs. II, IV, comp. my fig. 313). When Schiller, in order to show the derivation of the paraspores in *C. strictum* from the tetrasporangia, only adduces the facts that they only occur in the tetraspore-bearing plants, and that the tetraspore-formation decreases in the same degree as the paraspore-formation increases, it must be said that this proof is quite insufficient. The fact that

<sup>1</sup> SCHILLER'S C. strictum is certainly not the true C. strictum Grev. et Harvey. Dr. HENN. PETERSEN thinks that it is rather a form of C. diaphanum.

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the paraspores only arise in the tetraspore-bearing plants is probably connected with their number of chromosomes. Their nuclei are undoubtedly diploid, and it must be expected that they always give rise to tetraspore-bearing plants. It is in that respect interesting that in all the paraspore-producing species sexual individuals are either entirely wanting or extremely rare (*Ceramium*) in the Danish waters. And the fact that their development is in inverse proportion to that of the tetrasporangia is certainly the expression of a correlation similar to that existing in numerous Hepaticæ, Musci and many other plants between the sexual reproduction and the asexual propagation.

7. The occurrence of sexual organs and tetrasporangia in the same plant has been ascertained in several species in the Danish waters. It is a particularly common appearance in *Spermothamnion repens*, where the sexual organs almost always occur together with sporangia. In *Callithamnion tetragonum* too the antheridia and the procarps occur frequently in the tetraspore-bearing plants. In 1864 and 1878 THURET described a f. *amphicarpa* of *C. corymbosum* presenting the same combination but this form has not been observed in the Danish waters. In *C. Furcellariæ* I have once met with a procarp in a tetraspore-bearing plant, and in *Antithamnion Plumula* tetrasporangia were twice met with in a female plant. In *Antithamnion boreale* and *Rhodochorton penicilliforme* antheridia were detected, occurring in tetraspore-bearing plants, while female sex organs are still unknown.

8. Occurrence of the various organs of reproduction in the Danish waters. Sexual organs have not been met with in *Callithamnion Hookeri*, *Seirospora Griffithsiana*, *Plumaria elegans* and *Antithamnion cruciatum*, while sexual plants of these species occur elsewhere. The three first-named species propagate in the Danish waters principally by paraspores, but tetraspores have been met with in all of them. In *Antithamnion cruciatum* sexual organs seem altogether to be a rare occurrence. Sexual plants of *Spermothamnion repens* occur only in the North Sea, the Skagerak, the Kattegat and the northern part of the Sound while the species in the inner waters only bears tetrasporangia or is sterile. In *Ceramium diaphanum*, *C. strictum*, *C. Rosenvingii*, *C. Boergesenii* and *Antithamnion Plumula* the sexual plants are much rarer than the tetraspore-bearing ones. Of *Callithamnion corymbosum* only sterile plants have been met with in the inner parts of the area of the species (Sm, Su south of Hveen, Baltic).

9. Vegetative propagation occurs in *Rhodochorton Rothii*, fragments of the erect shoots loosening and producing from the plane of detachment a downward growing filament which is able to fix the fragment as a cutting to a new substratum. Similar cuttings were observed in a culture of *Seirospora Griffithsiana*.

## Fam. 12. Bonnemaisoniaceæ.

### Bonnemaisonia C. Agardh.

### 1. Bonnemaisonia asparagoides (Woodw.) Agardh.

C. Agardh, Spec. Algar. 1821, p. 197; Harvey, Phycol. Brit. I, 1846, pl. 51; J. Agardh, Spec. g. o. Alg. II, pars III, 1863, p. 779; Cramer, Physiol.-system. Unters. üb. die Ceramiaceen. Neue Denkschr. d. allg. schweiz. Ges. f. Naturw. 20. Zürich 1864, p. 52, Taf. VIII, figs. 4—11, X, figs. 1—12; Kützing, Tab. phyc. 15. Band, Taf. 32, 1865; Wille, Beitr. z. Entwick. d. phys. Gew. b. ein. Florideen. Nova Acta Leop.-Carol. Akad. 1887, p. 73, figs. 44—54; Golenkin, Algologische Notizen. Bull. soc. nat. de Moscou, N. S. VIII, 1894, p. 257; Bruns, Ber. deut. bot. Ges. 12, 1894, p. 179; Phillips, Developm. of the cystocarp in Rhodymeniales. Ann. of Botany, Vol. XI, 1897, p. 348, pl. 17 figs. 1—3; Kylin, Blasenzellen einig. Florid., Arkiv för Botanik. Bd. 14 No. 5, 1915; id., Entwicklungsgesch. u. syst. Stell. von Bonnemaisonia asparagoides. Zeitschr. f. Botanik VIII, 1916, p. 545; id., Über die Keimung der Florideensporen. Arkiv för Botanik, Bd. 14, No. 22, 1817, p. 12.

Fucus Asparagoides Woodward, Trans. Linn. Soc. Vol. II p. 29, 1794.

The structure and development of the alternately pinnate frond has been described by CRAMER, WILLE and KYLIN (1916). GOLENKIN, BRUNS and KYLIN (1915) have described peculiar gland cells situated among the cortical cells and containing a compound of iodine which is easily decomposed, producing free iodine. I have also observed, many years ago, the power of the species of giving a blue stain to paper. — According to KYLIN (1916, p. 549), rather short unicellular hairs may occur sparingly.

Tetrasporangia are wanting; all specimens are monoecious sexual plants. The sexual branchlets are alternate, opposite to the alternate sterile pinnulæ. The antheridia are produced on the surface of the oval male branchlets (KYLIN 1916, p. 551). The carpogonial branches develop singly on the female branches. Their development and that of the cystocarps has been followed by KYLIN (1916) who has found that it most resembles that of *Wrangelia* and *Naccaria*. OLTMANNS and KYLIN think that this group of genera makes transition from the *Nemalionales* to the *Cryptone-miales* and the *Gigartinales*. The germination takes place, as shown by GOLENKIN and KYLIN (1917), by the formation of a basal disc, from the margin of which numerous rhizoids are given off. The formation of the erect shoots were not observed. As emphasised by KYLIN, this mode of germination is very different from that of the *Rhodomelaceæ* to which the *Bonnemaisoniaceæ* have been considered related.

The species is annual. It has only been found rarely in a few localities in the northern and eastern Kattegat, in 18 to 24,5 meters depth, growing on various Algæ (*Delesseria sanguinea*, *Polysiphonia elongata*, *Laminaria saccharina*). The largest specimen observed (from Herthas Flak) was 13 cm long. Collected with ripe cystocarps in July and September.

Localities. Kn: Herthas Flak (!, Børgesen). - Ke: VZ, Groves Flak, VY, Fladen.

# Fam. 13. Rhodomelaceæ.

J. G. AGARDH (1863), Species, genera et ordines Floridearum. Vol. II pars 3.

- LILY BATTEN (1923), The Genus Polysiphonia, Grev., a critical revision of the British species based upon anatomy. The Journal of the Linnean Society. Vol. 46 No. 308.
- P. FALKENBERG (1901), Die Rhodomelaceen des Golfes von Neapel. Fauna und Flora des Golfes von Neapel. 25. Monographie. Berlin.
- L. KNY (1873), Ueber Axillarknospen bei Florideen. Festschr. z. Feier d. hundertj. Best. d. Ges. d. naturf. Freunde zu Berlin.
- L. KOLDERUP ROSENVINGE (1884), Bidrag til Polysiphonia's Morfologi. (Résumé français). Botan. Tidsskr. Bind 14.
- -, (1902), Ueber die Spiralstellungen der Rhodomelaceen. Jahrb. für wiss. Bot. Bd. 37.
- --, (1903), Sur les organes piliformes des Rhodomelacées. Overs. K. Danske Vidensk. Selsk. Forh. København.
- C. Nägell (1846), Polysiphonia. Zeitschrift für wiss. Botanik von Schleiden und Nägeli. 3. u. 4. Heft. Zürich.

R. W. PHILLIPS (1896), Development of the Cystocarp in the Rhodomelaceae. II. Annals of Botany X.

Fr. SCHMITZ und P. FALKENBERG (1897), Rhodomelaceae. Engler u. Prantl, Die natürl. Pflanzenfam. I, 2.

S. YAMANOUCHI (1906), The life-history of Polysiphonia violacea. Botan. Gazette, Vol. 42 p. 401-449, plates 19-28.

See further p. 297.

### Heterosiphonia Mont.

### 1. Heterosiphonia plumosa (Ellis) Batters.

Batters, Catalogue of Brit. Mar. Algæ. 1902, p. 83.

Conferva plumosa Ellis, Philosoph. Transact. Vol. 57, 1768, p. 424, Tab. 18, fig. c, d.

Conferva coccinea Hudson, Fl. angl. Ed. 2, 1878, p. 603.

Callithamnion coccineum Lyngbye, Tent., 1819, p. 144.

Dasay coccinea Agardh, Spec. Alg. II, 1828, p. 119; Flora Danica tab. 2456 (1845) (f. tenuis); Harvey,

Phyc. Brit. III, 1851, pl. 253; Areschoug, 1850, p. 42; J. Agardh, 1863, p. 1185; Kny, 1873, p. 108,



Fig. 336. Heterosiphonia plumosa. Cell showing chromatophores and nuclei, 350 : 1.

Taf. II Fig. 7; Janczewski, Dév. du cystoc. d. l. Florid. Mém. Cherbourg, Vol. XX, 1877, p. 129, pl. 4, figs. 19-21, pl. V, figs. 1-8; Buffham, Reprod. Organs, espec. Anther., Journ. Queck. micr. Club, Vol. III Ser. II 1888, p. 263, pl. XXII, figs. 19-20; Phillips, 1896, p. 187, pl. XII figs. 1-7.

Trichothamnion hirsutum Kütz., Tab. phyc. 14, tab. 90.

Heterosiphonia coccinea Falkenberg, 1901, p. 648, Taf. 18 Fig. 21; Kylin, 1907, p. 149.

The structure and development of the frond have been described by  $K_{NY}$  (1873) who first recognised the sympodial character of the ramification. The cells of the monosiphonous pinnules contain a number of small nuclei and numerous minute chromatophores (fig. 336).

The Danish specimens generally agree with  $\beta$ , *tenuis* J. Agardh, l. c. The older stems are usually naked, sometimes, however, beset with numerous adventitious branchlets.

As shown by BATTERS, I. c., the antheridia form a covering on the monosiphonous branches with the exception of the two or three basal and the four to six terminal cells which remain undivided. The antheridia (spermatangia) are not produced directly from the central cell, as asserted by BUFFHAM, but from a layer of small cells surrounding the central cell and budding the spermatangia on their outer face (fig. 337 B).

As regards the development and structure of the cystocarps, reference may be made to the papers quoted of JANCZEWSKI and PHILLIPS. The procarps are usually borne

on the fourth joint from the sympodial axis (PHILLIPS), from the last joint of the pushed aside main axis which in sterile plants becomes polysiphonous (FALKENBERG). The spores of the gonimoblast are seriate.

The tetrasporangia are produced in distinct stichidia arising in the upper part of the sympodia; their structure has been described by FALKENBERG (l. c. p. 649).

The Danish specimens only reach a length of 10 cm. They were found growing on stony bottom in 13 to 31 meters' depth, attached to stones or to Delesseria sinuosa or Furcellaria. It was dredged in July to September. Antheridia and tetrasporangia were found in August, young cystocarps in July.

Localities. Ns: aF, off Thyborøn, 14,5 miles, 31 meters. -Sk: ZK<sup>7</sup>, off Lønstrup, 4 miles, 17–19 m; YL, N.W. of Hirshals, 2,5 miles, 13 met. and deeper. - Kn: TO, Tønneberg Banke, north of Trindelen, 18 m; FF, Trindelen, 15 m. - Ke: ZG, Fladen, 18 m. -Su: Øresund, "in the deeper region of Algæ" (Lönnberg, Undersökn. rör. Öresunds djurlif, Uppsala 1898).

### Laurencia Lamouroux.

### 1. Laurencia pinnatifida (Gmel.) Lamouroux.

Lamouroux, Essai des Thalass.. Ann. du Mus. XX, 1813 p. 130; Greville

Alg. Brit. 1830 p. 108 tab. 14 figs. 1-5; Harvey Phyc. Brit. pl. 55,

1846; J. Agardh 1863 p. 764; Kützing Tab. phyc. XV, 1865 tab. 66; Kolkwitz, Beitr. Biol. Flor., Wiss. Meersunters. N. F. IV Abt. Helgoland Heft 1, 1900, p. 52; Falkenberg 1901 p. 248, Taf. 23 figs. 20-36; Kylin 1907 p. 138; id. 1917 p. 20; id. 1923 p. 123.

Fucus pinnatifidus Gmelin Historia Fucorum 1768, p. 156 tab. 16 fig. 3; Hornemann, Flora Danica tab. 1478, 1813; Smith, English Botany Vol. VII pl. 1202, 1808.

Fucus ramosissimus etc. Oeder Flor. Dan. tab. 276, 1765.

Gelidium pinnatifidum Lyngbye Tent. 1819 p. 40 tab. 9 C.

As regards the basal part of the frond strange discrepancies exist between the statements of the various authors. SMITH (Engl. Bot. 1808) and J. AGARDH describe it as a branched "root" ("radix fibrosa"). TURNER (1808) describes it thus: Root a flat disk throwing out a few creeping fibres. GREVILLE (1830) and HARVEY describe



625:1.

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it in a similar way; the figure of HARVEY shows cylindrical feebly branched creeping organs radiating from the base of the stem while the disc is not distinctly visible. According to LVNGBYE (1819) the basal part is a "callus explanatus, fibris brevibus interdum instructa". Kolkwitz found at Helgoland an extensive basal disc



Fig. 338. Laurencia pinnatifida. A, young plant gathered in September (Frederikshavn). 18:1. B, Basal disc growing on Fucus serratus, with numerous erect shoots (Hirshals June). 3:1. producing a number of distant erect shoots (1900 p. 52, fig. 6), but he does not mention any creeping shoots. In Danish specimens I found no creeping root-like organs but only a flat basal disc becoming thinner towards the border which has an even outline. This disc may sometimes have a considerable extension and produce numerous erect shoots (fig. 338). It is early formed in the sporeling; in the young plant represented in fig. 338 A it has increased considerably in circumference and has produced four new shoots. These arise from superficial cells.

The development of the erect shoots has been thoroughly studied by FALKENBERG and KYLIN. The growing point sunk in the apical groove of the shoot produces spirally arranged trichoblasts while the lateral branches, according to FALKENBERG arise as axillary shoots of the trichoblasts, but only of those which are placed in two longitudinal rows whereby the pinnate ramification and the compressed form of the frond arise. FALKENBERG found the trichoblasts well developed only in cystocarpbearing specimens having ceased to grow in length and to branch. According to KYLIN they are well developed during the development of the organs of reproduction, while they are very small during the vegetative development of the plant. I found them well developed and visible outside the apical groove in the specimens gathered in July to September; they were not visible externally in the specimens collected in winter and spring, and in the specimens collected in May and June they were in

several cases long, in other cases not visible outside. The long trichoblasts were found both in sterile and fertile specimens (fig. 338 A).

The antheridia are borne on cylindrical fertile trichoblasts closely placed in cup-shaped bodies near the tips of the shoots. These trichoblasts which cover the whole surface of the cup are much more numerous than the trichoblasts produced by the growing point in the centre of the cup and FALKENBERG therefore suggests "dass hier eine verkümmerte und verkannte oder normale Achselspross-Bildung vorliegt". The development of the antheridia has been recently described by KYLIN.

The procarps arise as in the other Rhodomelaceæ from the second segment of

the trichoblasts; they are developed in trichoblasts of various position, and the cystocarps are therefore placed on the edges and on the flat sides of the frond as

well. The development of the procarps and the cystocarps has been carefully studied by KYLIN (1923, pp. 125-129). In the ripe cystocarp the wall consists only of three or four cell-layers, the innermost ones being disorganised and transformed into a tough mucilage (FALKENBERG p. 246, pl. 23 figs. 20-21, KYLIN p. 128 fig. 80 d).

The tetrasporangia are immersed in the cortical layer of the upper ends of the frond; according to KYLIN (1923 p. 130) they arise from young cortical cells by divisions similar to those by which the sporangia arise in the pericentral cells of *Polysiphonia*.

The germination of the tetraspores has been examined by KYLIN (1917) who showed that a pluricellular basal disc is early developed. The young disc is composed of connate radiating filaments, it increases in diameter by marginal growth and early begins to produce new erect shoots by budding from the surface. The new shoots resemble the primary one (fig. 338 A).

The species has been met with in all the seasons. It occurs at low-water mark or a little deeper, down to 6,5 meters' depth. It grows most frequently on *Fucus vesiculosus* and *F. serratus*, further on stones and more rarely on *Chorda* 

> Filum a. o. algæ (Chondrus crispus, Furcellaria, Cystoclonium, and the blade of Laminaria digitata). It usually attains a length of 2 to 5 cm, more rarely up to 7 cm. The fructification takes place in summer. Antheridia have been met with in May and June, cystocarps in May to September, in the last month partly empty, and tetrasporangia in May (unripe) to August.

> According to GREVILLE and HARVEY, the species is annual, and it may certainly frequently be so also at the Danish coasts. Young plants are to be found in summer and autumn, July to September (fig. 338 A); they produce a number of erect shoots which remain sterile in autumn and winter and at the end of the winter attain a length of 3—5 cm. In winter the growth ceases but it recommences at the end of the winter. In March and April the new-formed tips of the frond are easily recognised and sharply limited against the old frond, but only about 1 mm long (fig. 339). In summer the new shoots have reached their full size and are distinguished from the old frond by the colour and

by the want of epiphytes (fig. 340). The fertile erect fronds probably die in autumn, but the basal disc seems to be able to continue the development, growing at the margin and producing new erect fronds fructifying next year. Thus, the basal disc shown in fig. 338 B, collected in June, is probably more than one year old.

The species occurs in the Danish waters with rather high salinity but requires D. K. D. Vidensk. Selsk. Skr., 7. Række, naturvidensk. og mathem. Afd., VII. 3. 52

Fig. 340. Laurencia pinnatifida. Limfjord July. The largest new frond has reached its full size; the old frond is darker, covered with epiphytes. 1,3:1.

Fig. 339. Laurencia pinnatifida. Portion of frond gathered in

April; the branches have recommenced growing. 3,5:1.



protected localities. It occurs most abundantly and most well developed in the Limfjord, undoubtedly owing to the high salinity and the high summer temperature; in some stony reefs in the Løgstør Bredning it was found to be the characterising species. The specimens growing in very sunny localities are yellow, owing to yellow cell-sap in the outer cortical cells, while the specimens growing in shady places are red-brown.

Localities. — Sk: Nørre Lyngby north of Løkken, washed ashore (Ove Paulsen); Hirshals, on stones west of the mole, under Fucus vesic. and serr., and on Fuc. serr. (fig. 338 B). — Lf: ZS, Nissum Bredning, off Kobberød, Rønnen and Søndre Røn by Lemvig; Malle (J. P. Jacobsen) and MG, off Hanklit in Thisted Bredning; Sallingsund, east side of Ørodde by Nykøbing and further north and south of Nykøbing; off Grønnerup; Knudshoved, Fur; off Lisehøj north coast of Fur; Ejerslev Røn, Amtoft Rev, Holmtunge Hage and Lendrup Røn in Løgstør Bredning. — Kn: Hirsholm (Hornemann, !) Kölpen, Deget and Busserev by Frederikshavn; Nordre Rønner; UB and ZL south-east of Nordre Rønner, 6,5 met.; stony reef by Jegens Odde. — Km: ZC, Kobbergrund, 4-4,5 m; Boels Rev between Randers Fjord and Mariager Fjord. — Sa: Rønnen in Begtrup Vig; Kalø Rev; Hofmansgave (Lyngbye, Hofm. Bang, Car. Rosenberg).

### Chondria Agardh (Harvey).

### 1. Chondria dasyphylla (Woodw.) Agardh.

C. A. Agardh, Spec. Algar. Vol. I pars post. 1822, p. 350; Falkenberg, 1901, p. 197, Taf. 22, figs. 4–18. Fucus dasyphyllus Woodward, Trans. Linn. Soc. Vol. 2, 1794, p. 239 tab. 23.

Laurencia dasyphylla Greville, Alg. Brit., 1830, p. 112, pl. 14, figs. 13-17; Harvey Manual, 1841, p. 70, Phyc. Brit. II, 1849, pl. 152; Kützing, Phyc. gener. 1843, Taf. 55 II, Tab. phyc. 15. Band, 1861, Tab. 43.

Chondriopsis dasyphylla J. Agardh, 1863, p. 809.

The morphology of the frond and of the reproductive organs have been exhaustively treated by FALKENBERG to whose work reference may be made. The plant forms tufts, several erect shoots issuing from the base; these shoots are 10— 11 cm high. It was found growing near land in a depth of 1 meter or a little deeper. All the 29 specimens collected by me in August bore ripe tetrasporangia. One specimen only collected by J. P. JACOBSEN bore cystocarps.

Localities. Ns: "Vesterhavet ved Thy" (J. P. Jacobsen). — Sk: Løkken, washed ashore; Hirshals, on stones east of the mole, in company with Gracilaria confervoides, Polysiphonia nigrescens, Ceramium rubrum a. o.; west side of Hirshals, August.

## Polysiphonia Greville.

### 1. Polysiphonia urceolata (Dillw.) Grev.

Greville, Flora Edinensis 1824 p. 309; Harvey Phyc. Brit. II, 1849 pl. 167; J. Agardh 1863 p. 970; Kützing Tab. phyc. Bd. 13 1863 Taf. 92; Kolderup Rosenvinge 1884 p. 24 (rés. p. 4) fig. 32; Buffham 1893 p. 298; Falkenberg 1901 p. 150; Kolderup Rosenvinge 1902 p. 347 pl. VI figs. 3-14; id. 1903 p. 449 figs. 2-3; Kylin 1907 p. 139; F. Tobler, Weitere Beitr. z. K. d. Florideenkeimlinge. Beih. z. Bot. Centralbl. Bd. 21 Abt. 1, 1917 Taf. 7 figs. 15-20.

Conferva arceolata Dillwyn Brit. Conf. p. 82, plate G (The name is originally due to Lightfoot). Hutchinsia arceolata Lyngbye Hydr. 1819 p. 110 pl. 34.

Hutchinsia stricta Ag., Lyngbye Hydr. p, 115 pl. 36 (e specim.)

Hutchinsia lepadicola Lyngbye Hydr. p. 113 pl. 35, c; Flora Dan. tab. 2313, 1840.

Hutchinsia roseola C. Agardh Sp. Alg. p. 92.

Polysiphonia formosa Suhr, Flora 1831; Harvey Phyc. Brit. II, pl. 168, 1849; Kützing Tab. phyc. Bd. 13 tab. 78, 1.

Polysiphonia pulvinata Flora Dan. tab. 2458. 1845 (?).

Polysiphonia roseola (Ag.) Areschoug Phyc. 1850 p. 59.

- Polysiphonia lepadicola (Lyngb.) Kützing Sp. Alg. 1849 p. 807; Liebman, Kröy. Tidsskr. II Hefte 5 1839, p. 478; J. Agardh 1863 p. 945.
- Hutchinsia abyssina Lyngbye Rariora Codana (ed. Warming) 1880, Vidsk. Medd. fra Naturh. Foren. 1879-80 p. 227.

The primary shoot of the seedling is erect but a lateral shoot is early produced at its base (fig. 341, comp. Tobler fig. 19) or sometimes two. Creeping branches appear later and form a system of procumbent shoots attached to the substratum by scattered rhizoids and giving rise to a great number of erect shoots forming a dense tuft. The procumbent branches are often very short-celled, the articles being much broader than long (fig. 342) while in other cases the articles are of equal length or a little longer than broad (fig. 343). The growing end of the decumbent branches usually grows upwards at last and becomes an erect shoot, but the procumbent filaments may remain creeping for a long time, in particular in the f. *lepadicola*,



### Fig. 341.

Polysiphonia urceolata. Sporelings, 9 days old. In A the trichoblasts are arranged in a spiral turning to the right. 227:1. Fig. 342. Polysiphonia urceolata. Lower part of an erect branch issuing from a procumbent branch. 95:1.

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where erect shoots may be entirely wanting. The procumbent and erect shoots issuing from a procumbent one are always of endogenous origin, budding from the central cell, usually very near to the rhizoids (fig. 343). Endogenous branches also frequently arise from the lower part of the erect shoots (fig. 342). The rhizoids which always arise from the pericentral cells, except the first rhizoid of the sporeling, sometimes obviously testify to a shortening, the cuticle being transversely wrinkled (fig. 343).

FALKENBERG has maintained that *P. urceolata* lacks trichoblasts (1901 p. 151). As shown by me (1903, p. 450), this may be true but only in autumn and winter, when the development of the plant has ceased, while the specimens collected in the months of March to June are normally provided with trichoblasts, and these organs may still be present in July and August. In the creeping branches, however, they



Polysiphonia urceolata. Procumbent branch with rhizoids and endogenous branches. 50:1.

are always wanting. The trichoblasts show the typical structure, having the first branchlet always on the right side (fig. 346); their cells contain one nucleus and small plastids which are usually colourless but may be feebly rose-coloured in early spring or in shaded localities. They are arranged in a spiral turning to the left<sup>1</sup> but are usually separated from each other by more than one joint. The branches occur in the spirals in the place of the trichoblasts, but the relation of frequency of the two kinds of organs to each other is very variable. The erect shoots often over a long stretch only bear branches arranged in a spiral with a divergence of 1/4 separated from each other by 3 to 5 joints, and the trichoblasts appear only at the upper end of the shoot intermingled with branches; but in other cases the trichoblasts appear already in the lower part of the shoots. At the upper end of the shoots in particular of the fertile male and female plants, the trichoblasts may be more densely placed, each joint bearing one trichoblast. The erect filaments issuing from the creeping ones are often without primary lateral organs over a long stretch from the base, but endogenous adventitious shoots may frequently occur here (fig. 342). Trichoblasts have been met with in specimens collected near land and in specimens from greater depths as well (f. inst. bM, south of Hveen Su 22,5 m). They are shed in summer, when the growth is sisted. This usually takes place in June or July, but specimens in vegetative development may still be met with in August; these specimens seem, however, always to be young plants produced from spores germinated in the same season.

<sup>1</sup> A rare exception is shown in fig. 341 A, where the spiral turns to the right.

1)  $7 e^{3} e^{5} e^{4} e^{2} e^{3} e^{3} e^{17} b^{3} b^{4} b^{4} b^{4} b^{3} b^{5} b^{10} b^{3} b^{5}$ 2)  $8 e^{7} e^{17} b^{6} b^{8} b^{3} b^{3} b^{3} b^{3} b^{4} b^{2} b^{2} b^{2} b^{2} b^{2}$ 3)  $10 b^{5} t^{3} b^{2} b^{4} t^{3} b^{3} b^{4} b^{3} b^{5}$ 4)  $10 (t)^{5} (t)^{3} (t)^{2} b^{3} b^{3} d^{3} d^{3}$ 

Schemes of branches of *Polysiphonia urceolata*. The figures signify the numbers of joints between the consecutive lateral organs. e endogenous branches; b ordinary exogenous branches; t trichoblasts; (t) basal cells of shed trichoblasts;  $\delta$  male trichoblasts; + tetrasporangia, the sign denotes the joint in which the sporangium is seated.... designates that the base of the branch was not observed. 1)-3) branches of male plant from Frederikshavn April. In 1) the basal portion of the branch is procumbent; from \* the shoot is erect. The endogenous branches were feebly developed. Always a divergence of 1/4. 4) and 5) from Store Middelgrund (**Ke**) May. 6) from Hirshals July.

The young segments of the shoots are lower than in the other Danish species, but the segments producing branches are higher and cut off by more inclined walls (fig. 344).

The antheridia cover the greater part of unbranched trichoblasts; these organs have a short two-celled stalk and terminate with a sterile filament composed of a small number of cells, most frequently three. A sterile branch does not occur in the antheridia-bearing trichoblasts, but I have once met with a male trichoblast bearing a fertile



Polysiphonia urceolata. Male trichoblasts, a normal, b branched. 124 : 1.

branch corresponding to the first branch in the sterile trichoblasts (fig. 345). The male trichoblasts are densely crowded in corymbiform clusters at the tip of the shoots, each segment often bearing one trichoblast. The male trichoblasts often appear suddenly without foregoing sterile trichoblasts. Fig. 344.

Fig. 344. Polysiphonia arceolata. Tip of shoot with young trichoblasts. The last segment is higher than the foregoing ones; it will produce a branch. 390:1.

The procarps arise as in the other species in the second joint of the female trichoblasts, the upper part of which takes the shape of a sterile trichoblast. The third joint remains short and undivided and the first sterile branch is given off from the 4th joint, usually to the right (fig. 346). Of 33 examined female trichoblasts 26 bore the first sterile branch on the right side, 7 on the left. A cystocarp with its ostiole protracted in a cylindrical neck is shown in fig. 247. A remnant of the sterile part of the trichoblast may sometimes be found on the fully developed cystocarp.

The arrangement of the tetrasporangia differs according to whether the filament bears trichoblasts or not. In the latter case the sporangia are seriate and the filament



Fig. 346. Polysiphonia urceolata. a, portion of female plant. b, young procarp-bearing trichoblast. 220:1.

is usually curved so that the sporangia are placed in a row at the convex side. When trichoblasts are present, the sporangia are placed to the right of the foregoing trichoblast (fig. 348 A). The sporangia-bearing joints have 6 pericentral cells. In the trichoblast-bearing shoots a small peripheric cell is further cut off at the base of the joint; in the joint next to a trichoblast this cell is situated immediately to the right of the trichoblast. In spore-bearing shoots without trichoblasts such a small peripheric cell was not cut off (fig. 348 B).

In a female plant with fully developed cystocarps containing apparently



Fig. 347. Polysiphonia urceolata. Ripe cystocarp. 68:1.

normal carpospores, sporangia were here and there met with in the filaments. The sporangia were developed in the usual manner (without formation of a small peripheral cell) but they were small and undivided and obviously abnormal. A very remarkable case is shown in fig. 349. A trichoblast has produced an aborted procarp in its second joint but has then over it been transformed into a sporangia-bearing shoot, with incompletely developed sporangia. The third joint



Fig. 348.

Polysiphonia urceolata. A, portion of tetrasporiferous branch with trichoblasts. B, portion of tetrasporiferous branch without trichoblasts. C, transverse section of tetrasporiferous joint after evacuation of the tetraspores. D, transverse section of a sterile joint of the same branch, with five pericentral cells. B 95:1. A, C, D 200:1. Fig. 349. Polysiphonia urceolata. A female trichoblast has been transformed from the fourth joint into a tetraspore-bearing branch. 150:11. was undivided as in the normal female trichoblasts, but the following joints had produced 4 pericentral cells, and in the 7th joint the formation of sporangia was beginning. YAMANOUCHI has formerly described abnormal tetrasporangia in female plants of *Polysiphonia violacea* (1906 p. 425, figs. 168—171). BUFFHAM found antheridia in tetrasporic plants of *Pol. urceolata* (1893 p. 298).

Tetraspores sown in July germinated immediately and gave rise to young plants provided with trichoblasts and producing in great part one or two vigorous branches at the base (fig. 341). The sporelings obtained by Tobler (l. c.) from carpospores showed no trichoblasts.

*P. urceolata* has been met with from low-water mark to deep water. The deepest observed localities are 31 meters in the North Sea, 26,5 m in the Eastern Kattegat and 22,5 m in the Øresund (south of Hveen). It occurs near low-water mark in all the waters except the Sound where it has only been met with in 5,7 to 22,5 meters' depth, without doubt owing to the varying and often very low salinity of the surface water.

The species is perennial through its creeping filaments. The erect, fructiferous filaments are thrown off after the evacuation of the spores, but the sterile ones may persist, and the species may be found in every season with erect filaments. The length of these varies from 1 to 15 cm and may even reach 23 cm; it does not diminish towards the limits of the occurrence of the species. — Antheridia have been met with in January to July, procarps in April to June, fully developed cystocarps in May but in particular in June to August and further in September (Skagerak), and as late as January I have met with cystocarps containing ripe carpospores by Frederikshavn. Tetraspores have been met with in May to August and in September (Hirshals). The germination takes place immediately, but the new plants seem only to fructify in the following year. The species is comparatively often found in a sterile state, but there is no general relation between the sterility and the size of the individuals.

The species grows in particular on stones and is very common on moles in harbours, but it occurs too on several Algæ, in particular on the stipes of Laminaria hyperborea in the Skagerak, further on Phyllophora membranifolia, Furcellaria fastigiata, Fucus etc., on Ascidiae and shells of molluscs and barnacles.

*P. urceolata* is not very variable. Several specimens from deep localities in the inner waters may be referred to f. *roseola*, remarkable by slender filaments and long joints. Small, poorly developed specimens consisting principally of creeping filaments have been described by LYNGBYE as a particular species, *Hutchinsia lepadicola* Lyngb. (*Polys. lepadicola* Ag.)

Localities. Ns: 6 miles S.E. to E. of Vyl light-ship, 17 m on Lam. hyperb., loose (A. C. Johansen); aF, off Thyborøn, 31 m; Thyborøn, on groins; XR, off Ørhage. — Sk: Dana 2904 23 m (C. A. J.); YM<sup>1</sup>, Bragerne, 2,5 m; ZK<sup>2</sup> and ZK<sup>13</sup>, off Lønstrup, 1 and c. 9 m; XO and other places off Hirshals 11—15 m; mole at Hirshals; Højen, within the shoals. — Lf: Krik, pier; Lemvig harbour; XY and LV in Nissum Bredning; Oddesund; Thisted harbour; MH, off Skrandrup on firm clay; Nykøbing and other places

in Sallingsund; Agersund harbour; Nibe, pier; Aalborg; Hals harbour. - Kn: Skagen harbour; Herthas Flak c. 20 m; Hirsholm; Deget; Frederikshavn harbour; off Laurs Rev; off Marens Rev; north of Læsø, on Hyas (E. Bay); Trindelen (Børgesen); fG, W. of Læsø Trindels light-ship. - Ke: Fladen IM, ZF, ZE, VY, 16-26,5 m; EV, south end of Groves Flak; EU, Lille Middelgrund, 14 m; IA, IB, HY, Store Middelgrund; off Gilleleje, Lyngbye (Hutchinsia lepadicola: 1. Marts 1833 in tergo Cancri Aran., and 26. Mart. 1833 in Lepad. Balano. Hutchinsia abyssina: Juni 1834 in Buccino undato and 31. Marts 1835 in testa Balani e profunditate 16 org. (30 m)); Gilleleje harbour. - Km: FL, south of Læsø Rende, 9,5 m. — Ks: Grenaa harbour; HS, Briseis Grund, 7,5—13 m; Nordvestrev by Hesselø (Lyngbye); Holbæk Fjord, on Mytilus. - Sa: KJ, south of Hjelm, 13 m; PJ, Ebeltoft Vig; PL, Wulffs Flak; Kalø Rev; FS, Vejrø Sund; PA, near Albatros, 7,5 m; PC, between Sejerø and Ordrups Næs; PF, north of Refsnæs; Hov (O. Paulsen); Hofmansgave (Lyngbye, Hofm. Bang, C. Rosenberg); inlet to Odensefjord (Lyngbye, Hutch. stricta). - Lb: Bogense harbour; Fredericia harbour (Hofm. Bang, !); Strib harbour; Middelfart; Fænø Sund; off Stenderup; Heilsminde; DF, Remmen; Assens harbour; Aarøsund; Aarø; DA, Bøjgden; CZ, Hornenæs; dH<sup>1</sup>, E. of Hesteskoen, 18-19 m; dQ, south of Lydø, 22 m; Sønderborg harbour (10 cm long). - Sf: Søby harbour; UV, north of Ærø, 13 m; Aasø, Langeland; Marstal harbour; Ærø (Kjærbølling). — Sb: Kalundborg harbour; cT, Ryggen; Stavreshoved; Kerteminde harbour; Nyborg, harbour and Avernakhage; DN, Vengeance Grund, 12 m; UK, Langelandsbelt, 12 m; Spodsbjerg harbour. - Su: Hellebæk (Ørsted); Blokhus Grund north of Helsingør, 13 cm long (Boye Petersen); Helsingør (Liebman, P. lepadicola); bM, south of Hveen, 22,5 m; Taarbæk Rev, 6 m. - Bw: Sønderhav and



#### Fig. 350.

Polysiphonia orthocarpa. A, portion of decumbent branch and the lowermost part of an erect branch given off from it. 50:1. B, trichoblast with axillary branch. 150:1. Brunsnæs in Flensborg Fjord, piers; pier at the East end of Sønderkov, Als; dP, Bredegrund south of Als; dK, Pøls Rev; DU, off Dimesodde, 11 m. – **Bm:** 7,5 miles E. of H ellehavns Nakke, 27 m (C.A. J.).

### 2. Polysiphonia orthocarpa K. Rosenv. n. sp.

Cæspitosa c. 7 cm alta, filis erectis numerosis, e filis repentibus exeuntibus, inferne rhizoideis numerosis, partim fasciculatis, substrato non adfixis, instructis, sursum paululum attenuatis, articulis tetrasiphoniis non corticatis, in parte inferiori filorum ad geniculas leniter incrassatis. Rami in axillis pilorum (trichoblastorum) oriuntur; rami axillarii secundarii, e cellulis basilaribus pilorum deciduorum orti, desunt. Fila inferne crass.  $135-160 \mu$ , articulis diametro 1,5-2,5-plo longioribus, in parte media articulis diametro 4-6-plo longioribus, superne crass. 40-60 µ. Tetrasporangia in ramulis torulosis longe spiraliter seriata. Antheridia ignota. Cystocarpia subglobosa, ostiolo apicali, non protracto. — Color fusco-purpureus. (Plate V fig. 1).

This species which was found in two localities in the Limfjord in some respects resembles *P. violacea* but it differs from it particularly by the much developed creeping filaments and the caespitose growth and further by the want of cortication and of secondary axillary shoots. By these characters it agrees with *P. Rhunensis* 



Fig. 351. Polysiphonia orthocarpa. Lower part of an erect filament with numerous rhizoids. 20:1.

Thur., to which it seems to be nearly related; but as it differs from it by other characters, especially the dimensions of the articles, the presence of rhizoids on the erect filaments, and the shape of the cystocarps, it seems legitimate to consider it as a distinct species.

The erect filaments issue in great number from creeping filaments fixed to the substratum by short rhizoids ending in attachment discs. These rhizoids are given off not only from

the basal but also from the apical end of the pericentral cells, from which they are separated by a cell-wall. The articles of the creeping filaments are two to four times as long as broad. Rhizoids are also given off from the lower part of the erect filaments, but these rhizoids are not fixed to any substratum; they are of equal diameter in their whole length and form no attachment disc. They are always given off from the undermost end of the articles, often two or three from the same article. In rare cases I have found them fixed by the end to the same filament from which they had issued.



Fig. 352. Polysiphonia orthocarpa. Portion of branch with tetrasporangia. 200 : 1.



Fig. 353. Polysiphonia orthocarpa. A young and two ripe cystocarps. 107:1, D. K. D. Vidensk. Selsk. Skr., 7. Række, naturvidensk. og mathem. Afd. VII. 3.

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The erect filaments are very slowly attenuated upwards; at the base they are 135  $-160 \mu$  thick.

The upper end of the shoots has the same aspect as in P. violacea. Each joint bears a trichoblast except the undermost 3 or 4 (or 5) of the branches. The trichoblasts, which remain rather long, have the usual appearance; their cells contain one nucleus only. The branches arise as axillary buds of the trichoblasts; they are separated by 4 or 5 trichoblasts without branches, but two branches frequently follow one another. Secondary axillary shoots do not occur, or only appear exceptionally on the lower rhizoid-bearing joints. The first trichoblast of the branches appears on the 4th, 5th or 6th joint. Endogenous branches may occur in the pro-



Fig. 354. Polysiphonia Rhunensis Thuret, from St. Vaast (herb. Thuret), an unripe, and a ripe cystocarp. 107:1.

cumbent filaments and in the lower part of the erect ones.

The tetraspore-bearing shoots have the same structure as in *P. violacea*. The joints have 6 pericentral cells and, under one of them, a short peripheral cell situated to the right of the basal cell of the trichoblast of the foregoing joint (fig. 352).

The antheridia are unknown.

The cystocarps are subglobose or slightly depressed (fig. 353). The ostiole is not protracted, it is situated on the apex of the cystocarp opposite to the point of insertion,

not on its ventral side as in *P. violacea* and in *P. Rhunensis*, of which I have examined an original specimen from THURET collected at St. Vaast (fig. 354). The series of cells forming the outer layer of the wall run in the same direction as the stipe, and the placenta is perpendicular on this direction (fig. 353), while in *P. Rhunensis* the cell-rows run towards the ventral side and the placenta has an oblique position to the stipe. In the latter species the ostiole is moreover a little protracted and, according to THURET (l. c. p. 85), often a little sinuous. The cells surrounding the ostiole in *P. orthocarpa* are low, not prominent.

The specimens from the Limfjord resemble *P. Rhunensis* so much that I have been inclined to consider them as belonging to the same species. They agree with it by the cespitose growth, numerous erect filaments issuing from a system of creeping filaments, by the want of cortication, further, as substantiated by examining original specimens of THURET's, by the branches arising in the axils of the trichoblasts and by the want of secondary axillary branches. Our species differs, however, from THURET's species by the erect filaments being thinner at the base ( $^{1}/_{4}$  mm in *P. rhunensis*) and less tapering upwards, by the presence of rhizoids from the erect filaments and by the apical, not protracted ostiole of the cystocarps. By the shape of the cystocarp it is also distinct from *P. violacea*, in which the ostiole has a more or less ventral position and is surrounded by a prominent border composed of rather large projecting cells. Loc alities. Lf: Under Lischøj, N.W. point of Fur, 1-2 m, apparently growing on diatomite (dan. Molér) with ripe sporangia in July; Amtoft reef, from a slight depth to 4 meters (unknown in which depth t has been growing). Sand and clay is retained between the erect filaments. With cystocarps in August.

### 3. Polysiphonia elongata (Huds.) Harvey.

Harvey in Hooker, Brit. Flora 1833 p. 333; Harvey Phyc. Brit. III 1851 pl. 292, 293; Kützing, Phycol. gen. 1843 Taf. 50 V; Tab. phyc. 14, 1864 Taf. 4; J. Agardh, 1863, p. 1004; Kny 1873, p. 107, Taf. II Fig. 5; Kolderup Rosenvinge 1884, p. 24, 1903, p. 405; Falkenberg, 1901, p. 126, Taf. 21, Fig. 6-9; Kylin, 1907, p. 144; L. Batten 1923 pp. 279, 297.

Conferva elongata Hudson, Fl. angl. II, 1778, p. 599. Ceramium elongatum Lyngbye, Hydr. 1819, p. 117. Ceramium brachygonium Lyngbye Hydr. p. 118, Tab. 36 C. Hutchinsia strictoides Lyngbye Hydr. p. 114, Tab. 35 D. Hutchinsia elongata Flora Danica tab. 1836, 1825. Polysiphonia strictoides Kützing Tab. phyc. 14, 1864, Tab. 10.

α, typica.

- β, Schuebelerii (Foslie) nob. (Plate V fig. 2).
- Comp. Børgesen and Jonsson, The distribut. of the Mar. Alg. of the Arctic Sea etc. Appendix to the Botany of the Færöes. 1908 p. XII.
- P. Schuebelerii Foslie, Nye aret. havalg., Christiania Vidensk. Selsk. Forh. 1881 Nr. 14 p. 3, tab. I fig. 1—3. Kolderup Rosenvinge, Grønl. Havalg. 1883 p. 798, pl. I figs. 1—2.

y, baltica nob. (Plate V fig. 3).

The morphology of the frond has been described by KNY and FALKENBERG. The trichoblasts are arranged in a regular spiral turning to the left, each joint bearing a trichoblast with the exception of the first 5 or 4, rarely of a greater number

of joints in the branches, which bear no lateral organs. The divergence of the trichoblasts in the spiral is a little greater than <sup>1</sup>/4. The cells of the trichoblasts contain one nucleus. In f. *baltica* the trichoblasts are simple or very feebly branched and usually contain well developed rose-coloured chromatophores. The branches appear in the places of trichoblasts in the spiral, and are usually separated by 5 joints, more rarely by 4 or 6. Upwards the branches often become rarer, in particular in the tetrasporiferous and the antheridia-bearing shoots, which in their upper parts are entirely branchless. The branches usually appear singly; branches on two consecutive joints may, however, sometimes occur.

Adventitious shoots from the basal cells of the fallen off trichoblasts (secondary axillary shoots) appear not rarely, in

particular on the lower part of the shoots. In specimens of f. *baltica* from Flensborg Fjord adventitious shoots appeared abundantly and early, before the trichoblast had been shed (fig. 364). The adventitious branches, however, usually reach only a slight degree of development in the first season. On the other hand,



Polysiphonia elongata f. Schuebelerii. Tip of shoot. The first pericentral cell in the 4th segment has been cut off to the right of the trichoblast. 560 : 1.

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adventitious shoots appear normally in the shoots of wintering plants. When the growth ceases at the end of summer, a number of shoots and tips of shoots are thrown off, and next spring numerous new shoots are produced, partly from the surfaces of the wounds, partly from the basal cells. Frequently a shoot is produced from each joint. When the new shoots are principally given



Fig. 356.

Polysiphonia elongata. A, portion of shoot showing the formation of the first cortical cells. B, nuclei and chromatophores of a pericentral cell. 270:1. C, portion of a branch showing the upper end of a pericentral cell with nuclei and cortical cells. 95:1.

off from the upper part of the wintering ones the form appears which J. AGARDH has named f. *microdendron* (l. c.). This form I have only found once (Klørgrund South of Hjelm in May).

In the usual form with short joints the branches are to a considerable extent connate with the following joint (fig. 356). In this form the branches are as a rule thin at the base and become thicker upwards. In f. *baltica* this is not so or only in a slight degree.

The cortication begins early, especially in the typical form. The primary cortical cells are here often of the same length as the pericentral cells, being cut off by a longitudinal wall (fig. 356). In the forms with longer joints, f. *Schuebelerii* and f. *baltica*, the primary cortical cells are shorter and cut off by an inclined wall (fig. 361). The pericentral cells contain numerous nuclei and the primary cortical cells are also plurinucleated (fig.

356), while the central cell contains one large nucleus, at least for a long time.

In the typical form, the pericentral cells of the thick main shoots are connected with several secondary pits traversing the transversal walls. In a transverse section one pit is found in the middlemost part of the wall and a number of up to ten in the periphery. The central pit is probably the first, arisen at a very early moment, while the others have only been formed in the following year. The cortical cells may also be connected by several pits in the same wall, in particular in the transversal walls. The secondary pits of the pericentral cells are much smaller than those of the central axis, but bigger than the pits between the pericentral cells in the other species of *Polysiphonia* and bigger than the primary pits connecting the central cells with the pericentral cells in *Polysiphonia elongata* (fig. 357).<sup>1</sup> Such multiple pits were not met with in f. *baltica*. On the other hand, the central cells of this

<sup>1</sup> Dr. LILY BATTEN figures three pits connecting two pericentral cells which are erroneously said to be central cells (1923 pl. 22 fig. 1).

form were often filled up by hypha-like cells, a phenomenon which, according to FALKENBERG, frequently occurs in the pericentral cells of *P. elongata*.

The attachment organ of the frond is conical, built up of numerous densely crowded descending filaments forming the continuation of the filaments of the cortication, and of rhizoids mostly given off from the latter (comp. L. BATTEN 1923 pp. 279, 297, fig. 47).



Fig. 357.

Polysiphonia elongata. A, longitudinal section through the central part of an old stem, showing the central cells and the pericentral cells connected with multiple secondary pits. 100:1. B, transverse section of a similar stem, at the level of a transverse septum, showing the pits. 290:1.

The antheridia occupy the main axis of the trichoblasts except the two first joints, the upper of which bears a sterile branch on the right side. Sometimes the third cell is also sterile and then bears a sterile branch on the left side. In the first case it happens that the branch becomes fertile and the trichoblast thus bears two antheridial bodies (fig. 358 to the right), and trichoblasts bearing three antheridial bodies were met with too (fig. 358 above). In the branch shown in the same figure an antheridial cushion even occurred on the stem (comp. L. K. R. 1903, p. 465).

In the procarp-bearing trichoblasts the first branch is seated on the 4th joint but not always on the right side, frequently on the left side. The ostiole of the cystocarp is fairly broad, not protracted and directed obliquely upwards, but more upwards than forwards (fig. 359, comp. Harv. pl. 292, 293). I have, however, met with cystocarps thicker than those figured by HARVEY and me and provided with a short spout.



Fig. 358.

Polysiphonia elongata. Portion of male plant, showing trichoblasts with two or three antheridial bodies and a cushion of antheridia on the surface of the stem. 124:1. The sporangiferous joints have 6 pericentral cells, 4 of which cover the sporangium. As shown by FALKENBERG (l. c. p. 128, pl. 21 fig. 9), a small peripheral cell situated to the right of the trichoblast of the foregoing joint is usually to be found (fig. 362); it is, however, not always present (fig. 360). When going from one trichoblast to the next two pericentral cells are passed.

The sporelings grow out to a vigorous straight primary shoot with early developed cortication, much bigger than the lateral branches.

J. AGARDH distinguishes two main forms of the species: I. Lyngbyei and II. Ruchingeri, the first thinner, with flagelliform filaments and the upper branches tapering upwards from a broader base, the latter thicker and more fleshy, with straight branches and the upper ones attenuated upwards and downwards. F. Lyngbyei is said to be most frequent at the coasts of Sweden and Denmark ("in

sinu Codano"), while the other occurs on the shores of the Atlantic Ocean. The characters mentioned seem, however, to be inappropriate as distinctive characters; thus

in most specimens from the Danish waters not referable to f. *baltica*, branches attenuated towards the base may be found. Nor has KYLIN considered this character as conclusive, having described under the f. *Lyngbyei* a new subf. *gelatinosa* with the branches attenuated downwards. This character is most prominent in the specimens from the North Sea, the Skagerak and the Northern Kattegat.

Most of the specimens found in the Danish waters have been referred to f. *typica* though they are somewhat variable according to the localities. When growing in slight depth and exposed to light they become breviarticulate, the joints in the upper part of the plant having only half the length or the same length as the breadth, and the main axes become at least 1 mm thick. In greater depths the joints become longer. The typical form



Polysiphonia elongata. Ripe cystocarp. 100 : 1.

is common in the Danish waters from the North Sea to the western Baltic Sea, descending to 19 meters' depth. The innermost places where it has been met with near low water mark are Svendborg (Sf), Kerteminde (Sb) and Hellebæk (Su). In the Great Belt south of Kerteminde the minimum depth of its occurrence is 6,5 m, in the western Baltic Sea it is 5 m and in the Sound south of Helsingør 10 m.

In the inner Danish waters *P. elongata* appears in more slender forms which, however, are closely connected with the typical form by intermediate forms. In the



Fig. 360. Polysiphonia elongata f. typica (from Frederikshavn). Portion of tetrasporiferous plant. 75 : 1. Fig. 361. Polysiphonia elongata f. Schuebelerii, from Bolsaxen). A, portion of frond showing pericentral cells and cortication. 70:1. B, transverse section of stem not yet corticated. 200:1.

Fig. 362. Polysiphonia elongata f. Schnebelerii, from Bolsaxen). A, portion of plant with tetrasporangia. B and C, transverse sections of tetrasporiferous joints. A 95:1. B, C 200:1.

Great Belt (Sb) a form agreeing exactly with *P. Schuebelerii* Foslie (see above) has been met with in several places in 6,5 to 19 meters' depth. It differs from the typical form principally in the longer joints, being up to 4 times as long as broad or longer where the cortication begins, and in the feebler cortication which entails a smaller diameter of the main axes (300—660  $\mu$ ). The first cortical cells are comparatively small and cut off by oblique walls. The pericentral cells occupy a great part of the transverse section of the old stem; they produce no new pits or a small number of multiple pits in the transverse walls. On the other hand, in some cases I found the central cell



Fig. 363. Polysiphonia elongata f. baltica. A, upper end of shoot; trichoblasts with chromatophores.

cortical cells. The main axis is only  $140-280 \mu$  thick. The trichoblasts are unbranched or slightly branched with well developed, feebly rose-coloured chromatophores; they are usually long kept. When adventitious shoots occur they may arise before the trichoblasts have been shed (fig. 364). This form is confined to localities with feeble salinity and rather feeble light (9-24,5 meters depth). Specimens from the deepest localities in the outer waters with high salinity may resemble f. *baltica* in some characters, but are so different in other respects that they cannot be referred to it. In the Limfjord, in depths of 7 to 10 meters, where the light is very feeble, owing to the very turbid water,

filled with hypha-like filaments. The trichoblasts are branched, in greater depths provided with feebly rose-coloured chromatophores. The frond may be 30 cm long or more.

In the Baltic Sea around Møen (Bm) and around Bornholm (Bb), where the salinity is much feebler, the species occurs in a still slenderer form which at first I judged identical with f. expansa (Ag.) which J. Agardh first found at the coast of Blekinge. An examination of the original specimen of Hutchinia expansa Agardh in AGARDH's herbarium in Lund showed me. however, that AGARDH's species cannot be referred to P. elongata as its branches arise in the axils of the trichoblasts, but that it is a form of P. violacea. I have therefore given the here described form of *P. elongata* from the Baltic Sea the name f. baltica. The frond of this form is very slender, up to 20 cm long, and has an intense red colour. The joints are 4-7 times as long as broad where the cortication begins. The branches are not attenuated towards the base. The cortication often begins rather late and advances more slowly down-

wards so that the pericentral cells do not become entirely covered by the



Fig. 364. Polysiphonia elongata f. baltica, from Flensborg Fjord. Secondary axillary shoot. 230 : 1. the specimens of *P. elongata* agree with the typical form in all respects. Specimens from the Kattegat collected in 17—19 meters' depth were certainly a little slenderer than those from higher levels and usually showed longer joints, 1—3 times as long as broad, but the branches tapered downwards and the trichoblasts were branched.

P. elongata occurs in all the Danish waters and also enters in the fiords. It descends to 20 meters' depth but has been recorded in 27 meters' depth in the eastern Kattegat and in 24,5 meters' depth near Bornholm (f. baltica). It grows on various substrata, stones, moles, shells of mollusks, various Algæ, as Fucus serratus, Laminaria digitata, etc. and Zostera. It occurs in very different plant associations but usually not as a dominant constituent. In oozy bottom it is frequently met with on mollusk shells. It is remarkable that it may occur rather abundantly in places where the flora is poor in species, f. inst. Fanø and Løgstør. It often attains a length of 23 cm, more rarely 35 cm, but only in protected localities. In autumn many specimens die but others are only denudated and recommence the growth in winter. New shoots may appear already at the end of December, and in January they are usually present though the growth is slow. Thus, new shoots more than one cm long were found in a specimen gathered on January 25th in the Great Belt; but it must be said that other specimens gathered in other localities in the same water were still in a resting stage. The growth is intense in April and May, it continues in June and July but in the latter month it decreases and usually ceases. The trichoblasts may remain still for some time, but in several specimens they are thrown off already in August. Otherwise this takes place in autumn, and at the same time a number of shoots, principally the fructiferous ones and the ends of the shoots are shed.

Antheridia were met with in January (unripe), April, May and July, and once even in August, ripe cystocarps in May to September, most frequently in July and August, unripe in April and May, ripe sporangia in May to August. The sporelings arising from the spores disseminated in summer continue their development, after wintering, the next year; but it is doubtful whether they can winter more than once.

Localities. *a, typica.* Ns: Nordby, Fanø; Esbjerg; Thyborøn, harbour and groins; off Ørhage, 5,5-7,5 m. — Sk: YU, Hanstholm, 2 m; within Bragerne, 2-10 m; off Løkken, 13 m; Dana St. 2900, 9 m (C. A. J.); FK<sup>2</sup>, off Lønstrup; Hirshals mole and off Hirshals, 2-11 m; Højen, within first and second shoals, 2-5 m. — Lf: LV, Nissum Bredning; MH, Thisted Bredning; Oddesund; Nykøbing (Th. Mortensen, !); four localities east of Mors; north of Fur, Lendrup Røn, Løgstør, Aggersund (Ostenfeld). — Kn: Skagen; fC, S. of Skagen, 15 m; FG, Herthas Flak; off Hulsig (Boye Pet.); Krageskovs Rev (KC and TV); Hirsholmene; Fladstrand (Hornemann); harbour of Frederikshavn and reefs off Frederikshavn, off Marens Rev, 20 m; harbour of Sæby; BP, off Sæby; Nordre Rønner; TL, NG, VT, fF, UC, UB, GM, north of Læsø; harbour of Østerby; TO (17 m), TP, TQ, NI, FF, FE, fG, Dana St. 3891, near Trindelen. — Ke: FC, FD, XA, east of Læsø; VY, ZE, fH, Fladen; Groves Flak, down to 26,5 m; IK, ET, Lille Middelgrund; HX, Store Middelgrund, 17 m; GI, Ostindiefarer Grund; OO, Søborghoved Grund; Gille-leje, Nakkehoved (Lyngbye). — Km: Læsø Rende; Dana St. 2619, 2884 (C. A. J.); YY, XD, XF south of Læsø; BN; TS; VQ, Svitringen; BM; BL; VP; bK, N.W. of Anholt, 15 m; BK, VM, near Tangen; NC; BI, Gjerrild Flak; Gjerrild bay (Lyngbye). — Ks: EP, Pakhusbugt, Anholt; OP, HQ, EJ, Lysegrund; D, K. D. Vidensk, Selsk, 7. Bække, naturvidensk, og mathem. Afd, VII. 3.

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RL, N.W. of Gilleleje; Grenaa harbour; HS, Briseis Grund; OS, Hastens Grund; OU, Schultz's Grund; FO, NB, Havknudeflak; FP, Jessens Grund; GF, Sjællands Rev; aU; D, Grønne Revle; EJ, entrance to Isefjord; NL and EH, off Lynæs; Lamme Fjord; Holbæk Fjord. — Sa: Very common, found in numerous places from 1 to 15 meters' depth. — Lb: Several places from 2 to 17 m. — Sf: Harbour of Svendborg, 1 m; BY; UV, 13 m; DZ. — Sb: 1 to 19 m.: DL; GT; DM; MN; GV; LM; harbour of Kerteminde; bay of Kerteminde; GQ; NU; AB; NP; NQ; NN, 19 m; UE; DN; Y; LH; LB, 17 m. — Sm: GZ; HA, Agersø Sund, 11 m. — Su: CS, off Aalsgaarde; Hellebæk (Budde Lund); Helsingør (Liebman); HK; PZ, east of Hveen; RZ, 13 m: bM, south of Hveen, 22,5 m; OH, off Vedbæk, 10 m. — Bw: bY, off Sønderskov by Sønderborg, 11 m; cD, dO, 5 m, dK, south of Als; LF, Vodrups Flak, 9,5 m; DV; LC, 11,5 m, south of Langeland.

 $\beta$ , Schuebelerii. — Sa: DK, Bolsaxen, 14 m. — Sb: Off Refsnæs, 19 m (Ostenfeld); LK, Elefantgrund (transitional form); UE, near Vresen, 7 m; UF, near Hov Sand, 8,5 m; DN, Vengeance Grund, 11,5 m. — Bm: 11,5 miles S. by E.  $\frac{1}{4}$  E. of Møens light-house, 19 m, ( $\bigcirc$  6, C. A. J.).

 $\gamma$ , baltica. — Su: SA, Flinterenden. — Bw: dN, Flensborg Fjord, 9 m; KX, Femerbelt, 19 m. — Bm: QY, Bjelkes Flak, 10 m; VG, north of Møens Klint, 17 m; bO, south of Møen. — Bb: SQ, south of Broens Rev, 8,5 m; YE, off Øleaa, 10,5 m; YC, 24,5 m and YD, 19 m, near Salthammer Rev; 3 miles S.S.E. of Nexø harbour (C. A. J.); (12 miles N. 1/2 E. of Arkona light-house 46 m ( $\bigcirc$  6, C. A. J.); the specimens much resemble that represented in Lakowitz, Algenfl. Danz. Bucht, Taf. II Fig. 5 under the name of *P. violacea* forma *tenuissima* which is perhaps identical with it).

### 4. Polysiphonia violacea (Roth) Greville, emend.

Hooker, Engl. Flora, Vol. II part I. 1833, p. 332; Harvey, Manual, 1841, p. 92; Phyc. Brit. II. 1849, plate 209; Areschoug, 1850, p. 51; J. Agardh, 1863, p. 988; Kützing, Tab. phyc. 13, 1863, pl. 97, 98; Kolderup Rosenvinge, 1884, p. 27, pl. 1—2, figs. 33—47; Reinke, Algenfl. d. westl. Osts., 1889, p. 30; Falkenberg, 1901, p. 115, pl. 1, figs. 17—19; S. Yamanouchi, 1906, p. 401—449, plates 19—28; Kylin, 1907, p. 140.

Ceramium violaceum Roth, Catal. bot. Vol. I, p. 150.

Hutchinsia violacea Ag., Lyngb. Hydr., 1819, p. 112 ex parte (tab. 35, fig. B, 1).

Hutchinsia stricta Lyngb. Hydr., 1819, p. 115 ex p. (test. specim.); Fl. Dan. tab. 1666, 1819. Hutchinsia divaricata Fl. Dan. tab. 2312, 1840.

a, violacea Aresch. l. c. p. 53, Alg. sc. exs. Nr. 65.

P. violacea  $\beta$ , sub-Brodiaei Aresch. 1850, p. 52, Exs. Nr. 5 (89).

β, fibrillosa (Dillw.) Aresch.

Areschoug, 1850, p. 52.

Conferva fibrillosa Dillw., Brit. Conf. 1809, p. 86, pl. G; Flor. Dan. tab. 1545, 1816.

Hutchinsia fibrillosa Ag., Lyngb. Hydr. 1819, p. 113.

Polysiphonia fibrillosa Grev. Harvey in Hook. Brit. Flora Vol. II p. 334, Phyc. Brit. Vol. III pl. 302, 1851. J. Agardh 1863, p. 991; Kny 1873, p. 104; Reinke, Algenfl. p. 31, Kylin, 1907, p. 141.

y, tenuis.

Ceramium violaceum  $\beta$ , tenuis Roth Catal. III p. 151 (?). Polysiphonia bulbosa Suhr, Aresch. Alg. sc. exs. Ser. I n. 9. Polysiphonia violacea  $\vartheta$ , bulbosa Areschoug 1850, p. 53. Polysiphonia violacea  $\epsilon$ , tenuissima Aresch. l. c. p. 54, Hauck, Meeresalg. p. 227. Polysiphonia roseola Kützing Tab. phyc. Bd. 13 Taf. 80.

### $\delta$ , aculeata (Ag.)

Hutchinsia aculeata Agardh Synopsis Alg. Scand. p. 59.
Polysiphonia aculeata J. Agardh, 1863 p. 947, Kützing Tab. phyc. Bd. 13 Taf. 71.
Polysiphonia aculeifera Kützing Tab. phyc. Bd. 13 Taf. 71.
Hutchinsia implicata Lyngbye Hydr. p. 111, Flor. Dan. tab. 1955.
Hutchinsia divaricata Ag. Syn. Alg. Scand. 1817 p. 59.
Polysiphonia divaricata Kützing Sp. Alg. p. 822, J. Agardh, 1863, p. 947.

Polysiphonia violacea is here taken in a larger sense than by earlier authors, not only *P. aculeata* (Ag.) but also *P. fibrillosa* (Dillw.) being included in it, while the latter has hitherto been regarded as a distinct species.

The morphology and development has been described by KNY (1873, p. 104, P. fibrillosa), myself (1884) and FALKENBERG (1901). The primary axis is usually very distinct; in the f. tenuis only it is very thin and not easily discernible from the longer branches. The basal disc is composed of numerous densely crowded rhizoids terminating in attachment discs (fig. 365, comp. L. Batten 1923 figs. 55, 59). According to FALKENBERG (1901, p. 116) adventitious, partly creeping branches are later given off from the base of the plant. This may be so, as I have convinced myself, but usually such adventitious shoots are not produced (comp. HARVEY Phyc. Brit. Plates 209 and 302). In some cases, however, I found a great number of small adventitious shoots arising from the basal disc, being first creeping and then ascending and producing erect branches, and I also found erect shoots issuing directly from the basal disc. Such adventitious shoots are perhaps more common in f. tenuis.

The trichoblasts are arranged in a regular spiral, with a divergence varying between  $\frac{1}{4}$  and  $\frac{2}{7}$  of the circumference. Each joint of the shoots bears a trichoblast with the exception of the lower-most joints of the primary axis and of the branches. The first trichoblast on the branches is most frequently placed on the third joint, the basal joint included, more rarely on the 4th, very rarely on the second joint; in a specimen collected at Gjelle-



#### Fig. 365.

Polysiphonia violacea. A, young plant growing on Polysiphonia elongata, June 15th; a procarp is developing in the trichoblast on the 20th joint. B, base of a hardly one cm high plant. 100 : 1.

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grund in the Great Belt in November it was, however, placed on the 5th or 6th joint. The trichoblasts are usually much branched, showing two generations of



Fig. 366. Polysiphonia violacea. Tip of shoot treated with glycerine. *I*—*IV*, trichoblasts; pericentral cells numbered according to age; *b*, basal cell of trichoblast. 390 :1. branches, particularly in the vigorous forms growing in shallow water (fig. 369 A). In other specimens the ramification is feebler, the trichoblasts bearing only one or two simple branches, or they may be entirely unbranched. Such simple trichoblasts are particularly found in slender specimens belonging to or approaching to f. *tenuis*, generally in specimens growing in deeper water or in shaded localities. They were met with in most of the specimens collected in November, at a season when the growth is very feeble. They occurred too in several specimens collected by Bornholm in July and August. The trichoblasts are usually hyaline; in specimens from deep water, however, they may contain feebly rose-coloured chromatophores. The cells contain one nucleus. The trichoblasts may be shed early, in other cases they may persist for a fairly long time; thus in several specimens from the Baltic Sea they were still present on the 40th to the 42nd joint from the top.

The primary branches arise at the base of the trichoblasts and develop simultaneously with them. They do not, however, occur at all the trichoblasts but are

usually separated by 4 or 5 joints; yet, two or even three primary branches often follow immediately after each other. The basal cells of the trichoblasts which are not accompanied by primary branches generally produce later branches which may be named secondary axillary branches. These branches arise at a considerable distance from the top, usually only when the trichoblast has fallen off, but not rarely before this has taken place; they may attain a considerable length but always remain much feebler than the primary axillary branches. Very often all the basal cells produce branches, though some of them reach only a small size. As an example is here given a diagram of a shoot, where t signifies trichoblast, t basal cell of a trichoblast fallen off, b primary branch and s secondary axillary branch:



### Fig. 367.

Polysiphonia violacea. Portion of central and pericentral cell showing nuclei, chromatophores (partly) and pits, p, connecting the central with the pericentral cells. 230:1.

ssssbssssbbtssssbssssbbttssbssssbbsstsbssssbbsstsbssssbbttttbbttttbb(top).

These secondary branches can be distinguished in the drawings of HARVEY (Phyc. brit. Plate 209) and KÜTZING (Tab. phyc. Vol. 13 Taf. 97 e, 98 e). They are very conspicuous in f. *aculeata* (fig. 374).

As in other species of *Polysiphonia*, torsions may occur in the long branches with the consequence that the primary branches may be placed in a longitudinal row over a long stretch (Plate VI fig. 1).

The central cell always contains a single nucleus; in the older cells it is rather large and situated in the middle of the cell. The pericentral cells after the formation of the secondary pits contain two nuclei which by continuous bipartitions produce the numerous small nuclei contained in the older pericentral cells. In one case c. 100 nuclei with a diameter of  $5-6\mu$  were counted in one pericentral cell, while the nucleus of the central cell measured a 20 is the measure in the formation.



Fig. 369. Polysiphonia violacea. A, trichoblast. B, trichoblast with antheridia. 200 : 1.



Polysiphonia violacea. A, cortical cell with three nuclei cut off from a pericentral cell. B, downward growing cortical filament on the point of establishing a secondary pit connecting it with another corticating filament. 230 : 1.

cell measured c. 30  $\mu$  in the greatest diameter (fig. 367). The central cell contains no chromatophores; the protoplasm

shows a fine longitudinal striation.

Cortical cells are always produced, but the cortication occurs in various degrees; it is most developed in f. fibrillosa, least in f. tenuis. It is usually not more pronounced than that the pericentral cells are visible between the cortical filaments; in the lower part of the main stem, however, the pericentral filaments may be completely covered, in particular in f. fibrillosa. The primary cortical cells are cut off from the undermost part of the pericentral cells by an oblique wall and originally contain more than one nucleus (fig. 368). They early begin to grow downwards in the outer wall between two pericentral cells, dividing by transversal walls. At their upper end they may also grow upwards under segmentation. The descending bark-



Polysiphonia violacea. Ripe cystocarp. 76:1.

filaments become connected with each other and with the pericentral cells by secondary pits (fig. 368 B). Two pits in the same wall may even occur.

The antheridia occupy the main axis of the male trichoblasts except the two lowermost cells, and the second cell bears a sterile branch on its right side. A torsion takes place, however, in the second joint with the consequence that the sterile branch issues on the outer side of the trichoblast

and thus serves to protect the antheridial body (fig. 369).

As regards the development and the structure of the cystocarps reference may be made to YAMANOUCHI (1906). A ripe cystocarp is shown in fig. 370.

In the tetrasporiferous shoots a considerable number of joints, usually without interruption, contain each one sporangium. As the sporangia always arise to the left of the trichoblast of the same joint, the sporangia are thus arranged in a spiral. The fertile joints have 6 pericentral cells, two of which are cut off from the cell which gives rise to the sporangium and which corresponds to the second pericentral



Fig. 371. Polysiphonia violacea. Branch with tetrasporangia. 200:1.

cell in the sterile joints (figs. 372, 373, comp. fig. 366). One of these secondary pericentral cells does not reach the base of the joint, and a small peripheral cell (p)is here later cut off from the inner cell which is thereafter divided by a horizontal wall in a short stalk-cell (s) and the mother-cell of the sporangium. The stalk-cell



#### Fig. 372.

Polysiphonia violacea. A, tetrasporiferous joint; b basal cell of trichoblast; p, small peripheral cell. B, transverse section of tetrasporiferous joint. 390:1. C, similar after evacuation; s, split through which the tetraspores have escaped. 230:1. is then connected through pits with the central cell, the sporangium, the two secondary pericentral cells and the small peripheral cell, p.

*P. violacea* which is one of the most common species of Algæ in the Danish waters is very variable. The single characters distinguishing the different forms, as the length of the joints, the degree of cortication, the degree of branching of the trichoblasts and the frequency of the secondary axillary shoots are evidently dependent on the outer conditions. *P. fibrillosa* 

has hitherto been regarded as a distinct species though in its morphology it exactly agrees with *P. violacea* and only differs by very variable characters such as those mentioned. HARVEY indeed observes of *P. fibrillosa* (Phyc. Brit. Pl. 302, 1851): "It is most nearly related to *P. violacea*, with which alone can it well be confounded, and from which it chiefly differs in its shorter and less multified ramuli, duller colour, and shorter articulations; but there are specimens occasionally found which seem almost to connect these two species together". J. AGARDH, REINKE and KYLIN admit too the relation of the two species but nevertheless consider them as distinct. After having

examined a great number of specimens from numerous localities in the Danish waters I have arrived at the apprehension that it is impossible to draw a natural line of demarkation between them. In too many cases it depends on an arbitrary estimate whether a specimen may be referred to the one or the other of the two species, and I have therefore arrived at the conclusion that P. fibrillosa must be regarded as a form of P. violacea distinguished principally by shorter joints and stronger cortication. The trichoblasts are strongly developed



Fig. 373.

Polysiphonia violacea. Division of tetrasporiferous joints. b, basal cell of trichoblast; p, small peripheral cell; s, stalk cell of sporangium;  $\times$  small cell establishing the secondary pit between the pericentral cells. 636 : 1.

and much branched, at the base up to  $28 \mu$  thick. The straw-colour of the frond emphasised by REINKE is entirely due to an intense light. It grows only in slight depths and in rather light places, and usually also in more agitated water, and these conditions undoubtedly produce the characters mentioned.

In f. *fibrillosa* the joints in the upper part of the frond are about  $1^{1/2}$  (1-2) times as long as the diameter. In f. *typica* they are longer, usually 3-5 times as long as broad. In this form the main axis is distinct as is the case also with f. *fibrillosa*. But the thickness of this axis is variable, and in the finer forms it is scarcely thicker than the principal branches. In f. *tenuis* the principal axis is thin and not discernible from the branches; the joints are longer, c. 6-9 times as long as broad, the cortication almost wanting, the secondary axillary shoots are scarce, and the trichoblasts simple or feebly branched, often with rose-coloured chromatophores. This form grows in localities with feebler light and less agitated water, principally in fjords and in great depths.

F. aculeata is a loose sterile form characteristic by its squarrose branches and by wanting cortication. It has usually numerous secondary axillary branches which in spreading at right angles give to the plant a characteristic appearance (fig. 374). Sometimes, however, the secondary branches occur only rather sparsely, and the plant might then be referred to *P. divaricata* Ag. which is otherwise not sufficiently different from f. *aculeata* to be distinguished from it as a different form. F. *aculeata* occurs in shallow water. It must be assumed that loose individuals of *P. violacea* drifted in shallow water may go on growing there and by the altered condition, in particular the stronger light, assume the appearance characteristic to this form. Spec-



Fig. 374.

*Polysiphonia violacea* f. *aculeata*. Portion of shoot with one primary and 6 secondary axillary branches. 36:1.

imens of f. *fibrillosa* growing in very sunny localities, e.g. the stony reef in Kalø Vig, may take an appearance reminding one of f. *aculeata* by squarrose branchlets.

P. violacea may complete its development in a short period. Most of the individuals probably only reach an age of a few months. This is at least the case with the specimens which grow on annual species of Algæ, e. g. Chorda Filum; they must have germinated in spring (May) or later, are fully developed in summer, and perish with the host plant in autumn. In favourable localities more than one generation may probably be produced in one summer. In the plant shown in fig. 365, collected June 15th, which was certainly only a few weeks old, a young procarp was already discernible in the trichoblast of the 20th joint of the plant, and another young plant of about the same size bore almost ripe antheridia. Most of the specimens certainly perish in autumn after fructification, but other

individuals endure the winter and recommence in spring the growth arrested during the winter.

The growth ceases or is at least much diminished in August, and several individuals then begin to lose the trichoblasts. In the following months the growth is likewise stopped or extremely feeble. In November all or most of the trichoblasts are thrown off, and that is also the case with the tips of many of the shoots. In December and January the species appears in the same stage (fig. 375). In the last part of December 1890, however, I found on the bottom of Holbæk Fjord, which at that time had been covered with ice during a month, specimens with well preserved growing points and trichoblasts. The growth recommences in the last part of the winter. In the wintering specimens new shoots are found in spring growing out from the basal cells of the decayed trichoblasts, while the tips of the wintering shoots have fallen off. It seems, however, to be only a small number of
specimens which endure the winter in a more advanced stage of development. In the northern part of the Kattegat, in the neighbourhood of Frederikshavn, I did not find any specimen of this species when collecting Algæ in December 1894 and Januar 1895, while it is very common there in summer. On the other hand full-grown specimens more frequently endure the winter in the inner waters, for I found such specimens in several places in the Little Belt and in the Great Belt

in December and January. In the northern Kattegat it probably passes the winter in very small specimens arising from spores germinated in autumn.

P. violacea fructifies in summer. Ripe sporangia occur in May to September; in May the sporangia are frequently unripe. Ripe antheridia were met with in May to September and in November. Ripe cystocarps occur in July to September. The spores germinate immediately; sporelings are frequently met with on various Algæ in summer. Three days old sporelings from tetraspores and carpospores sown in vessels with sea-water showed about 10 tiers of cells.

The frond usually reaches a length of 7-14 cm, not unfrequently up to 20 cm, more rarely up to 30 cm.  $\beta$ , fibrillosa does not reach the same length as  $\alpha$ , violacea, it scarcely grows over 13 cm in length. The longest specimens have been found in the following localities: Knollen, Øresund, 11-14 meters' depth, July, over 30 cm; Øresund east of Hyeen, 10-19 met., July, 25 cm; N.E. of Sejerø light-house, 11-14 met., July, 22 cm; Lille Belt off Stenderup wood, 13-15 met., July, 20 cm. The maximal size is not very different in the various waters. Outside Skagen,

however, the species does not reach the same size as in the more protected waters. It grows on all kind of firm substrata, stones, wood, but principally on various Algæ e. g. Chorda Filum, Fucus, Furcellaria, Polysiphonia nigrescens, P. elongata etc., further on Zostera. It occurs in depths of 0-19 meters, rarely deeper.  $\beta$ , fibrillosa grows principally on stony reefs in 0-7,5 meters' depth.

Localities. Ns: Does not occur at Fanø and Esbjerg. ZQ, jydske Rev, 24,5 meters (a). - Sk:  $\alpha$ : Lønstrup, near land;  $\beta$ : Hanstholm; Bragerne; Hirshals mole. — Lf: Very common in all parts of the fjord, most frequently  $\alpha$ , in deeper water  $\gamma$ ;  $\beta$  at Rønnen by Lemvig, Oddesund and Nykøbing (Th. Mortensen). — Kn:  $\alpha$  and  $\beta$  very common near land; wanting on Herthas Flak. Trindelen, FE, NI and  $dT^1$ , 9,5-11 m (a). - Ke: a, common to a depth of 28 m (ER east of Læsø.  $\gamma$ : ZE, Fladen, 15 m. — Km:  $\alpha$  and  $\beta$  common. bK, N.W. of Anholt, 15 m, approaching to  $\gamma$ ;  $\delta$ : BO, BM, BL east of Jutland, 5,5–9,5 m, with Zostera. – Ks:  $\alpha$  common, also in Isefjord: Holbæk Fjord, Frederikssund, PQ, near Boserup.  $\beta$ , several places. d, Lammefjord. — Sa:  $\alpha$  common to 14 meters' depth;  $\beta$  on stony reefs near land; δ Hofmansgave (Hofm. Bg., C. Rosenberg). - Lb: Principally α. β off Langøre near land. — Sf:  $\alpha$  most frequent.  $\beta$ : CT and Skaarup Ør (Rostrup).  $\gamma$  UX, Skjoldnæs, 9,5 m. — Sb:  $\alpha$ common.  $\delta$ : AC, off Knuds Hoved, 17 m. — Sm:  $\alpha$  common.  $\delta$  common: off Orenæsgaard, Petersværft, Kragevig, Guldborgsund. — Su:  $\alpha$  common.  $\beta$ : Kronborg (C. Rosenberg); QD, south of Saltholm; Dragør D. K. D. Vidensk. Selsk. Skr., 7. Række, naturvidensk. og mathem. Afd. VII. 3.



Fig. 375. Polysiphonia violacea. Tip of shoot in January. The trichoblasts have been shed; only the basal cells are to be seen. The two uppermost ones are perhaps rudimentary trichoblasts. 230 : 1.

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(not typical).  $\delta$  Kronborg (f. divaricata, C. Rosenberg). — **Bw:**  $\alpha$  Egernsund; Pøls Rev; LC, off Gulstav. – **Bm:**  $\alpha$  common.  $\gamma$  Præstø Fjord, Tromnæs, Falster (O. Paulsen). — **Bb:**  $\alpha$ : 0—11 m depth, up to 8,5 cm long; in several places with tetrasporangia, sexual organs and cystocarps not observed.

## 5. Polysiphonia Brodiæi (Dillw.) Grev.

Harvey in Hooker, Brit. Flora Vol. II part I, 1833, p. 328; Harvey, Phyc. Brit. Vol. II, 1849, Pl. 195;
J. Agardh, 1863, p. 993; Kützing, Tab. phyc. 14. Bd., 1864, Taf. 1; Kny, 1873, p. 103; Schwendener, Monatsber. d. Ak. Wiss. Berlin 1880, p. 333; Falkenberg, 1901 p. 34 Taf. 21 Fig. 12; Kolderup Rosenvinge 1902, p. 342, Taf. VI Figs. 1-2; id., 1903, p. 444 and p. 457; L. Batten, 1923, p. 303, figs. 61-63.

Conferva Brodiæi Dillw. Brit. Conf. 1809, pl. 107. Hutchinsia Brodiæi Lyngb. Hydr. 1819, p. 109, pl. 33 B; Flora Dan. 1840, tab. 2312 (?). Polysiphonia penicillata (Ag.) Kützing, Tab. phyc, 14. Bd., Taf. 1.

The erect shoots, with the exception of the primary shoot, issue from a system of creeping filaments with short articles, partly as continuations of these, partly as endogenous branches of them. The creeping shoots bear no trichoblasts but numerous rhizoids, and such organs may also be produced in abundance from the lower part of the erect shoots. These shoots, which are very flexible, on the Danish coasts attain a length of more than 20 cm; in almost their whole extent they bear a number of penicilliform shoots which are mostly much shorter than the main shoots. Long shoots are principally given off from the lowermost part of the primary axis; they are usually shorter than this, and transitional stages between the long and the short shoots frequently occur.

The trichoblasts of the erect shoots are arranged in a spiral almost always turning to the left. As shown by me (1902, p. 342), the spiral in 165 sporelings in 160



Fig. 376. Polysiphonia Brodiæi. Trichoblast seen from the back. 200 : 1.

cases turned to the left, in 4 or perhaps 5 cases to the right (2,5 and 3 per cent respectively), and in the numerous fullgrown plants examined I have met with one shoot only with a spiral turning to the right. According to KNV, the angle of divergence was, in plants from Cherbourg, 1/7 of the circumference, between the first trichoblasts of the shoots, however, 1/6. In the Danish specimens I found the divergences varying about 1/6, from a little greater than 1/7 to a little smaller than 1/5, most frequently nearly 1/6, and that not only at the base of the shoots. In the sporelings the divergence was 1/5. The first trichoblast appeared on the 5th to the 8th joint, and henceforth each joint bears a trichoblast (fig. 384).

The trichoblasts show the usual structure; they are well developed and are kept comparatively long. The primary branches (II) are alternate in two lateral series converging towards the axis, the branches of the second order (III) are likewise alternate in two series converging towards the primary axis of the tricho-

blast; the first branch of the second order  $III^1$  is directed towards the stem (fig. 376). Each cell of the trichoblasts contains one nucleus. For a transitional stage between a trichoblast and a stem comp. K. R. 1903, p. 457.

The number of pericentral cells is, as shown by J. AGARDH, 7--8, more rarely 6, in the full-grown plant. The first pericentral cell is cut off exactly under the first leaf or, more frequently under its right side (fig. 377). The cortication begins rather early, the primary cortical cells being cut off at the lower angles of the pericentral cells and growing downwards and dividing. A cortex of considerable thickness, consisting for a great part of hypha-like filaments, early covering the pericentral cells, is then formed. At the same time a plexus of hypha-like





Polysiphonia Brodiæi. A-C, segregate young segments of sporeling seen from the face, showing the successive divisions. D, E, similar segments, from older plant, the fourth from the top, showing the relation of the first pericentral cell to the trichoblast; D seen from above, E from below. F, young segments seen from the side. 626:1.

filaments appears between the central cell and the pericentral cells (fig. 378). It was detected by J. AGARDH (1863, p. 993), who thought that it arose by division of the central cell. Later on it was figured by FALKENBERG who rightly shows (1901, p. 34, Taf. 21 Fig. 12) that the hyphæ arise from the pericentral cells, which I can confirm. Secondary pits are produced in considerable number through the longitudinal

walls between the cortical cells mutually and between these and the pericentral cells.

The branches arise, as shown by KNY (1873), in the axils of the trichoblasts, however, not exactly in the median plane, but they are somewhat displaced to the left. The joint common to the trichoblast and the branch has 3 pericentral cells, two of which are situated to the left and one to the right of the median

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Fig. 378. Polysiphonia Brodiæi. Transverse sections of stem. A rather young. 200:1. B older with hypha-like filaments in the interior of the stem. × the central cell. 63:1.

B

plane of the trichoblast, as shown by KNY. The pit connecting the second cell of the trichoblast with the central cell of the basal joint appears at the upper end of the longitudinal wall between the middlemost pericentral cell and that to the right (fig. 379). The ordinary (primary) branches do not arise in the axils of all the trichoblasts. In the lower part of the long shoots none or only few are present, upwards they increase in number but decrease again in the fertile region, in particular in the tetrasporiferous and male plants. In the upper part of the plant two or three or even more branch-bearing joints may follow consecutively; on the other hand, the number of interjacent branchless joints may vary from one to many. The basal cell of the



originally branchless trichoblasts frequently later on gives rise to a secondary shoot which, however, as a rule attains only a small size. As examples some diagrams of shoots may here be presented: t signifies a trichoblast without primary branch, r a primary branch, s a secondary branch, (t) a basal cell of a shed trichoblast,  $\vec{\sigma}$  a male trichoblast.

long shoot: sssssss(t)(t)rrsrsr(t)(t)rt(t)rttrttrrrrtrtetrasporiferous plant: rsrr(t)(t)r(t)r(t)r(t)r(t)r(t)(t)r(t)(t)rtsimilar: ...ttrtttrtttttttmale plant: ...trtttrttcttttt

Fig. 379. Polysiphonia Brodiæi. Basal portion of branch showing the pit connecting the central cell of the basal joint with the rest of the trichoblast. 390:1.

The first lateral organ (trichoblast) of the branches is usually in the Danish specimens placed on the second joint; in specimens from Cherbourg, KNY found it on the second to the fifth joint.

As in most other species of the genus the antheridia are produced in the main axis of the trichoblasts except the two lowermost joints. At the right hand the upper of these cells bears a sterile branch which projects more than the antheridial body and may thus protect it. A sterile cell does not occur at the top of the full-grown antheridial body.

The carpogoniferous trichoblasts frequently show a curious aberration, some of the cells of their primary axis bearing two branchlets each (cp. K. R. 1903 p. 444). The fertile trichoblast shown in fig. 380 bears two branchlets on the fourth joint to the right and two on the fifth joint to the left. In other cases one joint only (the fourth) bears two branchlets, and in one case the 3rd joint, which normally bears no branch, bore one branch on the left side, the 4th two branchlets on the right side, the 5th one branchlet on the left side. The second joint of the female trichoblasts may even in rare cases bear a branch; such cases are shown in fig. 381. In fig. A the second, fertile, joint and the fourth bear each a branch to the right, the third bears no branch. In fig. B the second joint bears a branch to the right, the third one to the left and the fourth one to the right. In the latter case the first joint of branch 2 bears no branch as if it were a basal cell of a trichoblast; its second joint bears two branchlets. Branch 3 bears two branchlets on its first joint. In all cases where a joint bears two branchlets, the last-formed branchlet is placed



Fig. 380. Polysiphonia Brodiaei. Young female trichoblast, 220:1.

under the first and feebler than it. Accessory branchlets do not occur in all the female trichoblasts, and in some specimens (f. inst. from Thyborøn) they were not met with at all.

In the ripe cystocarps the orifice is enlarged and funnel-shaped, consisting of large cells (fig. 382).

The tetrasporangia arise at the left side of the trichoblast borne on



the same joint; they are produced by the second pericentral cell (comp. fig. 377). Two secondary pericentral cells are cut off from this cell and the



#### Fig. 381.

Polysiphonia Brodiæi. Female trichoblasts with supernumerary branchlets. The figures indicate the branches of the first order according to the joints of the primary axis of the trichoblast. (See texte). A 560:1. B 350:1.

most remote of them is usually a little shorter than the other, a small peripheric cell being later cut off from the basal cell of

Fig. 382. Polysiphonia Brodiæi. Ripe cystocarp. 63:1.

the sporangium. This small cell may, however, be wanting, the second secondary pericentral cell continuing to the base of the article (fig. 383).

Germination is easily realised in cultures (comp. K. R. 1902 p. 342). In August sporelings consisting of 6 joints or more and bearing trichoblasts were produced in two days. The lowermost article or the two first joints produced no pericentral cells but only feebly coloured rhizoids. The following one to four joints had 4 pericentral cells, the following 5, and shortly afterwards joints with 6 or 7 pericentral cells appear, the same number which is found in a transverse section of the lower part of the stem of a fullgrown plant. As mentioned above, the angle of divergence in the sporelings is 1/5 of the circumference. — Abnormal sporelings, showing two opposite rhizoids or two opposite vegetative poles were not unfrequently met with in my cultures.



Polysiphonia Brodiæi. Portion of tetrasporiferous plant with branch. 350:1.

This species has only been collected in the months of May to September. It has the appearance of being annual on the Danish shores. In May small specimens only were met with at Hirshals, and in April I did not find it at all in the same locality. Further it was not contained in the samples of Algæ from the groins of

Thyborøn collected and sent to me in March. It therefore seems probable that the plants die in autumn or in winter, leaving only the young plants produced by the germinating spores and the basal parts of some of the older plants, which pass the winter in a resting stage and again take up the

Fig. 384. Polysiphonia Brodiæi. Sporeling. The figures denote the number of pericentral cells in the joints. Fig. 385. Polysiphonia atrorubescens. A, portion of plant near the base; numerous rhizoids and endogenous branches. B, decumbent branch. C, joint of stem. A, B 26:1. C 68:1.

growth in spring. Antheridia were met with in all the months mentioned, cystocarps and tetrasporangia only in July—September. It grows in exposed places on moles, stones and wrecks at middle sea level. In moles and groins it forms a continuous vegetation at the ordinary limit of the sea.

Localities. Ns: Groins at Harboøre and Thyborøn; harbour of Thyborøn, outside. — Sk: Hanstholm, Roshage, stone on the shore; Lønstrup, stones on the shore, Hirshals, mole and reef; wreck by Skiveren; Højen, on pebbles within the innermost shoal and between the first and the second shoal, 1-4 meters. — Kn: Harbour of Skagen, outside eastern mole.

## 6. Polysiphonia atrorubescens (Dillw.) Grev.

Greville, Flora Edinensis, 1824, p. 308; Harvey, Phyc. Brit. Vol. 2, 1849, pl. 172; Kützing, Tab. phyc. 13. Band, 1863, Taf. 82; J. Agardh, 1863, p. 1035; Farlow, Mar. Alg. N. Engl. 1881, p. 174; Kuckuck, Bemerk. I, 1894. Wiss. Meeresuntersuch. N. Folge I. Bd., p. 253, Fig. 21; L. Batten, 1923 p. 289 fig. 26-29.

Conferva atrorubescens Dillwyn, Brit. Conf. 1809, pl. 70.

Polysiphonia Agardhiana Greville, Scottish Cryptog. Flora Vol. IV, 1826, plate 210; Kützing Tab. phyc. 13. Band, 1863, Taf. 49.

A number of vigorous endogenous creeping shoots are given off from the base of the primary shoot and from the long branches issuing from its base (fig. 385).<sup>1</sup> These shoots produce numer-

ous rhizoids (comp. KUCKUCK, BATTEN) and such organs are also given off in number from the lowermost part of the erect shoots. The rhizoids are separated from the pericentral cell by a wall and contain numerous nuclei. The creeping shoots bear no trichoblasts but produce endogenous shoots; they are not much branched, most of the branches issuing from their proximal part. Some of these shoots, arising from the upper side, become erect, others, given off from the flanks or from the under side of the shoots grow out in a horizontal direction. The branches arising at a greater distance from the base of the creeping



Polysiphonia atrorubescens. A, tip of tetraspore-bearing shoot with trichoblasts. B, trichoblast, 200 : 1.

shoots attain only a small size. The creeping shoots are usually somewhat incurved at the top, but not always upwards; they seem not to change from the horizontal to the vertical direction of growth, being transformed into erect shoot.

The long erect shoots are densely tufted, issuing endogenously partly from the lowermost part of the erect filaments, partly from the innermost part of the creeping shoots. They bear no trichoblasts from the base to a comparatively great distance upwards; often more than the first twenty joints are without trichoblasts, but endogenous branches may occur in this part of the shoots. The trichoblasts are as a rule separated from each other by more than one joint, frequently by two or three

<sup>1</sup> HARVEY incorrectly ascribes a scutate root to this species (Phyc. Brit. l. c.).

joints, sometimes even more. In the upper parts of the plants, however, in particular of the sex plants, the trichoblasts may follow immediately after each other on



Fig. 387. Polysiphonia atrorabescens. Basal portion of trichoblast with axillary shoot. 200:1.

the consecutive joints. In the male plants, the fertile trichoblasts are usually densely crowded at the upper end of the shoots, each joint bearing a trichoblast.

The angle of divergence of the trichoblasts must be determined at the upper end of the shoots, for torsions take place later. It is usually 1/5 or nearly so. In a male shoot I found it 1/6. On the other hand, in short branches I found a divergence of 1/3. The spiral always turns to the left; in one short shoot only I found a spiral turning to the right. The trichoblasts have the same structure as in the other species; they are much branched. The cells of the fully developed trichoblasts contain two or more nuclei; two nuclei most frequently occur (fig. 386), but four were repeatedly met with.

The branches arise as axillary buds to the trichoblasts, but only part of the trichoblasts, mostly those of the lowermost part of the shoots, are accompanied by shoots; these are placed at the left side of the trichoblasts. The first joint of the branches common to the branch and the trichoblast has three or four pericentral

cells. The pit connecting (the second joint of) the trichoblast with the central cell in the basal joint is situated in the longitudinal wall between the outermost pericentral cell to the right and the cell next to it (fig. 388 A). The branches are given off from the axes under a rather acute angle, and they are often connate with the joint above to some extent. It may even rarely occur that the second joint of the branch is entirely connate with the mother shoot. The first trichoblast of the branch is always situated on the left side of the 3rd to the 6th joint (fig. 388 B). The basal cells of the shed trichoblasts often produce secondary axillary shoots,



Fig. 388.

Polysiphonia atronubescens. A, portion of branch showing the pit× connecting the central cell of the basal joint with (the rest of) the trichoblast fallen off. B, portion of branch showing the basal cells (×) of the three first trichoblasts. 150:1.

developing into short shoots, sometimes fructiferous but often reaching only a very slight degree of development. In these shoots, as in the primary ones, the first trichoblast arises on the left side. As mentioned above, endogenous adventitious shoots, produced from the central cells, further occur on the creeping shoots and the undermost part of the long upright shoots, but they may also arise at the base of the normal branches in the upper part of the plant. They usually appear on the inner side of the branch, most frequently between the 2nd and the 3rd or between the 3rd and the 4th joint.

The upper trichoblast-bearing end of the shoots is curved, each trichoblast causing the axis to change direction. Later on, when the longitudinal growth takes place, the shoots are strengthened and each trace of bending is effaced. The number

of pericentral cells is 11-13 in the long shoots, lower in the short shoots (about 9). The older joints, in particular of the longer shoots, usually show a more or less marked torsion, the pericentral cells being spirally curved, an appearance already observed by the first observers of the species. The torsion is undoubtedly caused by the pericentral cells growing more in length than the central cell. The coherence between the first and latter and between the ends of the pericentral cells in consecutive joints must, however, oppose resistance to this torsion, and this resistance may sometimes cause that the pericentral cells have a sigmoid curvature (fig. 385 C). The torsion may go to the right or to the left, and the direction



Polysiphonia atrorubescens. Male trichoblasts with sterile branches, 200 : 1.

may change in various joints of the same shoot. — Cortication does not occur. The antheridia have been met with only once in a specimen from Hirshals (July 1914). The male trichoblasts may have the same appearance as in most other species, the antheridial body occupying the main axis of the trichoblast except the two first joints, the upper of which bears a sterile branched branch to the right.<sup>1</sup> But the fertile part of the trichoblast, which is always curved inwards, often bears sterile branches on the flanks in varying number (1 to 3 or more), issuing from the inner central axial cell-row (fig. 389). The antheridial bodies may then be a little irregular in shape and sometimes slightly branched. It also happens that the lower sterile branch is transformed into an antheridial body. The sterile branches of the antheridial bodies occurred in so great a number that they seemed to be a normal appearance.

The ripe cystocarps are nearly globular, about 400  $\mu$  in diameter, with a short stalk, the ostiole is small, situated in a slight depression and surrounded by small cells. The outer cells of the cystocarpial wall are connected with secondary pits, the formation of which is easily studied in this object.

D. K. D. Vidensk. Selsk. Skr., 7. Række, naturvidensk. og mathem. Afd. VII. 3.

<sup>&</sup>lt;sup>1</sup> According to THURET (Et. phyc. p. 86) the male trichoblast in this species bears no sterile branch on the coast of France.

The tetrasporangia occur in the upper ends of the long shoots and in the fusiform short shoots. They are situated to the right of the trichoblast in the tri-



Polysiphonia atrorubescens. Ripe cystocarp. 150 : 1.

choblast-bearing segments, in the foregoing trichoblast-less joints the sporangia are situated under the sporangium in the trichoblastbearing joint. The sporangia are covered by two secondary pericentral cells. A small peripheric cell is never found under one of these.<sup>1</sup>

*P. atrorubescens* occurs only in waters with a high salinity. It grows on stones and shells of mollusks at from one to 23 meters' depth or deeper. In the Skagerak it has mostly been found near land in 1 to 4 meters' depth growing on stones, in the northern Kattegat in 11,5 to 23 meters' depth or deeper in soft bottom growing on *Aporrhais, Turritella* a. o.

mollusks. Its non-occurrence in the upper regions of this water is probably due to the slighter and more variable salinity. It has only been collected in the summer months (June—August) and thus it cannot be stated whether the species is annual

or perennial on the Danish shores. In October it was only met with once in a denudate state. GREVILLE and HARVEY mention it as annual, while BATTERS states that it is to be found "all the year". In the Skagerak and the Limfjord it attains a length of 18 cm, in the Kattegat 13 cm. In the Danish waters it has been found with cystocarps



Polysiphonia atrorabescens. A, transverse section of stem. B, C, transverse sections of tetrasporiferous joints, C emptied. 200:1.

and tetrasporangia in June to August, with antheridia in July. It must be supposed that the spores germinate in summer and that the plants pass the winter in a feebly developed state.

Localities. Sk: YT<sup>3</sup> and YT<sup>5</sup>, Hanstholm 5,5 and 13 meters and YM, Roshage, near land, 2 m; Bragerne, YM<sup>1</sup>, 1,5-2 m; Grønhøj Strand, Miss Ellen Möller; Lønstrup, on stones near land, 1 m;

<sup>1</sup> J. AGARDH states (l. c. p. 1037) that he has found two sporangia in each joint in a densely branched specimen from Tanger collected by SCHOUSBOE. As this species has not been found near Tanger (comp. BORNET, Les Algues de Schousboe. Mém. soc. sc. nat. Cherbourg 1892 p. 315) it must be supposed that it has been confounded with another species, f. i. *Ophidocladus Schousboei* (Thuret). (Comp. DE-TONI Syll. Alg. IV, p. 1073).

Hirshals, on stones near land, 1-2 m; off Højen, on pebbles within the first shoal and between the first and the second shoal. — Lf: XY, at Mullerne, Thisted Bredning, 6,5 m; XV, north of Rønnen at Lem Vig; Oddesund, 6,5 to 10 m or deeper. — Kn: South of Skagens Gren, 13-15 m (Kramp); fC, 3

miles S.W. by S. of Skagen light-house, 15 m, denudate in October; YS<sup>2</sup>, north of Græsholm, Hirsholm, 15 m; YX, east of Nordostrev, Hirsholm, 23—28 m; south of Hirsholm, 13 m; XH and XL, east of Marens Rev, 11,5 —15 m. — Ke: FC, east of Flyndergrund, east of Læsø 17—18 m.

### 7. Polysiphonia nigrescens (Engl. Bot.) Grev.

Harvey in Hooker, Brit. Flora II, 1833, p. 332; Phyc. Brit. III, 1851, Plate 277; J. Agardh, 1863, p. 1057; Kolderup Rosenvinge, 1884, p. 13 (Résumé p. 2), plates I—II figs. 15—29; Hauck, Meeresalg. 1884, p. 244; Falkenberg, 1901, p. 129; Svedelius, Östersj. Hafsalg., 1901, p. 121; Kylin, 1907, p. 143; Lakowitz, Alg. Danz., 1907, p. 20; Kylin, 1923, p. 116; L. Batten, 1923, p. 306.

Conferva nigrescens Smith, Engl. Bot. 1806 Plate 1717.

Hutchinsia nigrescens Lyngb. Tent. 1819, p. 109 Tab. 33.

Hutchinsia violacea Lyngb. Tent. 1819, p. 112 ex parte, tab. 35 A.1-2. B.2.

- f. pectinata J. Agardh, l. c., p. 1058; Aresch. Exsicc. No. 63 and 57 (Polys. Brodiæi).
- f. fucoides J. Ag., l. c.
- f. flaccida Aresch., 1850, p. 49; Kylin, 1907, p. 143, Taf. 5 Fig. 1.
- f. reducta Svedelius, 1901, p. 121.

The morphology of this very common species has been described at length by me (1884) and later by FALKENBERG (1901). The trichoblasts are arranged in a spiral with rather large angles of divergence, about 2/5. They may occupy all the consecutive joints, including those bearing branches which may take the place of some of the trichoblasts in the spiral (comp. K. R. 1884 fig. 24). But it also happens that "sterile"

Fig. 392.

Fig. 392. Polysiphonia nigrescens. Frederikshavn December 31st. Tip of shoot without trichoblasts. 200 : 1.

joints occur between the trichoblast- or branch-bearing ones, e. g. that every second joint only bears a lateral organ, or the sterile joints may occur more sparsely and more irregularly. In other cases the shoots are entirely or almost entirely devoid of trichoblasts; the branches are then placed in a spiral or they are biseriate, alternate, separated by a varying number of joints bearing no lateral organs. The latter occurs particularly in the f. *pectinata* J. Ag. but also in the other forms (fig. 392, comp. FALKENBERG, p. 129). The main branches often begin by bearing only branches, no trichoblasts. Endogenous branches normally arise at the base of the primary axis and of the main branches (fig. 396), and at the base of almost all later well developed branches, mostly at their inner face (fig. 393, K. R. 1884, figs. 25-28); these



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endogenous branches may reach a considerable length. Secondary axillary shoots developed from the basal cell of trichoblasts also frequently occur, but these shoots



Fig. 393. Polysiphonia nigrescens. Endogenous adventitious shoot at the limit between the second and the third joint of the branch. Small cortical cells have been cut off from the lower end of the pericentral cells. 220 : 1.

usually reach only a small size (K. R. 1884 fig. 29); they sometimes arise before the trichoblast has been shed (fig. 395 A).

The trichoblasts show the usual structure; they have at least three generations of branchlets. The older cells contain a number of nuclei each (fig. 395 B). In specimens collected in April the trichoblasts had in a living stage a feeble rose tinge due to the cell sap, but the small round chromatophores were also feebly coloured. Later in the year the cell sap may have a brownish tinge.

The first joint of the branches is short and has only pericentral cells on its outer side, in a number of 4-6, the second joint of the branch being at the base in connection with the following joint in the mother axis. It may happen, however, that the first transversal wall of the branch does not reach the mother axis, but the first joint of the branch is at all events shorter than the following ones (fig. 394 A). A peculiar case is shown in fig. 394 B, where the third joint bears at the back

the basal cell of a trichoblast whereafter follows a bifurcation, the two branches being of equal strength and diverging equally from the original direction of the axis. This must probably be because the apical cell, after having produced a tricho-

blast-bearing segment, has been divided by a vertical wall in two equal parts, each giving rise to a branch, a true dichotomy thus occurring here.

In the upper part of the plants the first lateral organ on the branches usually occurs on the 3rd to the 5th joint, in the season of vegetation. The basal joint of the trichoblasts may sometimes produce pericentral cells, as if it were the basal joint of a branch (fig. 395 B). These trichoblasts must be apprehended as transitional forms approaching to the branches. A further transitional stage is shown in fig. 295 C, where the two lowermost joints are provided with pericentral cells and the upper of these has produced a tetrasporangium, while the upper part



Fig. 394.

Polysiphonia nigrescens. A, pseudodichotomy; the first joint of the branch (to the left) is long, with pericentral cells all round, though shorter than the following joints.
50:1. B, portion of young plant; probably true dichotomy (see text).

of the lateral organ has the character of a trichoblast, though it is unbranched. In winter (January) the plants as a rule bear no trichoblasts (fig. 392). The growth

seems to begin slowly in February. In April, specimens with corymbiform shoots and well developed trichoblasts are met with, in May the trichoblasts have in great part attained their definitive size and in the two following months growth gradually ceases. As the the fully developed trichoblasts are shed early, hairless specimens may be found already in July; in Sepspecimens become tember such more frequent, and in the following months they are almost exclusively met with.

The number of pericentral cells varies from 10 to 20, or more frequently between 12 and 17, but the average number is different in the different parts of the Danish waters as may be seen in the following table showing the numbers of pericentral cells found in cross sections of primary axes or principal long branches below the middle.



#### Fig. 395.

Polysiphonia nigrescens, from Søborghoved Grund off Gilleleje. A, a shoot has developed from the basal joint of the trichoblast. B, the basal cells of the trichoblasts have produced pericentral cells but no shoot. C, the two lowermost joints of an unbranched trichoblast have produced pericentral cells; the second joint a tetrasporangium. 200; 1.

	Localities over 11 meters' depth			Localities deeper than 11 meters		
	average number	numbers vary- ing between	number of observations	average number	numbers vary- ing between	number of observations
In the Constant Sharanah	15.1	10 10	0.0	A SAME	Submaries of	Wall Charles I have
North Sea and Skagerak.	10,1	12-18	26			
Northern Kattegat	15,3	11-20	21	14,2	12-17	6
Southern Kattegat	14	11-17	19	13	12-14	2
Samsø Waters, the Belts	(100000	a sur post				
and Sydfyn Waters	14,2	10-19	30	13,3	10-16	12
Smaaland Sea and Sound.	13,7	12-15	17		1.201	
Western Baltic and Baltic						
around Møen	- 13,1	11-16	16	12,2	11-14	5
Baltic around Bornholm	12,1	10-14	9	11	10-13	3

Number of pericentral cells.

The table shows that the average number gradually decreases on going from the North Sea to Bornholm, and it is also a little smaller in deeper than in shallow water. In a specimen from the deepest locality where the species has been met with, US, Store Belt, in 33-45 meters' depth, 9-10 pericentral cells were found.



#### Fig. 396.

Polysiphonia nigrescens. Young plant. The lowermost cell of the primary axis is the short primary rhizoid-cell fixed to the substratum; the second has produced no pericentral cells but several rhizoids. The following joints have produced pericentral cells, the numbers of which are indicated by the respective joints. A vigorous branch of endogenous origin is given off from the lower end of the third joint. 70:1. The number of the pericentral cells is for the rest rather variable in different parts of the same plant. In the sporelings the first joint after the primary rhizoid-cell has no pericentral cells but gives rise to numerous rhizoids; the following two or perhaps more have 4, and in the next following the number gradually rises to the number normal to the species (fig. 396). In the branches of the latest order, the number may be much lower; in a tetraspore-bearing specimen I found it reduced to 6 (fig. 401 *C*).

The pericentral cells usually contain numerous large starch grains. The nuclei were found situated at the inner and radial walls, not at the outer wall. The pericentral cells often contain peculiar starshaped bodies with curved rays which are probably a sort of crystalloids (fig. 397 B). They take a brown tinge when treated with iodine. They are very resistent to chemical reagents; they were not dissolved by KOH, HCl and Eau de Javelle, nor by boiling water. They seem to disappear at a later moment, for in older pericentral cells they were not met with. The inner and radial walls of older pericentral cells are transversely striped. In a tetrasporiferous branch

I found two nuclei in the central cells (fig. 401). At the level of the transversal walls between the joints, intercellular bodies like those described by me in *Polysiphonia fastigiata* as intercellular cuticular bodies (1884, p.10 (2), figs.11—14) occur; they occupy the angles between the central cell and the pericentral



cells, but are sometimes confluent and show some resemblance to cells (fig. 398).

The older parts of the long shoots are usually covered by a continuous cortex. The cortical cells arise as small cells cut off from the lower end of the pericentral cells.

The antheridia, as in the other species, usually occupy the principal axis of the fertile trichoblast except the two first Fig. 397. Polysiphonia nigrescens. A, pericentral cell showing chromatophores lying at the outer wall, January. 435:1. B, star-shaped bodies, probably crystalloids in pericentral [ cells. 300:1. After living

plants.

joints; the antheridial bodies are usually pointed (comp. HARVEY l. c. and BUFFHAM) and terminate in a short row of sterile cells, but that is not always the case (comp.

KYLIN 1923 p. 122). A sterile branch given off from the second joint is in many specimens normally present, in other specimens it is normally wanting, and the trichoblast is then unbranched. For the rest various arrangements may occur, as shown in fig. 399. As regards the development of the spermatia see KYLIN (l. c.).

The development of the cystocarp from the second joint of the female trichoblasts and the position of the branches of the upper sterile part of these trichoblasts in relation to that of the sterile trichoblasts have been mentioned by me in 1884. The development of the procarp and the cystocarp has recently been very carefully studied by KYLIN (1923 pp. 118—121). The ripe cystocarps have a conical upper part, tapering towards the orifice (fig. 400).



Polysiphonia nigrescens. Transverse section of stem, at the level of the transverse wall between two central cells. *p*, callus plate of the pit between the central cells. *c*, intercellular "cuticular" bodies. 200:1.

The tetrasporangia are, in the shoots

bearing a trichoblast on each joint, seated to the right of the trichoblast (or branch) borne on the same joint. When the internodia consist of more than one joint, the



Fig. 399.

Polysiphonia nigrescens. Male trichoblasts, differing from the ordinary type, dorsal view. A without branches, B-F with one or two branches, sterile or fertile, A 230 : 1.

sporangium was once observed amongst numerous sporangia divided in the ordinary tetrahedrical way,

position of the one following next to a trichoblast seems usually to be determined by the position of the following trichoblast. The tetrasporangia are covered in the front with two pericentral cells between which a split is formed through which the spores escape at maturity. On the flanks the sporangium is covered by two other pericentral cells. No short peripheral cell is produced as in several other species. A cruciately divided

The species is very common in all the Danish waters. It is perennial and may be found in well developed and large specimens in all the seasons. In winter there



Fig. 400. Polysiphonia nigrescens. Ripe cystocarp. 130:1.

is no or almost no growth, and the wintering shoots have no trichoblasts. In spring the plants are in full vegetative development with numerous hairs, and sexual organs occur. Thus antheridia and carpogonia were met with in April to June. Ripe cystocarps were met with in (May) June to September. Young tetrasporangia were found in April and May, ripe in May to September. The fructiferous branches seem to be thrown off in August and September, for in the following months the species was always found sterile. The denudate plants may produce new shoots in the following year as well as the young plants produced by the germinating spores in summer. The plants arising from early germinating spores may without doubt

produce ripe spores in the same season while those germinating in the later part of the summer probably pass the winter in a sterile state. The denudate specimens

bearing short remnants of the fructiferous shoots, may be referable to f. senticosa. Most of the specimens may be referred to f. fucoides. F. pectinata was met with in exposed localities in the North Sea and the Skagerak. In deeper localities in the inner waters slender specimens occur which may in part be referred to f. flaccida Aresch.<sup>1</sup> Other specimens from deeper localities were slightly branched and ought therefore to be referred to f. reducta Svedelius. described from the inner Baltic Sea. — The species thrives best in depths smaller than 15 meters, where it is very common, even in very light localities. Under that level it occurs rather rarely and only in small quantities.

<sup>1</sup> When ARESCHOUG (l. c. p. 49) says that the branches and branchlets in this form are subhorizontal, it does not seem to be justified.



#### Fig. 401.

Polysiphonia nigrescens. A, portion of tetrasporiferous branch;
b, basal cell of trichoblast;
c, central cell;
s, stalk cell;
sp, sporangium. B, similar in longitudinal section. C, D, transverse sections of sterile joints, E, F, of fertile joints of tetrasporiferous branches. A '95:1. B-F 200:1.

Thus in the North Sea it has only been found from low-water mark to 13 meters' depth, although several dredgings have been made in localities in deeper water. Further it was wanting in all the dredgings on Herthas Flak in the Northern Kattegat (19-22,5 meters), and in almost all the numerous dredgings made in the Eastern Kattegat. The species reaches a length of at least 20 cm; the largest specimens collected were 30 cm (Skagerak) and 35 cm (Lille Belt) long.

Localities. As the species is very common in shallow water, only localities deeper than 15 meters are recorded. In these specimens the joints were thrice as long as broad in the middlemost part of the frond. — Ns: From Esbjerg to Hanstholm, down to 13 m. — Sk: Down to 13 m. — Lf: — Kn: IX, near Trindelen, 19 m; YX, east of Nordøst-Rev, Hirsholm, 23—28 m. — Ke: Only in IN, Fladen, 15 m; EX, Groves Flak, 26,5 m; ET, Lille Middelgrund, 12 m; IA, Store Middelgrund, 16,5 m (f. reducta); GJ, Ostindiefarer Grund, 8,5 m and Søborghoved Grund, 8,5 m. — Ks: Hastens Grund, 16 m. — Sa: YV, 15 m. — Lb: Røgle Klint S. by E. 19—30 m; between Strib and Nederballe, 35—44 m; Fænø Sund, 28 m; dH<sup>1</sup>, east of Hesteskoen, 18—19 m (f. *flaccida*); dQ, south of Lyø, 22 m. — Sf: — Sb: cN, 18 m; Z, off Skagbo Huse, 19 m; AA, north of Nyborg, 22,5—26,5 m (f. reducta); NN, S.W. of Sprogø, 19 m; US, Langelandsbelt 37,5—45 m (f. *flaccida*); LB, Langelandsbelt, 17 m. — Sm: — Su: bM, south of Hveen, 22,5 m (f. reducta). — Bw: KX, Femerbelt, deeper than 19 m. — Bm: VG, 17 m and QS, 20,5 m, North of Møens Klint. — Bb: SR, 15—16 m and ST, 18 m, Rønne Banke (f. *reducta*); YC, Salthammer Rev, 24,5 m.

# Brongniartella Bory.

# 1. Brongniartella byssoides (Good. et Woodw.) Schmitz.

Fr. Schmitz, Die Gattung Lophothalia. Ber. deut. bot. Ges. 11, 1893, p. 217; P. Falkenberg 1901, p. 542, Taf. 19 Fig. 8-10; Kolderup Rosenvinge, 1903, p. 469.

Fucus byssoides Goodenough et Woodward, Trans. Linn. Soc. III 1797, p. 229.

Hutchinsia byssoides C. Agardh, Synops. Alg. Scand. 1817, p. 60; Lyngbye, Tent. 1819, p. 110, Tab. 34 B, C; Flora Danica Tab. 1905,2, 1827.

Polysiphonia byssoides Greville, Flora Edin. 1824, p. 309; Areschoug, Phyc. Scand. mar. 1850, p. 56; Harvey, Phyc. Brit. III, 1851, Plate 284; J. Agardh, 1863, p. 1042; P. Magnus, Bot. Zeit. 1872, p. 253; L. Kny 1873, p. 106; G. Thuret et E. Bornet, Études phyc. 1878, p. 86; L. Kolderup Rosenvinge, 1884, p. 25 (4), Pl. 2 Fig. 30; Hauck Meeresalg. p. 238; Buffham, 1888, p. 263; Reinke, Algenflora 1889, p. 31.

Polysiphonia Dillwynii Kützing, Phyc. gen. 1843, p. 430; Tab. phyc. 14, 1864, Tab. 23 (3).

Polysiphonia vaga Kützing, Phyc. gen. 1843, p. 431; Tab. phyc. 14, 1864, Tab. 24.

Polysiphonia asperula Kütz., Spec. Alg., p. 835, Tab. phyc. 14, Tab. 25.

Polysiphonia Lyngbyei Kützing, Phyc. gen. 1843, p. 431 (Hofmansgave).

Polysiphonia Bangii Kützing, Spec. Alg. p. 1849, p. 835; Tab. phyc. 14, Tab. 25 (Hofman Bang).

Lophothalia byssoides J. Agardh, Till Algernas Systematik, 6. Afdel. 1890, p. 59 (Lunds Univ. Årsskr. 26).

As first shown by KNY and confirmed by the writer and by FALKENBERG, the trichoblasts are arranged in a spiral turning to the left with an angle of divergence of 2/7 or nearly so. In luxuriantly growing shoots, the upper end of the axis is straight and overreaches the young trichoblasts which are curved upwards but not appressed to the axis (comp. FALKENBERG l. c. fig. 8). The trichoblasts have usually not more than two branches (FALKENBERG p. 544) but three branches are not unfrequently met with (comp. KOLDERUP ROSENVINGE 1884 fig. 30). On the other hand

D. K. D. Vidensk. Selsk. Skr., 7. Række, naturvidensk. og mathem. Afd. VII. 3.

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Brongniartella byssoides. Store Belt, May. Procumbent shoot giving off an erect shoot. The upper figure is the continuation of the lower, but eight joints without trichoblasts have been omitted; the lowermost joint in the upper figure is the 17th from the base. 50:1.

arise earlier, e.g. at the 8th to the 10th joint. The pericentral cells of the basal joint are cut off shortly after the formation of the axillary branch. The direction of these cells is usually very different from that of the pericentral cells of the following joints, coinciding with the direction of the trichoblast, while the direction of the axillary branch diverges almost at right angles from the trichoblast (fig. 405). As shown by FALKENBERG, it happens that no axillary shoots are produced in feebler branches, but notwithstanding that four pericentral cells are cut off from the basal cells of the trichoblasts. The same has been found by me in Polysiphonia nigrescens

unbranched trichoblasts also occur, f. inst. on the lower part of the erect shoots (fig. 402). The cells of the full-grown trichoblasts contain a number of nuclei.

The long shoots have 7 pericentral cells but in the shoots of higher order the number is frequently only 6 or even 5, and in the creeping shoots, too, only 5 or 6 pericentral cells were found. Cortication is wanting.

In the long erect shoots an axillary shoot is usually given off from the basal cell of all the trichoblasts; the lowermost trichoblasts, however, are often not accompanied by axillary shoots, and the same may sometimes be the case with single trichoblasts among the usual ones. The first joint of the axillary shoot, common to this and the trichoblast, has usually 4 pericentral cells, as stated by FALKENBERG (1901 p. 545), but the number may be smaller, e. g. 2, as described by KNY (1873, p. 106, comp. our fig. 404, 405 A). The normal axillary shoots arise comparatively late, on the kathodic side of the basal cell, according to FALKEN-BERG at the 20th to the 30th segment of the mother shoot; they may, however,



Brongniartella byssoides. A, transverse section of stem. B and C, transverse sections of tetrasporiferous branch. B, fertile joint after evacuation; C, sterile joint of tetrasporiferous branch. 200:1.

(see above p. 440). In normal axillary shoots the first trichoblast appears on the 3rd or 4th, more rarely on the 5th joint,



Fig. 404. Brongniartella byssoides. Communication of the second joint of the trichoblast with the central cell of the basal joint. 220:1. the basal joint included. At the base of the plants endogenous creeping filaments are to be found which bear no trichoblasts; they may bend upwards and become erect, trichoblast-bearing shoots (fig. 410). Endogenous shoots arise from the creeping and the lowermost part of the erect shoots, emerg-

ing at the limit between two joints. Their first joint has pericentral cells on all sides. In these shoots a great number of joints is often without trichoblasts; but when the trichoblasts appear they occur on all the joints (figs. 402, 410).

FALKENBERG under the designation stolons describes certain shoots which bear no trichoblasts but are provided with rhizoids and have a long conical point. Such shoots



Fig. 405.

Brongniartella byssoides. Lower part of trichoblasts with axillary shoots. The pericentral cells of the basal joint parallel with the longitudinal axis of the trichoblast, the axillary shoot nearly perpendicular to this direction. 350:1. are frequently met with in the Danish waters but they have not the character of stolons. They occur often indeed, mostly in the lower part of the plants, but they are not creeping, the numerous rhizoids are directed forward and not fixed to any substratum and therefore without attachment disc. and such shoots may also occur in the upper part of

Fig. 406. Brongniartella byssoides. Spiny

shoot without trichoblasts but with rhizoids or hairs. 30:1.

the plants. Their appearance is in correlation with a weakening of the growing power. In certain long shoots the trichoblasts become gradually feebler, finally their

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Fig. 407. Brongniartella byssoides. Shoot with antheridiabearing trichoblasts. June. 350:1. production ceases and then the rhizoids appear and the shoot becomes pointed. Such spiny shoots have been met with in specimens from the different Danish waters from the North Sea to the Belts, gathered in July to November. The form described and figured by KÜTZING under the name of *Polysiphonia asperula* (l. c.) shows these spinous shoots in great number also in the upper part of the plant. The rhizoids mentioned ought perhaps rather to be compared with the unicellular hyaline hairs occurring in other Florideæ; they are like these separated from the pericentral cell by a wall. As I have had no occasion of examining them in a living

state, it cannot be said with certainty whether they contain chromatophores or not.

The antheridia-bearing trichoblasts are simple with a two-celled stipe without sterile branch (comp. KÜTZING Tab. phyc. 14, Pl. 23 and THURET 1878). They are borne on short branches which also bear sterile trichoblasts but are usually unbranched (fig. 407). I always found them on particular individuals, but BUFFHAM found them intermixed with cystocarps on different branches of the same plant, and in another plant he found antheridia combined with tetrasporangia (1888, p. 263). LYNGBYE found these organs in specimens gathered at Gjerrild 1825 and mentions them in his herbarium as corpuscula antheræformia.

The procarps arise as usual in the second joint of a trichoblast. The third joint remains short and the fourth bears a branch on the right side. The ripe cystocarp has a cylindrical spout consisting of parallel cell-rows. The sterile part of the trichoblast is kept till the maturity of the cystocarp (fig. 408).

The tetrasporangia arise in shoots with more or less limited growth of the two last orders of ramification. In transversal sections of tetraspore-bearing joints I found 7 pericentral cells whereas sterile joints of the same shoot often showed only 6 or 5 (fig. 403). A small peripheral cell under one of the secondary pericentral cells was not met with. The sporangia apparently always arise to the right of the trichoblast borne on the same joint.



Fig. 408. Brongniartella byssoides. Ripe cystocarp. July. 130:1.

The different organs of fructification were always found in distinct individuals. Antheridia were met with in June to September, carpogonia in June to July and even later, cystocarps in August to October and tetrasporangia in July to November; as late as December sporangia, partly emptied, were met with. The principal season for the production of ripe spores is August to September.

The spores are able to germinate immediately after dissemination. I have not myself observed the germination, but Mr. BOVE PETERSEN has kindly at my request sowed carpospores in vessels with sea-water and brought me slides with the sporelings raised in the cultures. After one day the globular spore-cell showed a feeble proeminence, the first step of the arising rhizoid. The following day an elongated rhizoid-cell was formed and the still globular spore-cell was divided by parallel walls perpendicular to the direction of the rhizoid. The sixth day a number of (5–9) segments were formed, the upper end of the lengthened sporeling had taken a shape reminding one of that of the full-grown plants, but lateral organs had not



Brongniartella byssoides. Sporelings, 6 days old. 200:1.

yet appeared. Most of the segments had formed pericentral cells, but the division of the first segments was somewhat irregular and the number of pericentral cells



Brongniartella byssoides. Plants gathered January 3rd. A 200:1. B 95:1.

could not be determined with certainty (fig. 409). As the cultures had to be discontinued after 6 days, the further development is unknown, but it is probable that the sporelings produce early creeping filaments. Young sporelings were not met with in Nature, but in winter and spring I found only creeping filaments giving off short erect shoots (fig. 410). It has to be decided whether these creeping filaments originate from

sporelings produced the last year or from older plants, or from both. In the first case the species would be annual like our winter-crops, in the second case it would be perennial.

Brongniartella byssoides develops later as the species of Polysiphonia. In April the erect shoots are only 1 cm high, in May 1-3 cm, in June it is in active growth

and in July it usually attains the maximal size (23 cm). The growth seems to cease towards the end of July or in the beginning of August, in September the trichoblasts begin to fall off, but as late as November specimens with well preserved trichoblasts may be met with. At the end of the year the plants die, in many cases with the exception of the creeping filaments from which new shoots are given off next spring. The new shoots in winter bear at the top a tuft of simple or feebly branched trichoblasts which are incurved over the upper end of the stem (fig. 410).

In the Danish waters from the Skagerak to the Belts the species reached a length of 20 cm or a little more. In the western Baltic Sea the greatest length observed was 12 cm and in the Sound south of Helsingør only 5 cm. It does not usually occur in the fjords; in the Limfjord it has only been met with once, and in the Isefjord only in the entrance. It occurs in the sublittoral region. At Hirshals it was found near land in about 1 meters' depth, and in the harbour of Frederikshavn it was found in the same depth, but otherwise it has not been met with over 4 meters' level, in the Great Belt and the western Baltic Sea not over 6 meters' level, and in the Sound south of Helsingør only in 10 meters' depth. It has been found most frequently in 7,5 to 15 meters' depth and descends to 38 meters' depth. It grows most frequently on various Algæ, in particular *Furcellaria*, but also occurs on shells of Molluscs and barnacles and on stones.

Localities. Ns: ZQ, jydske Rev, 24,5 m; aF, off Thyborøn, 31 m; aE, 16 m. - Sk: YN<sup>1</sup>, YN<sup>2</sup>, within Bragerne, 6,5-10 m; SY, off Løkken; ZK12, off Lønstrup; off Hirshals, several places 11-15 m, near land, 1 m. - Lf: bU, Ejerslev Næse, 3-8 m, one specimen. - Kn: Off Skagen, 9,5 m; off Hulsig (Boye Petersen); Herthas Flak (Børgesen); around Hirsholmene, 5,5-7,5 m; Frederikshavn; off Frederikshavn; several places near Nordre Rønner; GM, Engelskmands Banke; TO, TP, ZA, Tønneberg Banke, 16-18 m; NI, FE, dS, a. o. pl., Trindelen, 8-16 m. - Ke: 4<sup>1</sup>/<sub>2</sub> miles S.W. <sup>3</sup>/<sub>4</sub> W. of Fladen light-ship, 30 m (C. A. J.); FD, east of Læsø; VY, Fladen; ZJ, EX, EV, Groves Flak; XA; EU, Lille Middelgrund, 14 m; ER, Fyrbanken, 28 m; Store Middelgrund, 10 m (C. A. J.); Ostindiefarer Grund; OO, Søborg Hoved Grund; bR, Vesterlands Grund off Gilleleje, 7,5 m. - Km: 6 miles S.S.W. 1/2 W. of Læsø Rende light-ship (C. A. J.); 5<sup>1</sup>/<sub>2</sub> miles N. by E. <sup>3</sup>/<sub>4</sub> E. of Østre Flak light-ship (C. A. J.); XD, XC, south of Læsø; VP, south of Læsø; ND, NC, BH, off Gjerrild Klint; Gjerrild Bugt (Lyngbye). - Ks: FO, NB, off Havknude; EM, Lysegrund; RL, west of Ostindiefarer Grund; near Hesselø (Lyngbye); D, north of Grønne Revle, 11,5 m; Tisvilde (Lyngbye); GG, GF, Sjællands Rev; EJ, entrance to Isefjord; EH, west of Lynæs. - Sa: FU, Begtrup Vig; MY, FT, north of Samsø; BE, off Sletterhage, 10 m; FS, Vejrø Sund; GD, GE, north of Sejerø; MP, Falske Bolsax; AS, Mejlgrund; FX, west of Tunø; AT, Svanegrund, 5 m; MQ, south of Paludans Flak, 11,5 m; Hofmansgave (Lyngbye, Hofman Bang, C. Rosenberg); AJ<sup>1</sup>, north of Æbelø, 4 m; AY, Ashoved; AX, Bjørnsknude, 9,5 m. - Lb: FZ, Kasserodde, 6 m; cX, between Strib and Nederballe, 35-44 m; Fænø Sund; north of Fænø Kalv; off Stenderup Skov, 13-15 m; Aarø Sund (Reinke); Lillegrund (Reinke); CD, Helnæs Hoved Flak, 4 m; CC, south side of Hornenæs, 7,5 m; dH<sup>1</sup>, east of Hesteskoen, 18-19 m; CF, west of Lyø; dQ, south of Lyø, 22 m. - Sf: UV, north of Ærø, 13 m. -Sb: Off Refsnæs; MN, north of Asnæs, 11 m; GS, south of Asnæs; LH, Elefantgrund; cN, S.W. of Musholm, 18 m; AA, north of Sprogø, 23-26 m; XS, Kløverhage; GZ, north of Egholm; DP, UJ, north of Onsevig; US, Langelandsbelt, 38 m. - Su: Off Ellekilde, 5,5 m, cast ashore north of Helsingør and at Hellebæk (C. Rosenberg, Ørsted, Joh. Lange); PZ, east of Hveen, 10-19 m. - Bw: LG, off Vidsø, Ærø, 9,5 m; bV, bX, off Kobbel Skov, 6-13 m; cG, west of Kegnæs; south of Als (Reinke); cE, Middelgrund, south of Als, 13 m; dK, Pøls Rev, 6-7 m; Vodrups Flak, 9,5 m; DU, off Dimesodde, Langeland, 11 m; KX, Femerbelt, 19 m or deeper.

# Rhodomela Agardh.

### 1. Rhodomela subfusca (Woodw.) Agardh.

- C. A. Agardh, Sp. Alg. I, 1821, p. 378, emend.; Harvey, Phyc. Brit. Vol. III 1851 pl. 264; J. Agardh, 1863 p. 883; Areschoug, Obs. phyc. III 1875, p. 6. N. Act. R. Soc. Ups. Ser. III Vol. X; Kjellman, N. Ish. Algfl. 1883 p. 146 (113); Kolderup Rosenvinge 1884, p. 33; 1902 p. 360; 1903 p. 459; Falkenberg 1901, p. 593 Taf. 11 Figs. 2-17; Kylin 1907, p. 145; id. 1923 p. 114.
- Fucus subfuscus Woodward, Linn. Transact. I, 1791, p. 131, tab. 12; Hornemann, Flor. Dan. tab. 1543, 1816.

Gigartina subfusca (Woodw.) Lamx.; Lyngbye Tent. 1819, p. 47, Tab. 10, 11.

Lophura gracilis Kützing Phyc. gen. 1843, p. 435, Taf. 53 IV.

Lophura cymosa Kützing Phyc. gen. p. 435; Tab. phyc. XV Tab. 36.

α, genuina.

Rh. subfusca Kjellm. l. c.; Kylin, l. c.

#### $\beta$ , lycopodioides (L.) Gobi.

C. Gobi, Alg. weiss. Meeres. Mém. Acad. Imp. St. Pétersbourg VII<sup>e</sup> sér. t. 26, 1878, p. 24. Fucus lycopodioides Lin. Syst. Nat. ed. 12, tom. II p. 717. Rhodomela lycopodioides Agardh Sp. Alg. I 1822 p. 377; J. Agardh, 1863, p. 885. Gigartina lycopodioides Lyngbye Tent. p. 45. Conferva squarrosa Oeder Flor. Dan. tab. 357, 1767.

y, virgata (Kjellm.) nob.

Rhodomela virgata Kjellman N. I. Algfl. 1883 p. 143 (110) tafl. 7; Kylin, 1907 p. 147; id., Stud. üb. die Entw. v. Rhod. virg. Sv. bot. Tids. Bd. 8 1914 p. 33.

 $\delta$ , tenuior (C. Agardh) Svedelius.

C. Agardh, Synops. Alg. sc. 1817 p. 32; Svedelius 1901, p. 124. Rh. subfusca f. gracilior J. Ag. Gobi, Rothtange Finn. Meerbus. 1877 p. 11.

 $\epsilon$ , abyssicola nob. Plate VI figs. 2–4.

From old time the *Rhodomelas* occurring at the shores of Northern Europe have been referred to the two species *Rh. subfusca* and *Rh. lycopodioides*, the near relation of which to one another has been emphasised by several authors. In 1883 KJELL-MAN tried to show that the first of these species must be divided into two corresponding with the forms *extrataniensis* and *intrataniensis* distinguished by ARESCHOUG in 1875. The latter, to which he gave the name *Rh. virgata*, is distinguished by the following characters: The vernal plant of the first year does not become black by drying and is flattened while *Rh. subfusca* becomes black and keeps cylindrical. The main axes are distinctly thickest in the middle and in their whole length bear branches gradually decreasing in length upwards, while *Rh. subfusca* has pronounced branchlets with limited growth. All these branches are shed in summer, the main axes only remaining. The organs of reproduction arise in winter on the branchlets which grow out on the long shoots from the previous winter, and which are shed after the fructification, while the corresponding branchlets in *Rh. subfusca* after fructification may develop as vegetative shoots, and the fructification in this species takes place later, in spring. KJELLMAN also found anatomical differences between the two species, the cells in the main axes of *Rh. virgata* decreasing gradually in size towards the periphery, while *Rh. subfusca* has a small-celled cortex rich in "endochrome", distinctly bounded towards the inner parenchyma consisting of large cells. *Rh. lycopodioides* is considered as a distinct species though nearly related to *Rh. subfusca*. Kjellman emphasises as distinctive characters the numerous curved branchlets hav-



Rhodomela subfusca. A (f. virgata) adventitious shoots near the base of a primary branch. 64:1. B transverse section of stem with a young adventitious shoot. 206:1.

ing their greatest thickness a little below the middle; they are arranged without any distinct order and are supposed to be adventitious.

While REINKE and FALKENBERG do not adopt *Rh. virgata* as a distinct species, KYLIN follows KJELLMAN, laying particular stress on the different season of fructification (Nov. to Jan. for *Rh. virgata*, April and May for *Rh. subfusca*) and on the fact that the new shoots which in *Rh. subfusca* develop in the last part of the winter and in spring, are at first both vegetative and fertile

but after fructification remain as vegetative, while the organs of reproduction in *Rh*. *virgata* are seated in particular shoots which are thrown off after fructification.

As to the branchlets of *Rh. lycopodioides* I have convinced myself, by examination of specimens from Iceland and Greenland, that numerous adventitious branchlets really occur in this species, arising from a single superficial cell growing out and dividing by a transversal wall, whereupon the outer cell becomes the apical cell of a branchlet. A similar formation of adventitious shoots has not only been met with in specimens from the Danish coasts otherwise fairly agreeing with *Rh. lycopodioides*, but also in specimens of *Rh. subfusca* and *Rh. virgata* (figs. 411 *A*). In the latter they were produced in particular near the base of the primary shoots. The occurrence of adventitious branchlets has thus no absolute value as distinctive character, and the same is, according to my experience, the case with the alleged shape of the branchlet and other characters, and I must therefore agree with the authors who have more or less distinctly suggested that *Rh. lycopodioides* might be considered a form of *Rh. subfusca*.

As to the two species *Rh. subfusca* and *Rh. virgata* as distinguished by KJELL-MAN, to which most of the Danish species can be referred, it must be confessed, that in their typical shape they are so distinct as to habit and anatomical structure that they have the appearance of being distinct species. The examination of a great number of specimens, however, has led me to the conclusion that they are only marked types of a very variable species produced by the influence of the outer conditions. The first occurs in particular near the lowwater mark, where it is exposed to the movement of the waves, whereas Rh. virgata grows in greater depth, in particular in streaming water but not exposed to the waves. In localities which are intermediary as to the outer conditions specimens intermediary as to the distinctive characters are also met with. In the outer characters it appears that e.g. individuals which



Rhodomela subfusca. Transverse sections of stems. A,  $\alpha$  genuina. B,  $\gamma$  virgata. 160:1.

if anything agree with *Rh. virgata* keep some branchlets which are not shed at the end of the period of vegetation, and do not show the above mentioned distinction



Fig. 413. Rhodomela subfasca f. virgata. Transverse section of stem. 80:1.

between vegetative and fertile shoots. Further, the above-mentioned greater thickness on the middle of the long shoots is often wanting. When in doubtful cases the anatomical structure, which according to KJELLMAN seems to offer a very good distinction, is taken into consideration one finds that this also is not reliable. As a rule the anatomical structure in Rh. virgata is as described by KJELLMAN (fig. 412 B), but not rarely a more or less developed small-celled cortex is to be found in the lower part of the long shoots in specimens otherwise agreeing with typical Rh. virgata. Such a cortex may be found on one side of the branch but not of the other (fig. 413), or several more or less confluent proeminences with similar structure or even a continuous cortex all round may be met with. Usually then some long shoots are provided with cortex, others not.

D. K. D. Vidensk. Selsk. Skr., 7. Række, naturvidensk. og mathem. Afd. VII. 3.

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Further, in some cases a feebly differentiated cortex may occur. Neither does the difference in the season of fructification emphasised by KYLIN seem to give a decisive



Fig. 414. Rhodomela subfusca f. abyssicola. Transverse section of stem. 150:1.

mark, for both species were found with sex organs in January and were frequently found with ripe sporangia in April and May in the Danish Waters.

In the inner waters, particularly the Baltic Sea, a fine form appears which in its extreme shape is very marked but which on the other hand is nearly related to the typical *Rh. subfusca* and to *Rh. virgata* as well. It is remarkable by its very thin and slender shoots and may be referred to f. *tenuior* Agardh, especially as it is characterised by SVEDELIUS (l. c.). In the ramification it usually resembles *Rh. subfusca*, the long branches bearing a considerable number of branchlets which are not shed, whereas in the anatomical structure it agrees better with *Rh. virgata* (comp. SVEDELIUS 1901 p. 125).

Another thin and slender form  $\epsilon$ , *abyssicola* nob. was gathered in the southern Little Belt south of Lyø in 22 meters' depth. Some of the specimens resembled *Rh. virgata* in habit (Plate VI fig. 2), others had a very thin principal axis and very distant thin and slender branches which were only slightly branched, in particular towards the top (Plate VI fig. 4). The trichoblasts were kept at least 4 cm below the top. These plants were still fructiferous on June 20th and bore sporangia and cystocarps in elongated

branchlets not different from the vegetative ones, thus behaving much as *Rh. subfusca*. A section of the main stem shows the same structure as in *Rh. virgata*, but the cells are smaller. The diameter of the stem was 320  $\mu$  (fig. 414). The plants are red and keep the colour when drying.

All the forms mentioned are thus here considered as forms of *Rh. subfusca* which may be divided in the following principal forms:

- α, genuina.
- $\beta$ , lycopodioides (L.) Gobi.
- r, virgata (Kjellman) nob.
- $\delta$ , tenuior (C. Agardh) Svedelius.



Fig. 415. Rhodomela subfusca growing on Portunus. Basal disc with primary and secondary shoots. 38:1.

 $\epsilon$ , *abyssicola* nob. F. axi primario distincto tenui, ramis remotis longis, parce præcipue apicem versus ramosis, trichoblastibus diu persistentibus.

The structure and development of the frond have been treated at length by FALKENBERG and KYLIN. Some supplementary remarks may be given here.

The fronds issue from a parenchymatous disc from which new shoots arise as adventitious buds without any order (fig. 415). According to FALKENBERG the lateral organs produced by the branching of the fronds are only branches except at the tips of the shoots which are closing their growth, where numerous hair-leaves are produced, on long stretches one on each joint, and above this region of hairleaves a formation of branches never takes place. The latter assertion, however, does not always hold good, for in the upper part of the branched shoots basal cells of shed trichoblasts are frequently found and single branches frequently occur between the trichoblasts still in function. The branches of the last order bear only trichoblasts. The trichoblasts and the branches are placed in a spiral with a divergence varying between 1/4 and 2/7 (often nearly 2/7). When occurring between the trichoblasts the branches take the place of the latter in the spiral without a change of the angle of divergence. The

spiral may be turning to the right or to the left, but there is no regular antidromy as stated by me in 1884 (p. 33 (5)). It seems that the spiral turns more frequently to the left than to the right, but my observations are not sufficient to ascertain that with certainty.

The trichoblasts have

the same structure as in Polysiphonia and other Rhodomelaceæ. The first branchlet of the trichoblast, however, is often given off from the third joint instead of from the second (fig. 416), or, though rarely, from the 4th, and unbranched trichoblasts may occur, e. g. in f. *tenuior*. The second joint is often shorter than the following ones whether it bear a

Fig. 416.

Rhodomela

subfusca. Fænø Sund February.

Trichoblast.

150:1.



Fig. 417. Rhodomela subfusca. Upper end of male plant. 124:1.

branchlet or not. The cells contain a single nucleus and numerous chromatophores which are distinctly red. FALKENBERG lays much stress upon this fact which he alleges

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Fig. 418. Rhodomela subfusca. Female trichoblasts. a-c of var. virgata. 220:1.

as supporting the opinion that "Die Blätter von Rh. subfusca stellen ein eigenartiges Mittelglied dar, über dessen Benennung man zweifelhaft sein kann" (l. c. p. 597). I cannot agree with the said author in this as there is only a slight gradual difference in the colour of the chromatophores in Rhodomela and in several species of Polysiphonia which have also rose-coloured chromatophores in spring and in deep localities. On the other hand the chromatophores of the trichoblasts in Rhodomela are often more or less decoloured during the spring, even in April.<sup>1</sup> The trichoblasts begin to develop in winter (January) and are fully developed in spring (March to May). In June they are shed at the same time as the growth ceases, and in the following months no trichoblasts are met with except the uppermost ones which are apparently without function. Vigorous trichoblasts with red chromatophores have been met with only exceptionally in mid-summer, in the beginning of August in a specimen found in great depth in the North Sea (31 m), and in specimens of the f. tenuior found at Bornholm (8.5–15 m).

As mentioned above, adventitious shoots may arise from superficial cortical cells of the stem in f. *lucopo*-

*dioides* and other forms. The fasciculate branches occurring frequently in the long shoots of various forms of *Rhodomela* are probably due to the production of such adventitious buds.

The antheridia, as I have shown (1903 p. 462), arise on the stems and on the tricho-

blasts (fig. 417). The fertile organs form corymbiform tufts at the ends of the shoots, or lateral on the long shoots in f. *virgata*. In some cases the fertile organs are apparently only branches, in others they are principally trichoblasts, but in both cases the main axis is usually covered with antheridia, and the formation of antheridia may extend to three generations of branches

<sup>1</sup> Further it must be remembered that the assimilating trichoblasts in *Brongniartella* are just as distinct from the stem as those in *Polysiphonia*.



Fig. 419. Rhodomela subfusca f. virgata. Cystocarp. May. 95:1.

(fig. 417, comp. FALKENBERG p. 597). As regards the development of the spermatia reference may be made to KYLIN'S paper (1914, p. 55 pl. 3 figs. 13-18).

The procarps arise in the second joint of the trichoblasts (fig. 418, comp. K. R. 1903 p. 459, KYLIN 1914 p. 42). The sterile upper part of the latter remains for a shorter or longer time at the upper end of the developing cystocarp; it may still be found sometimes in the ripe cystocarp (fig. 419). It may be simple or branched. The development of the procarp and the cystocarp has been described at length in the important papers of KYLIN

(1914 pp. 41—54 and 1923 p. 114).

The tetrasporangia arise in short branches forming small tufts at the ends or on the sides of the long shoots, the latter principally in the f. virgata, two in the same joint, in a number of consecutive joints. In the lower part of the branch, under the first lateral organ, they are arranged laterally, to the right and to the left of the median plane. The first trichoblast is inserted over one of them. In the joint following after a trichoblast (or a branch) the sporangia are arranged in a similar way to the right and to the left of it, and the orientation of the sporangia is





Rhodomela subfusca f. virgata. May. A, longitudinal section of tetrasporiferous joint before division of the sporangia. B, tetrasporiferous joint after evacuation of the tetraspores. s sporangia, st stalk-cell, c central cell, b, basal cells of trichoblasts. 200:1.

thus constantly changing in the trichoblast-bearing region. The pericentral cells, from which the sporangia are produced, are first divided by two oblique walls by which two cover-cells are cut off (comp. KYLIN 1914 fig. 11). These cells are shorter than the mother-cell, the lower part of which therefore is free outwards and which afterwards is divided by a horizontal wall into two cells, the upper of which becomes the sporangium. The lower cell, the stalk-cell, is then divided by one or two periclinal walls cutting off one or two shorter peripheric cells that cover the stalk-cell. The other pericentral cells divide in the usual manner by horizontal walls in such a manner that the upper cell remains in pit-connection with the central cell while the cover-cells of the sporangia are connected with the stalk-cell (fig. 420 A, KYLIN p. 61). The pits connecting the central cell with the sterile pericentral cells are situated at a much higher level than that connecting it with the stalk-cell (fig. 420). At the stage of maturation the central cell, the stalk-cell and the pericentral cells contain several nuclei. For further details in the development of the sporangia see Kylin 1914.

The germination has not been observed by me, but I have once found a spore-

ling on Callithamnion Hookeri, which is shown in fig. 421. The basal part was disc-shaped, as in the adult plant, but it was only developed on one side.

Rhodomela subfusca is widely distributed in the Danish waters, growing on stones and various Algæ (Fucus, Laminaria). It usually descends only to a depth of 20 meters, but it has been found once in the North Sea in 31 meters' depth (Jydske Rev, f. a), and f. tenuior has been repeatedly recorded in depths from 25



Rhodomela subfusca. Plantlet growing on Callithamnion Hookeri. 210:1.

to 38 meters near Bornholm. The forma  $\alpha$  occurs from low-water mark to a depth of about 15 m or a little more, but it is most typical near low-water mark. F. lycopodioides has only been met with rarely in the Skagerak, washed ashore or by dredging in slight depths near land. F. virgata has been met with in all the waters within Skagen in depths from 4 to 20 meters, most typical in the Belts. F. tenuior has been found in the Baltic Sea and particularly round Bornholm, in depths from 8,5 to 38 meters. F. abussicola has only been met with once in the Little Belt in 22 meters' depth. - The vegetative development begins in winter (January) and is usually arrested in May or June whereupon the trichoblasts and fertile shoots are shed. The organs of fructification begin to develop in winter and the spores are evacuated in spring.

Localities. Ns: a: Jydske Rev 31 m and some other loc. off Lodbjerg light-house and off Ørhage, very sparsely.  $\beta$ : washed ashore by Klitmøller (Hornemann). — Sk: Several places from Hanstholm to Hirshals, from low-water mark (Hirshals) to 15 m, mostly  $\alpha$ , more or less approaching to  $\beta$ , lycopodioides at Bragerne, Løkken and Hirshals. - Lf: Several places from Rønnen by Lem Vig to Løgstør Bredning, but not well developed, usually intermediary between a Fig. 421. and  $\gamma$ , virgata. — Kattegat:  $\alpha$  very common,  $\gamma$  very common, also in the Isefjord; here also f. tenuior. — Sa:  $\alpha$  and  $\beta$  very common down to 17 meters' depth. — Lb:  $\alpha$  and in particular  $\gamma$  very common,  $\alpha$  from low-water mark to 15 m,  $\gamma$  from 7-30 m;  $\epsilon$ , abyssicola: dQ, south of Lyø, 22 m. - Sf:  $\alpha$ ,  $\gamma$ . - Sb:  $\alpha$ : LK, Elefantgrund; Kerteminde; GY, south of Sprogø; NN, 19 m.  $\gamma$ : in numerous places, 5-19 m. — Sm:  $\gamma$  in numerous places 4-12 m. — Su:  $\alpha$ , off Aalsgaarde, Charlottenlund.  $\gamma$ , in several places, 5-10,5 m. - Bw: a, UP off Kramnisse Gab 8,5 m; KU, Schønheyders Pulle 7,5 m; KR, near Korselitze Grund.  $\gamma$  several places 7–20 m. – Bm:  $\alpha$ , HG, Præstebjergs Rev.  $\gamma$ , several places from 7 to 20,5 m. & SD, north-east of Møen, 23,5 m, loose. - Bb: The species is common at Bornholm in depths from 5,5 to 25 m, but descending to 40 meters' depth, more rarely near low-water mark, e.g. at Rønne (!) and at Rø (C. A. J.) in 1-2 meters' depth. Some specimens have been referred to f. genuina; their stem was provided with cortex. These specimens were found near land in 1-10 meters' depth. But also in great depth specimens were found which, though small and slender, most resembled f. genuina (Dana St. 3116, 5,5 miles N.N.E. 1/2 W. of Hammershus light-house, 35-40 m, C. A. J.): their stem had a well developed cortex. Most of the specimens from the waters around Bornholm may be referred to f. tenuis though they not rarely approach to f. genuina or to f. virgata. They are rather small; their height does not usually exceed 15 cm and the shoots are slender. The awl-shaped branchlets emphasised by Svedellus as characteristic to f. tenuior are not always present; in other cases they are very numerous. A small-celled cortex is wanting as in Svedelius' specimens. On all sides of Bornholm.

# Odonthalia Lyngbye.

# 1. Odonthalia dentata (L.) Lyngbye.

Lyngbye Hydr. 1819, p. 9 tab. 3 A; Ørsted De reg. mar. 1844 p. 52; Harvey Phyc. brit. I 1846 Pl. 34;
J. Agardh, 1863, p. 899; Wille, 1885, pp. 30, 50, Tab. IV figs. 48—49; id. 1887, p. 69 figs. 32—37;
Buffham 1893, p. 297, Pl. XIV figs. 32—36; Falkenberg 1901, p. 604, Taf. X figs. 6—22.

Fucus dentatus Lin. Syst. nat. ed. 12, vol. II, p. 718. Fucus pinnatifidus Oeder Fl. Dan. Tab. 354, 1767. Rhodomela dentata Lyngb., Rar. cod. 1880 p. 225.

The morphology of this species shall only be mentioned here rather shortly as it has been treated at length by FALKENBERG (1901). As mentioned by this author, p. 605, the two-edged shape of the frond is caused partly by the formation of a wing on each side of the frond, partly by the congenital coalescence of the lower parts of the shoots The branch-bearing segments are, in the sterile parts of the frond, separated by 2-4 segments bearing no branch (fig. 422). The ectoblastesis (L. K. R. 1920 p. 20) is very prominent. As emphasised by FALKENBERG, there are no trichoblasts. The pericentral cells divide early and thus become covered by a layer of smaller cells which divide further and the outermost of which are so arranged that four transversal rows correspond to the height of a primary segment (comp. FALKENBERG p. 606, our fig. 422 B). It deserves further notice that triangular initial cells are to be found in the edge of the frond, in particular where the outline is convex, one for each secondary segment (fig. 422 B). There is thus resemblance with the edge of *Delesseria* but with the difference that the initial cell is seated in the lower (basiscopic) corner of the segment while in *Delesseria* it is to be found in the upper corner. In Apoglossum ruscifolium, however, I also found marginal initial cells with the same orientation as in Odonthalia (comp. p. 459). FALKENBERG has

delineated these initial cells in *Odonthalia* (l. c. Pl. 10 Fig. 12), but he has not shown the produces of their divisions.

The frond of the last year has a slightly projecting mid-rib which contains the central cell in the centre. This cell is comparatively narrow but becomes very long and is connected with the contiguous central cells through a large primary pit; it contains several nuclei but produces no starch. The other cells of the inner tissue have a larger diameter (fig. 423 A) but are



Fig. 422. Odonthalia dentata. Tips of growing plant. I—III the successive generations of branches. 350:1.



Fig. 423.

Odonthalia dentata. A, transverse section of frond from the last year. B, longitudinal section of cells of the inner tissue (pericentral cells or inner cortical cells), connected by three secondary pits. 150:1.

shorter and are connected with each other by one to three, mostly secondary pits in the transversal walls (fig. 423 B). They contain several nuclei and produce many starch grains when the growing period has ceased. The cells surrounding the central cell are longer and constitute together with it a conducting system (comp. Wille l. c.). The older, at least one year old parts of the frond are provided with a more distinct mid-rib projecting on both faces of the frond. Its appearance may be somewhat irregular, the rib being present on a certain stretch, disappearing further downwards and then reappearing definitely, and the two ribs are not always exactly

opposite to each other. This rib is composed of cell-rows directed outwards and then in a bow obliquely downwards and united into a compact tissue, the surface of which is even. WILLE's fig. 48 (1885) evidently represents a transverse section of such a mid-rib. He regards this tissue as belonging to the assimilating system; it has in my opinion rather

a mechanical function.

The germination has not been observed, but young plants, about 3 mm high, were found in the northern part of the Sound off Aalsgaarde, on a shell of Cyprina islandica in a depth of 19 meters (fig. 424). The smallest one (A) which did not reach 2 mm in length was entirely unbranched. It had a terete stipe continuing in a narrow lanceolate lamina, the upper part of which is shown in fig. D. Numerous marginal initial cells similar to those shown in fig. 422 B are to be found in the edge. A couple of some-



## Fig. 424.

Odonthalia dentata. A-C, plantlets found growing on Cyprina islandica, B and C, with an adventitious hranch. D, upper end of A more highly magnified. E, young adventitious branch. A 50:1. B, C 18:1. D, E 260:1.

what more developed plants showed an adventitious shoot issuing from the stipe, produced from a superficial cell (fig. 424 B, C, E). The normal branching at the apex seems only to begin when the plants have attained a size of about 3 mm. In a young 7 mm high plant the primary shoot was terete at the base but a short distance upwards flattened and at a higher level branched in the usual way. The young fronds are fixed to the substratum by a circular basal disc composed of densely united radiating cell-filaments. In a more ad-

the regularly radiating filaments are united to the margin.

The organs of reproduction are as a rule confined to small adventitious shoots





Odonthalia dentata. Female sexual branchlets with ripe and aborted cystocarps. See text. At \* procarps are apparently developing in the last segment cut off from the apical cell. A 95:1. B 50:1.



Fig. 425.

Odonthalia dentata. Female sexual shoots. The procarps arise partly in the third joint of the branches. In B a procarp will probably arise subterminally in the main axis \*. 200:1.

vanced stage the basal disc is a flat expansion having a circular or lobed outline;

borne on the margin of the frond.

The antheridial shoots are according to BUFFHAM (1893) and FALKENBERG (1901, p. 607) pale simple or bifid leaflets, the surfaces of which are covered with antheridia. They have hitherto not been observed in the Danish waters.

The female shoots are much branched, slightly winged or quite cylindrical. According to FALKENBERG (1901, p. 606) the procarps constantly arise in the second joint of the fertile shoot. That is, however, not always the case, for I not unfrequently found them in the third joint (fig. 425 A, C), and it seems that they may also arise in higher situated joints (fig. 426 B, to the right). The sterile upper part of the procarp-bearing shoots (the calcar) is as a rule unbranched, incurved, but it not unfrequently happens that it is branched and produces new procarps (fig. 426). It seems that the end of the shoot may also produce a procarp arising from the last segment cell (figs. 425, 426\*).

The tetraspore-bearing shoots are cylindrical,

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much branched, forming small fascicles of stichidia each containing two series of sporangia.

O. dentata is perennial; it attains a length of up to 20 cm, thus in the most southern locality recorded in the Sound. It has only been met with in the months of April to September. The new shoots must arise in winter; in spring they are of a fresh red colour in contrast to the shoots of the foregoing year. The organs of fructification must develop in winter. According to ARESCHOUG the species is fructiferous in winter (Dec. to March) at the west coast of Sweden, and that is probably also the case in the Danish waters, but tetraspore-bearing specimens have been met with as late as May, and cystocarp-bearing ones were collected in April and even in June (Store Belt). On the other hand, specimens were found in May with adventitious shoots having shed the outer fructiferous part.

The species is confined to the waters with high salinity and slightly varying temperature; it has therefore principally been met with in the deeper parts of the eastern Kattegat in 15 meters' depth and deeper. In slighter depth it has only been collected in one place in the northern Kattegat on the north side of Hirsholmene. In the Great Belt it has only been found in one place in 19 meters' depth, and in the Sound south of Helsingör only in one place in 22,5 meters' depth in the deep channel. It grows on stony or gravelly bottom and may be fixed to *Litothamnia*, barnacles or mollusks, has also been found on *Fucus serratus* and *Polysiphonia elongata*.

Localities. Kn: East of Tyskerens Rev, Hirsholmene, c. 11 m; VX, Böchers Banke, 29 m. — Ke: IL<sup>1</sup>, IM, ZE<sup>1</sup>, ZE<sup>2</sup>, ZF, IP, IQ, Dana St. 2922 (C. A. J.), Fladen, 15-30 m; Groves Flak, 24,5 m; IK, Lille Middelgrund, c. 18 m; RU, 26,5 m; IA, Store Middelgrund, 17 m. — Ks: Lysegrund (Lyngbye, Rhodomela dentata, Rariora codana, p. 225); near Hesselø (Lyngbye); off Isefjord, buoy at Grønne Revle in S. 3 miles, 15 m (Biolog. Station). — Sa: The Herbarium of the Bot. Mus. of Copenhagen contains a denudate specimen of Polysiphonia elongata bearing in Hornemann's handwriting the following labelling: "hab. ad littus Hofmansgave saxis adnascens ded. Lyngbye". This bears some small specimens of O. dentata, c. 1 cm long. — Sb: Off Refsnæs, 19 m (C. H. Ostenfeld). — Su: Off Aalsgaarde (Th. Mortensen), off Hellebæk (Ørsted); frequently cast ashore at Julebæk and Hellebæk; bM, south of Hycen, 22,5 m.

# General Remarks on the Morphology of the Danish Rhodomelaceæ.

The following remarks deal particularly with the genus *Polysiphonia* which has been most thoroughly studied as to the morphology. Further information on the morphology of this interesting family must be sought in the quoted papers of FALKENBERG, KYLIN a. o.

1. The hair-shaped organs which were named leaves by NäGELI (1846) were repeatedly studied by various authors. I treated them in 1903 and gave them the name trichoblasts; they might also be named hair-leaves. Vegetative trichoblasts occur in all the Danish species of Rhodomelaceæ except *Odonthalia* and *Heterosiphonia*. In *Polysiphonia* they occur only in the erect shoots, not in the creeping ones. In this genus they are usually hyaline though provided with small colourless plastids. In most of the Danish species, however, I have observed that in specimens gathered in spring or in great depths these bodies were true chromatophores giving to the trichoblasts a light rose colour. This phenomenon is particularly conspicuous in *Polysiphonia elongata* f. *baltica* which just occurs in deep water. In *Rhodomela* the chromatophores of the trichoblasts are distinctly rose-coloured, but they are finally decoloured in the adult trichoblasts which are shed at the beginning of the summer. In *Brongniartella byssoides* they are persistent and remain coloured during the life of the plant.

In *Polysiphonia nigrescens* the cell-sap of the trichoblasts may be rose-coloured in April, later brownish.

The ramification of the primary axis of the trichoblasts is regularly alternate, biseriate. The first branchlet is always given off on the anodic side (to the right when the spiral turns to the left), from the second joint, in *Rhodomela* often from the third. In the female trichoblasts the first branch is given off from the fourth joint and most frequently on the anodic side. In female trichoblasts of *Pol. Brodia* two branches were found on the same joint, one above the other (p. 381).

2. Unicellular hyaline hairs do not occur in the Rhodomelaceæ. Only in *Brong*niartella byssoides such organs may sometimes be met with in peculiar pointed shoots without trichoblasts (comp. p. 406); but they might perhaps better be interpreted as a sort of rhizoids.

3. The branches arise in different manners.

a) In Polysiphonia urceolata, P. elongata, P. nigrescens and Rhodomela they are produced directly from the youngest segment under the apical cell, usually in the place of a trichoblast in the spiral. In some species, at any rate, the branchproducing segments are higher than those which give rise to the trichoblasts or do not produce any sort of lateral organs (P. urceolata, fig. 344, P. elongata). To this group belongs Odonthalia, which is destitute of trichoblasts, and Heterosiphonia which has a sympodial growth.

b) In the other species of *Polysiphonia*, in *Brongniartella byssoides*, *Chondria dasyphylla* and *Laurencia pinnatifida* the normal branches arise as a xillary buds of the trichoblasts. In *Brongniartella* they arise rather late when the trichoblast has reached a pluricellular stage. In *Polysiphonia* they arise much earlier, simultaneously with the trichoblast or nearly so, and it seems that the branch-producing trichoblasts are, at their first appearance, bigger than the sterile ones (comp. K. R. 1884 p. 29, rés. p. 5, figs. 34—40). The branches in *Polysiphonia* are thus not branches of the trichoblasts as OLTMANNS thinks (Morph. u. Biol. d. Alg. 1904 p. 609). The basal cell common to the trichoblast and the branch belongs as to its lowermost part to the stem. The first joint of the branch, common with the trichoblast, cuts off pericentral cells on its outer surface, but the central cell of this joint keeps the protoplasma continuity with the trichoblast through a longitudinal wall between the pericentral cells or the segmental wall between the first and the second joint (figs. 379, 388, comp. K. R. 1903, p. 468).

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c) Secondary axillary shoots arise from the basal cells of shed trichoblasts. They occur normally in *P. violacea*, giving rise to the shorter branches characteristic to this species, appearing between the longer primary branches, further in *P. elon-gata*, particularly in older, wintering plants, and in *P. Brodiæi*, more rarely in *P. nigrescens* (K. R. 1884, p. 19, rés. p. 3) while they have not been met with in *P. urceolata* and in *P. orthocarpa*. Thus they occur also in species having no primary axillary shoots. In some cases they appear before the trichoblasts have been shed (figs. 364, 394).

d) Endogenous branches produced from the central cell of older joints occur in particular in the species of *Polysiphonia* with creeping shoots and in *Brongniartella*. The creeping shoots always arise endogenously and produce new endogenous shoots; they issue normally near the base of the principal stems in *P. urceolata*, *P. orthocarpa*, *P. atrorubescens* and *P. nigrescens*. In the latter species an endogenous shoot often appears in the axil of the longer branches, near the base of the branch (fig. 393).

e) Adventitious branches arising from peripheric cortical cells occur in *Rho*domela and Odonthalia; they have not been met with in *Polysiphonia*.

4. The rhizoids are unicellular. In *Polysiphonia* and *Brongniartella* they are produced from the pericentral cells or in the corticated species also from the cortical cells. In the sporelings, however, the first rhizoid originates from the lowermost cell of the plant and the next following from the first joints which do not produce pericentral cells (figs. 384, 396). The rhizoids are separated from the pericentral cells by a wall (comp. DERICK 1899 p. 251). Dr. LILY BATTEN did not observe a wall at the base of a rhizoid in any species of *Polysiphonia* that she had observed (1923 p. 276). Such a wall is, however, really present in all of the Danish species. In *P. urceolata* only I found rhizoids in open connection with the pericentral cell. A shortening of the rhizoids was stated in *P. urceolata*. Rhizoids are wanting in *Laurencia pinnatifida, Rhodomela subfusca* and *Odonthalia dentata*, the organ of attachment of which is a continuous pseudoparenchymatous disc.

5. Torsion of the stems in *Polysiphonia* and *Rhodomela* frequently occurs. In *P. atrorubescens* it is a constant feature, but the direction of the torsion varies. The twisting may cause that the branches become uniseriate for a longer stretch (*P. violacea, P. Brodixi, Rhodomela*).

6. In most of the species the central cell contains one nucleus which remains undivided, while the pericentral cells are always polynucleate. In *Polysiphonia ni*grescens and *Rhodomela subfusca*, however, it becomes plurinucleate by division of the primary nucleus.

7. By the germination of the spores (of *Polysiphonia* and *Brongniartella*) the cell is first divided by a transversal wall whereby a cell is cut off that becomes the first rhizoid cell. In *Brongniartella* the rhizoid was perceivable before the appearance of the wall. The sporeling is then divided by parallel walls into segments, the first one or two of which (in *Polysiphonia*) do not produce pericentral cells,
which only appear in the second or third and following joints. In *P. Brodicei* and *P. nigrescens*, which have 7-8 and 12-17 pericentral cells respectively, the next following one to four joints had 4 pericentral cells (figs. 384, 396), an interesting fact when we remember that a great number of the species of this genus have constantly 4 pericentral cells. The normal number of pericentral cells in the said species is gradually reached in the following joints.

8. Secondary pits are produced not only between pericentral cells but also between the cortical cells and between these and the pericentral cells (*Pol. violacea*, *P. Brodiæi*). Cells connected with more than one secondary pit in the same wall occur in *Pol. elongata*, *Rhodomela* and *Odonthalia*. In *Pol. elongata* the pericentral cells are first connected by one secondary pit, but later on, in the following year, a circle of further secondary pits arises in the same wall (fig. 357).

9. The tetrasporangia arise in a pericentral cell. According to FALKENBERG (1901 p. 88) they always originate in the *Polysiphonice* from the oldest pericentral cell in the segment. This is, howewer, not in accordance with my observations. As early as in 1884 I have ascertained that the sporangia in P. fastigiata take their rise in a lateral pericentral cell separated from the oldest one by two or three sterile pericentral cells (1884 p. 10, rés. p. 2, figs. 1-3). In P. violacea and P. Brodiaei I found that the first pericentral cell is cut off to the right of the trichoblast, while the fertile pericentral cell is always situated to the left of the trichoblast borne on the same joint, and is probably the second pericentral cell. The fertile cell cuts off two secondary pericentral cells, and the inner cell is then divided by a horizontal wall into a stalk cell and a spore-mother-cell or tetrasporangium. In the species of *Poly*siphonia with 4 pericentral cells a small peripheric cell is further cut off under one of the secondary pericentral cells which is a little shorter than the other, and this little cell is always situated beside the basal cell of the trichoblast of the foregoing joint, on its right side. This cell is always present in P. violacea and P. orthocarpa. In P. urceolata and P. elongata it may be present or wanting; in the first named species it was present in the trichoblast-bearing stems, while it was wanting in the stems without trichoblasts. It is further usually present in P. Brodiai which has 7—8 pericentral cells, but it is wanting in *P. atrorubescens* and *P. nigrescens* where the number of pericentral cells is greater. In the species with 4 pericentral cells in the sterile joints the number of pericentral cells in the fertile joints is always 6, though there are always only two secondary pericentral cells.

# Fam. 14. Delesseriaceæ.

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- R. KOLKWITZ, (1900), Beiträge zur Biologie der Florideen. Wissensch. Meeresuntersuch. Neue Folge. IV. Band. Abt. Helgoland Heft 1. Kiel und Leipzig.

- P. KUCKUCK, 1894, Bemerkungen zur marinen Algenvegetation von Helgoland. (I). Wissensch. Meeresuntersuch. Neue Folge. I. Band.
- W. NIENBURG, 1908, Zur Keimungs- und Wachstumsgeschichte der Delesseriaceen. Botan. Zeitung 1908, p. 183, Taf. VII.
- R. W. PHILLIPS 1898, The Development of the Cystocarp in Rhodymeniales: II. Delesseriaceae. Annals of Botany, Vol. 12.
- N. WILLE, 1885, Bidrag til Algernes physiologiske Anatomi. K. Sv. Vet. Akad. Handl. Bd. 21 No. 12. Stockholm.
- , 1887, Beiträge z. Entwickelungsgeschichte der physiolog. Gewebesysteme bei einiger Florideen. N. A Leop. Car. Ak. Bd. LII Nr. 2. Halle.

See further p. 297 and p. 402.

My investigations on the Danish Delesseriaceæ, which have been directed to the structure and development of the frond, were almost finished when I received Kylin's important paper (1923) which contributes so much to the morphology of this family. My observations are in full accordance with those of Kylin to which I can, however, give some additions. Two matters only must here be emphasized.

1. The presence of secondary pits, first pointed out by me (1888) in *Membranoptera alata*, was ascertained in all the species in question, both in the ribs and in the monostromatic frond. In the mid-ribs of the fronds multiple pits occur in the transverse walls of most of the long cells. These pits are in most cases all of secondary kind, arising at different moments between two pericentral or similar cells that were not before-hand connected by pits. In *Phycodrys rubens*, however, secondary pits are also formed between the cells of the axial cell-row, though these cells are from the first connected by a primary pit. The secondary pits are here formed in the periphery of the wall while the primary pit is central (figs. 429, 430).

2. The germination has only been observed in Apoglossum ruscifolium by TOBLER, but young specimens of the other species were found in nature. In Apoglossum ruscifolium, Delesseria sanguinea and Membranoptera alata the primary axis of the plantlet becomes a typical frond provided with a mid-rib. In Delesseria sanguinea this primary frond seems to obtain only a moderate length, but in Membranoptera alata and probably also in Apoglossum ruscifolium it becomes the main axis of the frond, and in Membranoptera it early begins branching. In Phycodrys rubens, on the other hand, the primary axis of the young plant develops into a thorough monostromatic frond without mid-rib, reaching only a length of half a cm or a little more; the typical fronds arise as adventitious shoots from the stalk of the primary shoot. The accordance of this primary frond with the normal frond in Nitophyllum corroborates the opinion put forth by earlier authors, in particular by KYLIN, that this species must be referred to the Nitophylleæ.

# Subfam. Nitophylleæ.

# Phycodrys Kützing.

## 1. Phycodrys rubens (Huds.) Batters.

Batters, Cat. Brit. Mar. Algæ. 1902 p. 76.

Fucus rubens Hudson Fl. Angl. 1762 p. 475 (not seen).

Fucus roseus O. Fr. Müller, Flora Danica tab. 652, 1775.

Fucus sinuosis Gooden. & Woodw., Linn. Transact. III 1797 p. 111.

Delesseria sinuosa (G. & W.) Lamour. Essai, 1813 p. 124, Lyngbye Hydr. 1819 p. 7 Tab. 2 B; Harvey, Phyc. Brit. III pl. 259, 1851; J. Agardh, 1852 p. 691; Magnus, Bot. Erg. d. Pommerania Exp. Kiel 1873 p. 75; Nägeli u. Schwendener, Das Mikroskop, 2. Aufl. 1877 p. 563; Wille, 1885 pp. 30, 51, fig. 51, 1887 pp. 65-69 figs. 21-31; Kuckuck, 1894 p. 255; Phillips, 1898, p. 189.

Phycodrys sinuosa (Huds.) Kützing. Phyc. gen. 1843 p. 444 Taf. 68 II; Tab. phyc. XVI 1866 pl. 20; Kylin, 1923 p. 64.

The apical growth of the frond has been studied repeatedly (NäGELI and SCHWENDENER, WILLE, NIENBURG, KYLIN). NIENBURG has stated the occurrence of intercalary cell-divisions<sup>1</sup>, but the succession of the divisions and the genetic connection of the cells has only been correctly described by KYLIN (1923) who payed especial attention to the pits connecting the cells. In my figures 427 and 428 the pits connecting the cells have not been drawn. The sequence of the division walls can, however, to a certain degree be concluded from a comparison of the consecutive segments cut off from the apical cell, but the fact stated by KYLIN, that the primary cell-row of the segment issues from the lowermost cell produced by intercalary division of the primary cell in the axial cell-row, cannot be recognized. Intercalary divisions occur early in the axial cell-row; they appear already in the second seg-

ment from the top (KYLIN figs. 44, 45) or a little later, in particular in narrow fronds (figs. 427, 428), where the primary segments do not become so much deepened as in KYLIN's fig. 44.

The secondary initial cells situated in the upper edges of the primary segments are able to grow out into lobes, and as the two initial segments of a segment always behave in the same manner, the lobes are always opposed. In the frond shown in fig. 427 the three consecutive segments produced each a lobe on each side, and it seems to be normally so that the number of lobes in a normal leaf corre-



Phycodrys rubens. Tip of frond. April. 260:1.

sponds to an equal number of consecutive segments. The distance between two consecutive lobes or between the nerves belonging to them in an adult leaf thus indicates the height obtained by the primary segments which may be 3--6 mm.

<sup>1</sup> SCHMITZ has undoubtedly observed these cell-divisions in *Del. sinuosa*, but he has not expressly cited this species in this connection.

The border of an older frond shows numerous triangular initial cells (fig. 431) which are the end-cells of cell-rows of the third or fourth order, which really exist in



Fig. 428. Phycodrys rubens. Tip of narrow growing frond. 260:1.

spite of NIENBURG's assertion (comp. 1908 pp. 195, 206). These initial cells do not grow out except by producing adventitious shoots.

The structure and development of the mid-rib has been described by WILLE and KYLIN. The development begins with longitudinal divisions of the primary cell-row in the middle of the frond,

and the cortication proceeds at both sides of it. A transverse section of the mid-rib shows a row of large cells with rather thick walls traversing the midrib (fig. 429). These cells are lengthened in the longitudinal direction of the frond and show multiple pits in the transversal walls. The cells situated on both sides of the median row have a similar character

to these, but they have a smaller diameter and are shorter (comp. WILLE 1887 fig. 28, KYLIN 1923 p. 70 fig. 45); they are also provided with (secondary) pits in the transversal walls. The



Fig. 429. Phycodrys rubens. Transverse section of midrib. c, central cell with a central primary pit and four secondary pits. 150:1.

middlemost cell of the transversal cell-row must be designated as the central cell; its transverse walls contain the primary pit of the primary segment walls or of the



Fig. 430.

Phycodrys rubens. Longitudinal sections of inner cells in the mid-rib. A in the living state, B and C fixed and stained, showing the pits and the nuclei. A 200:1. B, C 450:1.

intercalary walls; it is shown in the middle of the middlemost cell-wall (c) in fig. 429, but the same wall shows four secondary pits in the periphery of the wall by which the cell is connected with the next following central cell. The transverse walls of the other cells in the transverse cell-row are only provided with secondary pits, usually four, all situated near the periphery of the wall. Fig. 430 shows longitudinal sections of the inner cells in a mid-rib; C is a central cell showing at the upper end

a primary and two secondary pits, B a transverse wall with four secondary pits. As pointed out by WILLE the inner cells of the rib have, a mechanical and a conductive function as well. This tissue is covered on both sides by an assimilatory system composed of radiating filaments of short cells (fig. 429, comp. WILLE 1885, fig. 51, KYLIN l. c.).

The lateral veins are opposed, in accordance with their origin from the primary cell-rows of the consecutive segments, and run out in the lobes. Lateral veins of the



#### Fig. 431.

Phycodrys rubens. A, marginal part of frond showing formation of secondary pits (\*). i intercalary division wall. 450:1. B, group of cells showing secondary pits. In the middlemost cell the inner contour is the outline of the cell at high level; the outer contour showing the pits is at a lower level. 380:1.

second order may also occur, but they are much feebler. The later arising marginal shoots give further rise to lateral veins in the leaves. By treatment with iodine the veins take a darker stain owing to their richer contents of starch (July).

Secondary pits are also produced in great numbers in the monostromatic part of the frond; but they arise only at a considerable distance from the top. In the living plant it is impossible to observe their formation, as it takes place only in the middlemost part of the walls while the parts of the cells situated at the surfaces of the frond do not participate in the process. The formation of the secondary pits seems to continue rather long; their number increases downwards and inwards from the border. In a leaf examined by me the cells situated near the border (not including the marginal cells) had averagely 2,5 pits, while the cells in some distance from the border had averagely 3,6 pits, a difference due to the greater frequency of the secondary pits. The secondary pits are recognizable by the transmigrating cell being not completely incorporated in the receiving cell but remaining at all events for a

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long time as a triangular projection, after the entrance of the nucleus in the receiving cell (fig. 431). No wall separating two cells in the monostromatic part of the



Fig. 432. Phycodrys rubens. Multicellular papilla. 150:1.

leaf contains more than one pit.

The shape of the frond is rather variable according to the different length and breadth of the lobes and to the different manner in which the growth recommences after the rest of the winter. In some cases a number of the lobes resume the growth from a broad base and form new leaves as prolongations of the lobes of the old leaf. In other cases the apical cells of the lobes give rise to a leafy shoot with a narrow stipe, and it has then a similar character to the other marginal shoots arising from single marginal cells, probably principally from initial cells of the third order. Most of these shoots, which may be very numerous, reach only a small size and become fertile. Adventitious shoots may also arise, in older

leaves, from the middle-rib and from the side-ribs. KYLIN found tetrasporiferous leaflets projecting from the veins (1923 p. 65); I found the same. Long narrow shoots

are frequently produced, mostly at the base of the plants, but sometimes also from the upper end of the shoots. They often bear multicellular papillæ (fig. 432) which take the function of hapters when meeting a firm substratum, f. inst. other Algæ. Such papillæ, which have first been described by P. MAG-NUS (l. c. p. 75), occur frequently in this species, also in the broader forms of the frond and frequently cause the fronds to be entangled with each other and with other Algæ.

Germinating spores have not been observed in cultures, but young plants have repeatedly been found in nature, principally in hydroids. The small plant shown in fig. 433 *A* is most probably a sporeling of *Phycodrys rubens*, as it has been found by dredging in April in company with adult specimens of this species while other species of *Delesseriaceæ* were not present. This young plant shows much resemblance to the sporelings of *Nitophyllum punct*-



# Fig. 433.

Phycodrys rubens. A sporeling found in April off Refsnæs (Store Belt). 270:1. B plantlet found in July in the Little Belt on Sertularia. 63:1.

atum described and figured by NIENBURG (1908 Taf. VII). Like these it lacks the regular apical cell-divisions characteristic of the older shoots of the *Phycodrys*-plants; the monostromatic frond is composed of uniform cells which are rather irregularly divided, intercalary divisions being very frequent, and no mid-rib is present. Our sporeling differs, however, from those described by NIENBURG in being erect, while the latter, according to the said author, are decumbent, growing along the sub-stratum (l. c. p. 185). This primary shoot has been found again in a number of older

plantlets collected in July; it had reached a considerable size, up to 6 mm long and 2 mm broad or more, and had a broadly lanceolate shape, but otherwise showed the same character as before. It was thoroughly monostromatic, composed of uniform, irregularly disposed cells becoming smaller upwards, and terminated in an apical cell divided by transversal walls, but showed no trace of a mid-rib. The base of the primary shoot was contracted in a short stalk fixed to the substratum by a basal disc. From the stalk one or more adventitious shoots showing the typical apical growth and a well developed



*Phycoargs rubens.* A, plantiet found in July in the Little Belt on Sertularia, with lobed primary frond; at the base a young adventitious shoot. 20:1. *B*, tip of the primary frond in *A*, showing the apical cell. 260:1.

mid-rib were given off; the mid-rib could be traced to the very base (fig. 433 B). The primary frond in an advanced stage terminates in an apical cell dividing like that of the typical fronds, and the first divisions of the primary segments are similar to those mentioned above of the normal fronds, but intercalary divisions occur early and continue in still greater number than in the ordinary leaves and cause the arrangement of the cells to become much more irregular than in these (fig. 434 B). The cells in the middle of the frond do not show any tendency to longitudinal arrangement and no divisions parallel to the surface of the frond occur. Secondary apical cells appear and may give rise to slight sinuosities of the outline (fig. 434 A above) but normally they do not occasion branching. Primary fronds with one lateral lobe such as that represented in fig. 434 may, however, sometimes be met with. Even in these fronds no rudiment of a mid-rib was discernible. The primary fronds thus agree perfectly well with the normal fronds in *Nitophyllum* (comp. NIENBURG 1908). The discovery of the primary frond in *Phycodrys rubens* is in good

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accordance with the opinion pronounced by earlier authors (SCHMITZ, PHILLIPS, NIENBURG), and recently more precisely by KYLIN, that this species must be referred to the *Nitophylleæ*.

Antheridia have been met with in one specimen collected in November in the Great Belt; it was well developed, 5 cm long, while KUCKUCK only found antheridia on dwarfy specimens at Helgoland. The antheridia were borne on marginal lobes and leaflets on the upper part of the plant, about 1 mm long. The antheridial patches are usually surrounded by a narrow sterile border (fig. 435 A). In young leaves KYLIN found the antheridial sori forming bands parallel to the margin (1923 p. 65).



*Phycodrys rubens.* A, part of male frond with antheridia in particular leaflets, November. B, two cystocarps in particular leaflets. 16:1. The development of the antheridia has been described by the same author (p. 77).

The procarps arise in great numbers in the upper part of the fronds without any relation to the veins. The development and structure of the procarps and the cystocarps has been studied by PHILLIPS and recently most carefully by KYLIN (1923 p.71) whose description may here be referred to. The cystocarps were, in the Danish waters, only met with in a few specimens dredged in the Little Belt; they were almost

all placed in special marginal leaflets usually containing one cystocarp only (fig. 435 B), otherwise near the margin in the larger leaves.

The tetrasporangia arise in the Danish specimens only in small marginal adventitious folioles, never in larger leaves. The folioles, as shown also by KYLIN, may arise from the face of the frond, and sometimes even from old mid-ribs without membrane, much as in *Del. sanguinea*. They contain two layers of tetrasporangia which are only separated by one median layer of cells. Their development has been described by KYLIN (1923, p. 73) who emphasises that the mother-cells of the sporangia arise in the inner cortical layer, whereas in *Del. sanguinea* they are superficial cells.

*Ph. rubens* is rather variable in the size and shape of the frond, but the forms are connected with each other by intermediate forms. It is widely spread in all the Danish waters except the fjords, usually in the ordinary, rather broad form. In the North Sea and the Skagerak, however, it reaches only a moderate length (about 4 cm). In the northern Kattegat, too, it does not reach the full size (7 cm). In the inner waters it becomes larger, it not unfrequently attains a length of 10 cm and more. The largest specimens were found in the Great Belt and the Sound, in depths of 15 to 23 m, where they reach a length of up to 18 cm and a breadth of 1-2 cm

excluding the lobes. These, the most well developed specimens can be referred to f. *quercifolia* Turn., distinguished by the outline of the frond resembling an oak-leaf and by the rounded lobes. In smaller depths the size of the frond is smaller; that appears very plainly when comparing the rather numerous specimens collected in the Great Belt. In those dredged in depths of 1 to 17 meters the length was at most 8 cm, the breadth at most 1 cm, while the specimens collected in greater depths,

where the salinity is higher and the conditions less variable, reached a length of 10-18 cm and a breadth of 1,3-2 cm and analogous differences were found in the Sound.

A much branched loose form (f. *ægagropila*) was found in fast flowing water in Svendborgsund at 5,5 meters' depth.

As a noticeable form may be named f. *lingulata* Ag., characterized by its narrow frond with stalked lingulate almost entire marginal shoots. This form is, however, closely connected with the typical form through intermediate specimens. The smaller breadth of the frond is evidently an effect of the unfavourable conditions in the water with feebler salinity and great variations in temperature and salinity. In the Western Baltic Sea the frond still reaches a length of 10 cm and a breadth of up to 1 cm, but in **Bm** and **Bb** the frond is only 0,5— 1,5 mm broad. The frond is then almost linear or linearilanceolate and reminds one of *Membranoptera alata* from which it is, however, distinct by the more or less lan-



Fig. 436. Phycodrys rubens f. sublinearis. From Bornholm, cast of Dueodde, 38 m. 2:1.

ceolate segments of the frond. The margin is for long stretches even or only provided with few feeble teeth (fig. 436). These specimens which may be named f. *sublinearis* usually seem to be loose; they occur together with *Furcellaria* and *Mytilus* and attached to these, but apparently only by lateral hapters, and it is doubtful whether they have arisen directly from spores.

Tetrasporiferous specimens occur more frequently than sexual ones. Antheridia have been met with once only in November and cystocarps in two or three localities in March, while tetrasporangia have been found in numerous specimens collected in the months December to May. In the last-named month the sporangia were, however, usually entirely or partly emptied.

The species occurs in depths from 1 to 40 meters. In the southern parts of the Belts and the Sound and in the southern waters it has, however, not been met with in smaller depths than 5,5 m, and at Bornholm only in 19 to 38 meters' depth. It grows partly on stones, partly and principally on other Algæ as *Furcellaria*, *Laminaria*, *Halidrys* and many others, further on shells of mollusks, hydroids, *Hyas* etc.

Localities. Ns: ZQ, jydske Rev, 24,5 m; aF, off Thyborøn, 31 m; XR, off Klitmøller, 12 m; YT, Hanstholm, 15 m. - Sk: eV; Dana 2902; eY; eZ; several places off Lønstrup, off Hirshals, mole at Hirshals, everywhere were scarce. - Lf: Wanting. - Kn: Skagen harbour; Herthas Flak; Krageskovs Rev; around Hirsholmene; Frederikshavn, harbour and environs; UC, TL and ZP, at Nordre Rønner; several places near Læsø Trindel, 11-21 m. - Ke: Fladen, 16-30 m; Groves Flak, 19-32 m; Lille Middelgrund; ER, Fyrbanken, 28 m; IE; RU; RV; Store Middelgrund; Gilleleje. - Km: Læsø Rende: BN, off Asaa: Dana St. 2884 (C. A. J.). - Ks: Grenaa harbour; PF, Jessens Grund, 4 m; EJ, EM, Lysegrund; at Hesselø (Lyngbye); RL, 15 m; D, north of Grønne Revle, 11 m; aU, off Lumbsaas, 13 m; GF, GG, Sjællands Rev, 4-8,5 m. - Sa: GD, north of Sejerø; PC, MY, north of Samsø; stony reef in Begtrup Vig; Aarhus harbour; FV; FX; FY; GC, east of Æbelø; Hofmansgave (Lyngb., Hofm. Bang); AH<sup>1</sup>, Lillegrund at Fyns Hoved, 13 m; Korshavn; MP; DK, Bolsaxen; PF, off Refsnæs. – Lb: AX; OB; AL (Baaring Vig); AN: Middelfart harbour; common in the belt at Middelfart; Fænø Sund; cX: DG; dC; DF; DD; DE; DA; CC; CY; dQ; dE; dH, east of Hesteskoen. - Sf: CU; UV; Svendborgsund several places, f. *ægagropila* at 5,5 m depth. - Sb. Very common: GT, off Asnæs; GU; GS; AG; GV; cN; Kerteminde harbour; NU; cL; GP; NN; Z; AB; AC; BS; BT; between Sprogø and Korsør (Magnus); UE; DN: UF: UH; UT: DP; UI: Spodsbjerg; LH: DQ; DR: US, over 38 m; US<sup>1</sup>; DS; DT; LB; UR. - Sm: HA, HB, Agersøsund; CK; Q. - Bw: bX, off Kobbel Skov; CD, CE, Middelgrund south of Als; dO; dP; dK, Pøls Rev; DX, Vodrups Flak; UY, Vejsnæs Flak; DV; DU; UL, Øjet, 20 m; LA; KX; KU; UM, 25 m. - Bm: HG, Præstebjergs Rev; VH, south of Møen; VG, n. of Møens Klint; QS; SD; QO; QM; PR, off Dragør. - Bb: F. sublinearis: Rønne; XZ<sup>1</sup>, Davids Banke; SP, off Svaneke, 28 m; YD; YA, east of Dueodde, 38 m.

# Subfam. Delesserieæ.

## Apoglossum J. Agardh.

#### 1. Apoglossum ruscifolium (Turner) J. Agardh, 1898 p. 194; Kylin 1923 p. 83.

Fucus ruscifolius Turner, Trans. Linn. Soc. t. 6 p. 127, tab. 8 figs. 1-2, 1801.
Delesseria ruscifolia (Turn.) Lamouroux, Essai 1813 p. 124; Harvey Phyc. Brit. II pl. 26, 1846; J. Agardh 1852 p. 695; Kützing Tab. phyc. XVI tab. 12, 1866; Buffham 1893 p. 296 pl. 14; Kuckuck 1894

p. 256 (antheridia); Phillips 1898 p. 188; Kolkwitz 1900 pp. 45, 46; Nienburg, Z. Entwickl. d.



#### Fig. 437.

A, Apoglossum ruscifolium (Biarritz), part of mid-rib in superficial view. e endogenous branch budding from the central cell which is not visible. 700:1. B and C, Hypoglossum Woodwardii, similar views; the central cells are shown behind the cortical cells. '240:1. Florideenkeimlinge, Hedwigia Bd. 51, 1912, p. 299; Kylin, Keimung der Florideensporen, Arkiv f. Botanik 1917 p. 21.

Two specimens only of this pretty little Alga have been met with in the Danish waters, I must therefore refer the reader for the structure and development of the frond and of the organs of fructification to the recent paper of KYLIN (1923). It must only be noted that, according to my observations many years ago at Biarritz, the adventitious branches do not arise from any superficial cell of the mid-rib, as maintained by KYLIN (1923 p. 85), but by endogenous budding from the central cell. I have found the same in Hypoglossum Woodwardii Kütz. (Delesseria Hypoglossum (Woodw.)) (fig. 437).

The first stages of the germination have been observed by KYLIN (1917 p. 21). NIENBURG, who studied the further development, found that the sporeling is early divided by parallel walls into four cells. By irregular divisions of the two middle-most and partly of the lowermost and the upper of these cells, a flat body without mid-rib is produced which corresponds to the primary frond in *Nitophyllum* and continues in the primary frond, showing the typical structure.

Apoglossum ruscifolium has been met with in two localities in the northern and eastern Kattegat in great depths with salt water, 20—22,5 m, in July, in each place only in one specimen. They were both provided with tetraspores. The largest specimen was 2 cm high, 4 mm broad. According to KUCKUCK it accomplishes its course of life in scarcely more than four weeks. ARESCHOUG states, however, that it has been found fructiferous at the western coast of Sweden in July to September.

Localities. Kn: XJ, Herthas Flak, c. 20 m. - Ke: ZF, near Fladens light-ship, 22,5 m.

## Delesseria Lamouroux.

## 1. Delesseria sanguinea (L.) Lamouroux.

Lamouroux, Essai 1813 p. 124; Lyngbye, 1819 p. 7 pl. 2; Flora Danica tab. 2198,2 1836 (f. lanceolata Ag.); Kützing, Phyc. gen. 1843 p. 445 pl. 67; Harvey, Phyc. Brit. II pl. 151, 1849; Buffham, 1893, p. 296 pl. XIV figs. 28—30; Kuckuck, 1894 p. 255; Kolkwitz, 1900 p. 41; Kylin, 1907 p. 136; Svedelius, Svensk Botan. Tidskr. Bd. 5, 1911 p. 200, Bd. 6, 1912 p. 239, Bd. 8 1914 p. 1; Kylin, 1923 p. 92.

Fucus sanguineus Linné Mantissa 1767 p. 136; Oeder Fl. Dan. tab. 349 1767.

Hydrolapathum sanguineum Stackhouse Tent. 1809 p. 67 (not seen); J. Agardh, Sp. g. ord. Vol. III 1876 p. 370; Le Jolis, Liste.. Cherbourg 1864 p. 133; Wille, 1887 p. 57 figs. 1-13; J. Agardh, Analecta alg. cont. IV 1897 pp. 22, 41.

Wormskioldia sanguinea Sprengel, Syst. veg. IV 1827 p. 331; J. Agardh, 1851 p. 408.

The cell-divisions in the tip of the frond are very regular (comp. WILLE, KYLIN). As emphasised by KYLIN (1923 p. 93), intercalary cell-divisions do not take place in the primary cell-row but in the cell-rows of the second and third orders. These divisions are marked with an \* in my fig. 438 *B*. The cell-rows of the third order are given off from the lower side of those of the second order, and the cell-rows of the fourth order equally from the lower side of those of the third order (fig. 438, comp. KYLIN 1923 fig. 61). The pericentral cells cut off from the primary cell-row are early divided by a transverse wall (fig. 443). The cells surrounding the central cell-row are therefore of half the length of the central ones. As the central cells never divide by transverse walls they become very long. They are connected with one another by a broad pit in each transversal wall. The nucleus early divides into two, and the divisions continue, in consequence of which the older central cells contain numerous nuclei. The first transverse wall dividing the young pericentral cell is situated

under the pit connecting it with the central cell (comp. KYLIN 1923 fig. 62 a) and this pit is later to be found near the upper end of the central cell. The lowermost cell resulting from this division is at first not connected with the central cell by a pit,



Fig. 438.

*Delesseria sanguinea.* A, growing point of young leaf; the division of the apical cell has begun. B, lateral part of the same leaf; the intercalary division walls are marked with an \*. C, marginal portion of frond at a longer distance from the top, showing the secondary pits (\*). D, young adventitious shoot given off from a mid-rib. A, B 560: 1. D 200: 1.

may also sometimes project from the upper side. Veins of the third order may be met with and anastomoses of the veins may occur near the border. The branching of the veins is wrongly represented in Flora Dan. pl. 349.

The leaves do not normally branch, and branched leaves do not seem to have been mentioned in the literature. I have, however, observed some cases of branched leaves; as they have been met with in three different places, branched leaves may

but such a connection must later be established for in a more advanced stage the lower end of the central cell is also connected with the surrounding cells by pits (fig. 439 A, C). The pericentral cells are connected longitudinallybymultiple, usually three pits of which all or at least two are secondary.

The lateral veins of the first order arise in the upper border of the primary segments. Lateral veins of the second order are given off from the lower side of the primary ones; only near the margin of the leaf small veins perhaps be found to be not quite uncommon. The branching is caused by a secondary apical cell becoming a primary one. When the branch has arisen at an early moment it may give rise to a pseudodichotomy (fig. 440 A); if it arises later, it becomes feebler and the branching more distinctly monopodial (fig. 440 B, C). Opposite branches have never been observed.<sup>1</sup>

Secondary pits are produced in great numbers, not only in the veins but also in the monostromatic frond (438 C). Two pits may exceptionally occur in the same wall between two cells in the latter.

The new leaves, as is known, arise as adventitious shoots from the mid-rib. The first stages of development have not been observed, but the new leaves seem to arise from a superficial cell. They are at first almost filiform (fig. 438 D) but soon become flat. In the lower part of the young leaves several cells early grow downward giving rise to rhizine-like filaments that strengthen the connection with the mother axis and establish a union of the conductive systems of the two axes which does not exist to begin with (comp. fig. 444). A small number of adventitious leaves may arise early, in spring, and grow out in the summer (comp. HARVEY l. c.), but most of the leaves arise in autumn (or perhaps early in winter). In January they have only a small size, they grow out in early spring and reach a considerable size already in April and the growth ceases in the beginning of summer, usually in June or perhaps already in May.

In the mid-rib the inner cortical cells are segregated by numerous rhizoids or conductive hyphæ (WILLE 1887 p. 59; KYLIN 1923

<sup>1</sup> As mentioned by KYLIN (1923 p. 92), SCHMITZ and HAUPTFLEISCH's fig. 238 *B*, which shows a ramification, does not represent *Delesseria sanguinea*. Fig. *A* according to KYLIN is a *Hypoglossum*, probably *H. Woodwardii*; fig. *B* is probably *Membranoptera alata*.



Delesseria sanguinea. Cells from the mid-rib in longitudinal sections. A, central cell. B, inner cortical cells showing secondary pits. C, central (c) and pericentral (p) cells, the latter showing three secondary pits. A, C 350:1. B 560:1.



Fig. 440. Delesseria sanguinea. From the Baltic, south of Als. Branched leaves. 1<sup>1</sup>/<sub>4</sub>:1.

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D. K. D. Vidensk. Selsk. Skr., 7. Række, naturvidensk. og mathem. Afd. VII. 3.

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p. 95). As shown by Kolkwitz (l. c.) starch is deposited in the mid-rib of the new leaves in June, and in summer and autumn they are densely filled with starch

> grains. The lateral veins are also filled with starch and therefore become dark brown by treatment with iodine.

The basal portion of the frond is disc-shaped or conical and composed of densely united rhizines (Kolkwitz p. 45). It may, however, also be branched, composed of cylindrical members resembling the hapters of the Laminariæ (fig. 441). The basal portion is, according to KOLKWITZ, filled with starch in August and September; it gives rise to new adventitious shoots.

The germination has not been observed, but plantlets which could be identified with this species were repeatedly met with in summer, mostly growing on Hydroids, often in company with plantlets of *Phycodrys rubens* but easily distinguished from them by the lanceolate outline of the primary frond which is provided with a very distinct mid-rib from the base to the top (fig. 442). As shown in fig. 443, the cell-

divisions at the top of the frond agree exactly with those of the later fronds and the mid-rib has also the same structure as in these (comp. Kylin 1923 fig. 61). Near the base, however, the cortication of the mid-rib is less advanced than in the middle of the young frond (fig. 442 B). As in the later fronds, the margin shows a number of secondary apical cells, but while these are otherwise always situated so that the right angle of the cell is directed upward, the marginal apical cells of the primary frond often show the inverse situation, the wall by which they have been cut off being inclined upwards and the right angle of the cell therefore being directed downward. It not rarely happens that two marginal cells situated beside one another show different orientation, the one directed upward, the other downward (fig. 443 B). The downward directed apical cells remind one of those described above (p. 459) in Odonthalia dentata. Adventitious shoots early arise in the lowermost

Fig. 441. Delesseria sangui-

nea. Basal part of

frond consisting of several cylindric

hapters. Natural

size.



Delesseria sanguinea. A, plantlet from the Little Belt, July, 1,7 mm long. 43:1. B, lower part of the same showing adventitious branch. 200:1.

part of the primary frond, which has the character of a stipe, probably produced by a superficial cell (figs. 442, 444).

The laminæ of the leaves begin to disorganise in September, and this process advances more or less quickly during the autumn and winter and so that only the mid-rib remains. In exposed localities the disorganisation may begin earlier and the mid-rib may be denudated in September, whereas in sheltered localities, e. g. in the belts the laminæ keep till the next spring, having then a brownish colour.



Fig. 443.

Delesseria sanguinea. Parts of 7 mm long plantlet, primary shoot. A, apical part showing cell-divisions. B, marginal part showing secondary, variously orientated apical cells. C, lateral veins and secondary pits. 560:1.

The fertile folioles arise in the autumn as adventitious shoots on the mid-ribs of the leaves from the foregoing winter. The development and structure of the organs of fructification has been thoroughly described by SVEDELIUS and KYLIN and will not therefore be mentioned here. The three kinds of fructification always occur in separate individuals. The antheridia-bearing leaflets were met with in September and October; they reach a length of 5 mm. The procarp-bearing leaflets produce a great number of procarps situated on the mid-rib, but one cystocarp only is developed in each shoot. Ripe cystocarps were met with in January and may certainly

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also occur in December and in the following months. Still in May numerous cystocarps may be found. Ripe tetrasporangiferous leaflets were met with in January to May, but the dissemination of the spores apparently takes place mostly in winter. The sporophylls reach a length of 20 mm.

The age reached by the individuals of this species is not easy to determine with certainty, not only because the basal disc is able to produce adventitious shoots, as emphasised by KOLKWITZ (1900, p. 45), but also owing to the fact that new vegetative shoots may be produced not only in the autumn or in winter, but also in spring or early in summer on the new leaves, and there may thus possibly be



Fig. 444. Delesseria sanguinea. Adventitious branch of plantlet producing downward growing filaments at the base. 420 : 1.

produced two generations of shoots in one year. When in single cases, in specimens from the Little Belt, I have ascertained the presence of 7 generations of shoots in one specimen, it is therefore not permitted to conclude that it was 7 years old, though it is not improbable that it was really so. Kolkwitz thinks that *D. sanguinea* becomes "kaum älter als einige Jahre". I estimate the maximal age to be 4-5, perhaps 7 years.

Delesseria sanguinea reaches its greatest frequency and the best development in comparatively deep water with fresh flow, as in the eastern channel of the Kattegat and in particular in the Belts and the Sound, where it is often predominant. In such places

it often attains a length of 30 cm or a little more. In the open waters as Ns and Sk and in Kn it does not thrive by far so well and only reaches a length of up to 20 cm. Still in the western Baltic (Bw), in the deep channel between Lolland and Fehmern it reaches the maximal length. But in Bm it reaches only 18 cm and at Bornholm only 9 cm in length. The maximal length of the leaves varies about 10 cm in most of the Danish waters, in Kn and Ke between 7 and 18,5 cm, in Sb between 6 and 17 cm, in Su and Bw between 7 and 14 cm. In Bm it is only 5-8 cm and at Bornholm 2-5 cm. The greatest breadth of the leaves is reached in the Northern and Eastern Kattegat where it is 1,5-7,5 cm, most frequently 2,5-4,5 cm. In Sb the breadth is 1,3-4 cm, in the Sound 1,4-3 cm, in Bw only 0,8-1,5 cm, in Bm 0,3-1,3 cm and in Bb only 0,3 cm (comp. Plate VII figs. 1-4). The breadth of the leaves seems therefore to be more influenced than the length when the salinity of the water is diminished.

*D. sanguinea* occurs in all the Danish waters except the Limfjord and other fjords. It does not grow in depths smaller than 4—5 meters and descends to 30 meters' depth at least; in Sb it has been met with in 40 meters' depth. It prefers water with a salinity of  $20 \ ^{0}/_{00}$  or higher and with rather low summer temperature. It is characteristic to stony bottom in the deep channels in our inner waters, where it occurs in great specimens with several generations of shoots.

Localities. Ns: ZO, jvdske Rev, 24,5 meters; aF, 31 m; XR, off Ørhage; eT, 34 m; YT, off Helshage, Hanstholm, 5,5-13 m. - Sk: eX, N.W. of Bragerne, S.E. of Bragerne, 10,5 m; washed ashore at Svinkløv; Dana St. 2900, 2899 (C. A. J.); several places off Lønstrup, 7,5-19 m; Bredegrund and Møllegrund off Hirshals; bF, Skagbanken. - Kn: Herthas Flak, c. 22 m; around Hirsholm; Frederikshavn; VT and GN, near Nordre Rønner; VT; common at Læsø Trindel, 10-24 m. - Ke: Fladen, several places, 16-30 m; Groves Flak; several places, 19-30 m; XA; RU, 26,5 m; Store Middelgrund (Børgesen, !); GJ, Ostindiefarer Grund; OO, Søborghoved Grund, 8,5 m; bR, Vesterlands Grund at Gilleleje, 7,5 m. - Km: Læsø Rende, Dana St. 2884 (C. A. J.); XC, south of Læsø, 7 m. - Ks: Lysegrund (Lyngbye, HO, OP !); OT, Hastens Grund, 9,5 m; near Hesselø (Lyngbye); RL; D; GG, GF, Sjællands Rev: FP, Jessens Grund, 4 m. - Sa: PA, GD, GE, PC, near Sejerø: PG, near Hatter Rev: Koldby Kaas, outer side of mole; aV; MP, DK, Bolsaxen; AH<sup>1</sup>, Lille Grund; Hofmansgave (Hofm. Bang); entrance to Odense Fjord (C. Rosenberg). - Lb: Middelfart; off Kongebro; Fænø Sund, 19-34 m; off Stenderup; DA, off Bøjgden; dH, dH<sup>1</sup>, east of Hesteskoen; CF, dQ, south of Lyø, 22 m; LG, off Vidsø, Ærø. - Sf: BY, BX, Svendborgsund; UV, north of Ærø. - Sb: GT, off Asnæs; GU; LK, Elefantgrund; cN; NU; cL, 25-27 m, NO, NN, near Sprogø; GP; DN, Vengeance Grund; UE; UF; UG; LH, West Side of Langeland; UH; UT; DQ; US, c. 40 m; US<sup>1</sup>; DR; LB; UR. - Sm: HA, Agersø Sund; VC; HC; CR; KQ. - Su: Hellebæk; north of Kronborg cast ashore (Liebman, C. Rosenberg a. o.); bM, south of Hveen, 22,5 m. - Bw: bV, N.E. of Kobbel Skov; cD, cE, dO, 5 m, south of Als; Pøls Rev; DX, Vodrups Flak; UL, Øjet, 20 m; LA, UQ, KY, KV, KU, south of Lolland; KT, Gedser Rev; Kadetrenden, 24,5 m. - Bm: KS, KR, HG, east of Falster; bO, 15 m (O. Paulsen); VG, QS, N.E. of Møen; 7,5 miles E. of Hellehavns Nakke (C. A. J.); 20 miles E. by N. of Møens light-house (C. A. J.); 13,5 miles E.S.E. of Møens light-house, 24 m (C. A. J.); QN, QM, Køge Bugt. - Bb: Adler Grund, 20 and 30 meters (C. A. J.); SH, Rønne Banke; YH, off Rønne, 24,5 m; 8 miles S. 1/2 E. of Rønne harbour, 11-19 m (C. A. J.); XZ<sup>1</sup>, Davids Banke, 29 m; 3 miles S.S.E. of Nexø harbour, 21 m (C. A. J.); YC, near Salthammer Rev, 24,5 m.

### Membranoptera Stackhouse.

# 1. Membranoptera alata (L.) Stackhouse.

Stackhouse, Tentamen marino-cryptogamicum. Mémoires de la soc. imp. des Natur. de Moscou, Tom. 2, Moskwa 1809 p. 85 (teste Kylin); Kylin 1923 p. 108.

Fucus alatus Hudson, Fl. Angl. 1st ed. 1762 p. 578 (not seen); Oeder Fl. Dan. tab. 352, 1767.

Delesseria alata (Huds.) Lamour. Essai 1813 p. 124; Lyngbye 1819 p. 8 pl. 2; Hornemann Fl. Dan. tab. 2129, 1836; Harvey Phyc. Brit. III 1851 pl. 247; J. Agardh 1852 p. 683; Wille 1885 pp. 31, 64, id. 1887 p. 62 figs. 14—20, 79; Kny Wandtaf. Taf. 77. 1886, Erläuterungen p. 334; Buffham 1893 p. 296 figs. 22—24; Phillips 1898 p. 183 figs. 17—19; Kolderup Rosenvinge, Sporeplanterne 1913 p. 112 fig. 158.

*Hypoglossum alatum* Kützing, Phyc. gen. 1843 p. 445, pl. 66; Tab. phyc. Bd. 16 tab. 16, 1866. *Pteridium alatum* J. Agardh 1898 p. 225.

The apical cell-divisions of the frond have been described and figured by KNY (1886), WILLE (1887), myself (1913) and recently by KYLIN (1923). The latter author shows that the structure of the tip of the frond resembles that of *Delesseria* sanguinea but differs from it 1) in the absence of intercalary divisions, 2) in that the lateral pericentral cells do not divide by transversal walls, and 3) by the branching of the frond by the secondary apical cells transforming into primary ones. After the division of the primary segment cut off from the apical cell by two longitudinal walls, the two lateral cells are divided by inclined walls in a number of segments of



Membranoptera alata. Tip of frond from Frederikshavn, May.

the second order, the first of which are included, the outer end meeting the lower primary segment wall, while the younger segments of the second order reach the border of the frond. The number of included segments of the second order is variable, it is greatest in the broader forms (comp. KNY 1. c., K. ROSENVINGE

1913 p. 22 (from Cherbourg) and KYLIN 1923 fig. 70), while in the narrow forms from the Baltic Sea it may be only 1 or 2 (fig. 447). Their number can be recog-

nised in the older parts of the frond by the aid of the lateral veins of the second order arising in the upper border of the segment



Fig. 447. Membranoptera alata f. baltica, from Bornholm. Tip of frond. 350 : 1.

of the second order (fig. 446 *A*), just as the lateral veins of first order arise in the upper border of the primary segments. In the branch - producing segments one segment of the second order only is as a rule included (fig. 445, lower branch on the right hand; comp. KNY l. c., se-



Membranoptera alata. A, tip of frond showing the mid-rib and the lateral veins. B, portion of membrane showing the veins. 19:1.

cond branch from the top on the right; K. R. 1913 fig. 158 last branch; KYLIN 1923 fig. 70 *a*). But it also happens that the first segment of the second order reaches the border of the frond (fig. 445 last branch on the right, comp. KNY l. c. last branch on the right, KYLIN 1923 fig. 70 *c*). When the first segment of the second order of the branch-producing

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segment is included the vein situated in its upper border anastomoses with the vein of the foregoing primary segment (fig. 446 A). The primary segment situated immediately over a branch may sometimes be included (fig. 452, segm. 9). The branches are as a rule regularly alternate, but superposed branches may occur (fig. 445).

The mid-rib arising by tangential divisions, not only of the median cell but also of the adjacent parts of the primary segments, early attains a considerable thick-



Membranoptera alata. Portion of membrane showing two lateral veins and secondary pits. The limits of the primary segments are marked with an arrow. 260 : 1.

ness and the lateral veins are also early developed, the cells in the upper border of the primary segments lengthening and



Membranoptera alata. A, longitudinal section of young shoot. B, C, transverse sections of shoots. D, longitudinal section of lateral vein. 390:1.

dividing by walls parallel to the flat, in consequence of which the inner conducting cell becomes covered by a shortcelled layer on both sides (fig. 448 *D*). Lateral veins of the second order are also early developed in the upper border of the segments of the second order. According to HARVEY (Phyc. Brit. pl. 247 fig. 8) the lateral veins of the second order spring upwards and downwards as well from the primary ones; this is,

however, not correct, they are only given off from the lower side (fig. 446). Lateral veins may also spring from the mid-rib between the prim-

ary lateral veins (fig. 446). The divisions parallel to the flat of the frond extend from the mid-rib towards the margin, so that the greater part of the frond consists of more than one layer of cells; the margin itself, however, is always monostromatic (fig. 448 *B*, *C*, comp. KYLIN 1923 p. 111). The veins are rather close owing to the want of growth beyond the apical portion of the frond.

Secondary pits are produced in great numbers and, in the membranaceous portion of the frond, in particular in the walls perpendicular to the longi-



Fig. 450. Membranoptera alata. Adventitious shoots from an axil. 350:1.

tudinal axis of the frond, thus establishing a longitudinal connection between the cells of the flat. A longitudinal arrangement of the cells not agreeing with the distribution corresponding to the succession of the cell-divisions then frequently appears (fig. 449).

Adventitious shoots arise in various number from the axils of the branches; they have no fixed position but develop from marginal initial cells or from other



Fig. 451. Membranoptera alata. Young plants growing on Membranipora pilosa. A, with a young branch near the top. B, with an adventitious shoot near the base. 19:1. cells near the margin (fig. 450).

In the Baltic Sea a very narrow form occurs, the frond of which is only c. 1 mm broad, at Bornholm even only c. 0,3 mm broad (Plate VII fig. 7). While in the typical form the frond is rounded above with two or three branches near the top, the frond from the Baltic is much less branched; the shoots are pointed, frequently without any branch near the top (fig. 447). The frond is polystromatic almost to the margin. Of the segments of the second order only one or two are included; sometimes even the first one reaches the margin of the frond (fig. 447, 7th segment from the top).

The mid-rib becomes very convex on both sides. Within a thin assimilatory cortex it is built up by 1) primary longitudinal cell-rows, the cells of which are principally jointed by secondary pits, often three in each transversal wall, 2) conducting hyphæ given off from the former (comp. WILLE 1887 p. 62 figs. 14—20, 79). In a cross section a transversal row of primary cells is present, the middlemost of which, the primary axial cell, may have a smaller diameter than the others. All the inner cells of the mid-rib contain several nuclei.

Sporelings produced in cultures were not obtained and very young plantlets were not met with in Nature, but young plants that could be referred with certainty to this species were collected in July, e. g. growing on *Membranipora pilosa* at Herthas Flak. They were 1/3 to 1/2 cm long, not branched, with a terete stipe continuing in a

vigorous mid-rib from which opposed lateral veins were given off (fig. 451). The apical cell-divisions agreed exactly with those of the adult plants (fig. 452). In one of the larger plants the ramification had begun, the first branch having been formed near the top (fig. 451 A). As shown in fig. 452, this branch differs from those of the older fronds in that it is more symmetrical, the first segments being equally developed in the anterior and the posterior side; the following segment of the primary axis is therefore included, and the rib of the branch is not as usual in its outer part situated in the anterior border of the segment of the mother axis from which it has arisen. The primary axis appears to develop

into an ordinary branched frond. The stipe is fixed to the substratum by a conical disc formed by densely united rhizines. Adventitious shoots early appear in the stipe.

The antheridia occur, as shown by BUFFHAM (1893 p. 296 figs. 22-24) in minute leaflets arising from the apices of the plant and, especially, in groups from the axils (comp. Kylin 1923 fig. 69a); they cover the whole surface except a marginal zone which is sometimes very narrow, and the lower portion of the leaflet



Membranoptera alata. Tip of the plantlet represented in fig. 451 A. The figures indicate the number of segments from the top. 350:1.

may also be sterile (fig. 453). According to KYLIN, the development and structure of the spermatangia and the spermatia is similar to that in *Apoglossum ruscifolium*.

The procarps arise in the mid-rib in adventitious shoots or in the upper part of the frond; their development has been described by PHILLIPS (1898) and KYLIN



Fig. 453. Membranoptera alata. Male leaflets. 2,7:1.

(1923). The cystocarps occur singly on the midrib in the said parts of the frond.

The tetrasporangia occur in sori in adventitious branchlets or in the ultimate branches of the frond. According to Kylin (1923 p. 113), they develop from superficial cortical cells in the same way as in *Delesseria*.

Membranoptera alata occurs in all the Danish waters except the fjords and perhaps the waters around Bornholm where it has only been met with as washed ashore. It reaches a length of 14 cm in the Northern Danish waters, 12 cm in the Sound and the Belts, 8 cm in **Bw**, 7 cm in **Bm** and 5 cm in **Bb**. The breadth is rather variable.

In the northern waters it usually varies about 2 mm, it frequently amounts to 3 mm more rarely to 4,5 mm. In the Great Belt and the Sound a breadth of 3,5-4 mm may still be reached in deep salt water. In **Bw** it is rarely more than 2 mm broad, in **Bm** 1/2-1 mm (in one specimen 1,5 mm). A specimen from Bornholm was only 0,3 mm broad (comp. Plate VII figs. 5-7).

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The narrow Baltic form (fig. 447, Plate VII fig. 7) is much feebler and less branched than the typical form and thereby rather characteristic. It is, however, connected with the typical form by transitional forms. It may be named f. *baltica*. Some of the specimens of this form were loose on the bottom, especially those found north of Møen.

The vegetative growth begins in winter and ceases in summer. Antheridia were met with in October and November, cystocarps and tetrasporangia in January to April. The species has been found growing on stones and on various Algæ (*Farcellaria*, *Fucus serratus*, *Halidrys*, *Ahnfeltia*, *Laminaria* etc.). It has been met with from low-water mark to 27 meters' depth.

Localities. Ns: Rømø, cast ashore (Møller); YT, off Helshage, Hanstholm, 13 m. - Sk: Roshage, Hanstholm, near land, 2 m; Dana 2902 (loose?) (C. A. J.); eY, 15 m; Bragerne, 1-2 m; Dana 2900 (loose?) (C. A. J.); off Lønstrup, 7-9 m; off Hirshals, 12-15 m (Børgesen, !); Hirshals mole and stones near land, 1-2 m. - Lf: Wanting. - Kn: Herthas Flak; Hirsholmene; Krageskovs Rev, 5 m; Strandby, 1 m: Frederikshavn, harbour and stony reefs; GM, north of Læsø; Trindelen, FE, IX. - Ke: fH, Fladen, 17 m; Store Middelgrund (!, C. A. J.); GI, Ostindiefarer Grund; OO, Søborghoved Grund; Gilleleje (Lyngbye). - Km: Læsø Rende, Dana 2884, 9 m (C. A. J.). - Ks: Grenaa harbour; Jessens Grund, 4 m; OP, EM, HQ, Lysegrund, 6-10 m: RL; near Hesselø (Lyngbye); GF, Sjællands Rev, 8 m. - Sa: GD, GE, north of Sejerø; FT; FS; PG; YV, 15 m; MP, Falske Bolsax; DK, Bolsaxen; AH<sup>1</sup>, AH, Lillegrund north of Fyns Hoved. - Lb: NV, Middelfart; LG, off Vidsø, Ærø. - Sf: Ærø, Kjærbølling. - Sb: GT, off Asnæs; cN, S.W. of Musholm; Kerteminde harbour; GP, off Halskov; near Sprogo (Magnus): NN; NO; NP; Nyborg (Hofm. Bang); UE; DN, Vengeance Grund, 12 m; UT; US<sup>1</sup>, 20 m; DR, off Albuen; DT; LB, 17 m; UR. - Sm: HA, Agersø Sund, 11 m; VC; HC, off Knudshoved Odde; Q; KP, 3 m; HI and KQ, 4 m, Grønsund. - Su: Hellebæk (Ørsted), washed ashore north of Helsingør (C. Rosenberg a. o.); bM, south of Hyeen, 22,5 m: OG, Taarbæk Rev; TB, off Skovshoved, 5 m; OG<sup>1</sup>; RH, Knollen; PR, off Dragør. - Bw: cE, south of Als; UY, Vejsnæs Flak; UY; UL, Øjet, 20 m; KY; KX; KU, KV, Schønhevders Pulle. - Bm: (f. baltica) KR, KS, HG, east of Falster; VH, QY, south of Møen; OZ, RC, VG, east side of Møen; 7,5 miles east of Hellehavns Nakke, 27 m (C. A. J.); QS; QR; VD; SD; QN; QM, off Køge: QF, south end of Flinterenden. — Bb: (f. baltica) washed ashore at Rønne (R. T. Hoff).

# EXPLANATION OF PLATES

All figures are photographs of dried specimens, 4/5 nat. size.

# Plate V.

1. Polysiphonia orthocarpa, from Amtoft Reef, Limfjorden.

2. Polysiphonia elongata f. Schuebelerii, from the Great Belt north of Langeland (UF).

3. Polysiphonia elongata f. baltica, from YC, east of Bornholm, 24,5 meters' depth.

# Plate VI.

- 1. *Polysiphonia violacea*, from Hirsholm 11 meters' depth showing secondary axillary shoots and torsion.
- 2-4. Rhodomela subfusca f. abyssicola, from dQ south of Lyø 22 m, June; fig. 3 with tetrasporangia.

# Plate VII.

1. Delesseria sanguinea, from N.E. Reef by Hirsholm, July.

2. - , from Øjet (Bw) 20 m, May 21st. With cystocarps.

3. - , from VG, north of Møens Klint, 17 m, May 28th.

4. - , from YC, east of Bornholm, 24,5 m, July.

5. Membranoptera alata, from Læsø Trindel, April, Børgesen.

6. - , from Frederikshavn, outside of harbour, May.

7. - , from Præstebjergs Rev, east of Falster, 7,5 m, November.





Pl. VI





