# THE MARINE ALGÆ OF DENMARK

## CONTRIBUTIONS TO THEIR NATURAL HISTORY

# PART II RHODOPHYCEÆ II. (CRYPTONEMIALES)

BY

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WITH TWO PLATES

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#### KØBENHAVN

BIANCO LUNOS BOGTRYKKERI

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# III. Cryptonemiales.Fam. 4. Dumontiaceæ.Dumontia Lamour.

#### 1. Dumontia incrassata (O. F. Müll.) Lamour.

Lamouroux, Essai. Mus. d'hist. nat. Paris 1813; Batters, Catalogue, 1902, p. 93.

Ulva incrassata O. Fr. Müller, Flora Danica tab. 653, 1775.

Ulva spongiformis O. Fr. Müller, Flora Danica tab. 763 fig. 2, 1778 (?). Fragment not determinable with certainty.

Ulva filiformis Hornemann, Flora Danica tab. 1480,2, 1813.

Gastridium filiforme Lyngbye, Hydr. p. 68 tab. 17.

Gastridium filiforme var. intestiniformis Liebman, Flora Danica tab. 2457, 1845 = f. crispata Grev.

Dumontia filiformis (Hornem.) Greville, Alg. Brit. p. 165 tab. 17 (cystocarp); Harvey, Phyc. Brit. pl. 59 and 357B; Nægeli, Die neueren Algensysteme 1847, p. 243 Taf. IX fig. 4-8 (structure of frond); J. Agardh, Spec. II p. 249, III p. 257; Kützing, Tab. phyc. 16. Band Taf. 81 (transverse section of tetrasporebearing plant; Schmitz, Befr. Flor. 1883 p. 18,20, fig. 22 (carpogonial filament); Reinke, Algenflora d. westl. Osts. p. 26; G. Brebner, On the Origin of the filamentous thallus of Dumontia filiformis. Journ. Linn. Soc. Bot. Vol. 30, 1895, p. 436; Kuckuck, figure of a young basal disc in Oltmanns' Morph. I, p. 573; Okamura, Icones of Jap. Alg. Vol. I No. IV pl. 16 figs. 1-8, p. 65.

The fronds arise from a crustaceous disc produced by the germinating spore. A 5 days old plant is shown in fig. 74 A. It is not much larger than the tetraspore from which it arose, but it is divided into a number of small cells and has become a hemispherical body from the border of which short one- or two-celled filaments proceed.<sup>1</sup> A later stage is figured by KUCKUCK (OLTMANNS l. c.); a group of short-celled filaments is here seen given off from the upper side of the disc, and it is said that only one of these filaments serves to form the erect frond, some of the others forming the bark on the base of it. The basal discs may be perennial (REINKE, BREBNER); they form large expansions on stones, *Mytilus, Chondrus* a. o. In sunny localities they have a light violaceous colour and often show radial folding (in a dried state), in greater depths they are darker, They are easily distinguishable by their structure and by the occurrence of groups of short-celled filaments giving rise to new erect fronds. As shown by BREBNER (l. c.) the fronds may be endogenous

<sup>1</sup> The germination of the tetraspores has quite recently been described by KVLIN (Über die Keimung der Florideensporen. Arkiv för Botanik. Band 14. N:o 22. Stockholm 1917, p. 9). The author kept the sporelings in culture during more than two months but did not obtain any production of erect shoots. The sporelings produced after 10 days long unicellular hairs, but after addition of nitrate to the culture no hairs were produced. or exogenous and, according to this author, the cells of the short-celled filaments are divided by intercalary divisions.

The structure of the frond has been described in 1847 by NÆGELI (l. c.). It terminates in an apical cell which is said to be divided by oblique cell-walls producing segments at all sides, and this is affirmed by SCHMITZ and HAUPTFLEISCH (ENGLER U. PRANTL, Nat. Pflfam. I, 2 p. 517); it is however at least not general. The young fronds arising from the basal disc have at all events an apical cell divided by horizontal parallel walls, and this is also the case with young slender branches (fig. 74, B, C). In thicker shoots still in development I have found the segment walls



Dumontia incrassata. A, five days old plant from germinating tetraspore. B, upper end of side branch showing transverse segment walls. C, tip of young frond November), the segment walls in the main axis slightly inclined. D, young hair. E, transverse section of frond showing a young sporangium. F, transverse section of frond showing the development of the antheridia. A 300:1. B, C, E 390:1. D, F 630:1.

somewhat inclined, but not so much that they reached the foregoing segment wall (fig. 24, C). The cells of the frond contain a single nucleus and a number of discshaped chromatophores.

Some of the surfacecells may produce a hyaline hair of the same character as in other Florideæ (fig. 74, D). In spring (March to May) they are most developed, numerous, long and rich in protoplasm; at other seasons they are often wanting.

The frond is at first cylindrical, but in an advanced age it becomes irregularly compressed and crisped (f. *crispata* Grev.). In winter and in shaded

localities it is dark red-brown, while in sunny places in spring and summer it has a light yellowish colour, the tips at last becoming green.

The central cavity contains a thin slimy matter which seems to consist of pectic substances; it forms a network in the cavity, the meshes containing probably only water.

The sporangia are, as is well known, immersed in the wall of the frond; they are born of a cell in the inner cortex bearing moreover at least two cortical filaments (comp. KÜTZING Phyc. gen. tab. 74 II). The sporangium is connected through a pit with the bearing cell but not with other of the cortical cells (fig. 74, E); thus it is terminal and not intercalary as in *Dilsea*. The division is always cruciate; but

it is often somewhat irregular, the longitudinal walls being inclined. I have not been able to decide if real cell-walls are formed between the spores in the sporangium. The latter is surrounded with a distinct wall consisting of more than one layer; at the lines of separation between the spores the inner layer is seen to be continuous, without penetrating between the spores. The sporangia develop in the main axis as well as in the branches down to 1 to 2 cm. from the base.

The antheridia (spermatangia) form a continuous layer on almost the whole surface of the male individuals. They are cut off by inclined, often upwards convex, intersecting walls of the upper end of the antheridia-bearing cells (SVEDELIUS' spermatangial mother-cells), at two (or perhaps more than two) sides (fig. 74, F). The form of the antheridia-bearing cells is rather variable according to the varying length and breadth; they contain a single nucleus but seem to be destitute of chromatophores. Beneath a fully developed antheridium a new one can arise, a little cell very rich in contents being cut off in the same direction as the former. In the middle of fig. 74 F above, the oldest antheridium is seen to be connected through a pit with the youngest one formed right under it. The continued formation of antheridia thus takes place by intercalary divisions, and the antheridia are placed in two (or more) series, but owing to the evacuation of the spermatia, at most two antheridia are to be seen at the same time in the same series. The antheridial development in this plant thus does not correspond with any of the types set up by SVEDELIUS (Martensia, K. Sv. Vet. Ak. Handl. Band 43. No. 7. 1908 p. 76).

The development of the cystocarp was found to agree with what OKAMURA found in examining Japanese specimens. The carpogonial branches arise from the inner part of the wall of the hollow frond, frequently from a cell in a longitudinal filament or from a cell given off from it. They are 5-celled and curved, in particular at the upper end, where the carpogonium is cut off by an oblique wall intersecting the underlying wall (comp. SCHMITZ 1. c. fig. 22, OKAMURA 1. c. fig. 4).

The auxiliary-cell filaments, being very numerous, as the carpogonial filaments as well, have a similar position to these. They are somewhat curved, and consist of 4 to 5, more rarely 6, rather low cells with rich contents. They are frequently placed quite near the carpogonial filaments; it may even happen that a carpogonial filament arises from the base of an auxiliary-cell filament (fig. 75 A). After fecundation, fusions take place between the carpogonium and one or more cells in the carpogonial filament, resulting in the formation of a great fusion-cell of very irregular form, giving off sporogenous filaments in various directions; in fig. 75 E 4 such filaments are present. The auxiliary cells with which they become connected are usually the second cell from the base of the auxiliary-cell filaments, sometimes the third or even the fourth cell. After fusion, the auxiliary-cell, when giving rise to a cystocarp, produces, at the convex side of the filament, a number of cells which after several divisions form a group of carpospores placed around a placentar cell originating from the auxiliary cell (or the fusion cell). A curious anomaly is shown in fig. 75 F. In the ventral part of the carpogonium no nucleus was visible, but



Fig. 75.

Dumontia incrassata. A, two carpogonial branches, the upper representing a side branch of an auxiliary-cell filament. B, carpogonial branch; the carpogonium does not reach the third cell from the top. C, carpogonial branch and auxiliary-cell branch. D, carpogonial filament after fecundation; the fertilized carpogonium has fused together with the three uppermost cells of the carpogonial branch, has become very enlarged and formed sporogenous filaments. E, the fertilized carpogonium has fused with one or two cells of the carpogonial filament and has given rise to four sporogenous filaments. At right a four-celled auxiliary-cell filament; the auxiliary-cell after having fused with a sporogenous filament has produced a young gonimoblast. F, the trichogyne of the unfertilized carpogonium contains two nuclei, while the ventral part contains no nucleus. The lowest or second cell from the base has fused with a sporogenous filament and produced a new sporogenous filament. H, auxiliary-cell filament; the auxiliary cell has fused with a sporogenous filament and produced a new sporogenous filament. H, auxiliary-cell filament, the sporogenous filament from another carpogonium. G, auxiliary-cell filament; the auxiliary cell has fused with a sporogenous filament and produced a new sporogenous filament. H, auxiliary-cell filament, s, sporogenous filament. t, trichogyne. A, B, D, E, G, H 380:1 C, F 610:1. I 220:1.

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in the middle of the trichogyne two bodies were found which were probably nuclei. As no spermatia were found fixed to the trichogyne, the two nuclei must have derived by division from the original carpogonial nucleus, the undermost representing probably the sexual nucleus, the upper the trichogynal nucleus. It must however be admitted that the upper end of the trichogyne was not quite distinctly visible. This filament is further remarkable in that the second cell from the base acts as an auxiliary cell, having fused with a sporogenous filament from another carpogonium. It is however not fully clear if the great fusion cell has arisen from the second cell or by division from the first cell, which is rather small and half enclosed by it. In the first case the carpogonial filament has been 6-celled.

The species is widely distributed on the Danish coasts, and occurs often abundantly. It grows particularly in somewhat sheltered localities, and attains there the greatest dimensions. In Sk, Lf, K, Sa, Lb and Sf it has been found only at lowwater mark or a little lower; on the other hand, in the southern and eastern waters (southern parts of the Great Belt and of the Sound and the Baltic) it has also been met with in depths of 4 to 12 meters, and it occurs in a similar manner in the western Baltic according to REINKE (1. c.), while it otherwise appears to grow only at a slight depth. On the shores of North Europe it grows, where tide occurs, in the middlemost part of the littoral region ("à mi-marée"). The explanation of this peculiar distribution in the western Baltic and the adjacent waters might perhaps be sought in the lesser salinity of these waters. It deserves to be mentioned in this connection that the species, according to CROUAN (Fl. Finist. p. 144), in the neighbourhood of Brest occurs particularly where fresh water runs out. When growing at low-water mark in Danish waters of comparatively high salinity, the plants are also temporarily exposed to fresh water at least by rainy weather during low-water. On the other hand it will be seen from the following maximal lengths for specimens collected in a series of localities in the Sound ranged from North to South that the length decreases with much decreasing salinity: Hellebæk 47 cm, Humlebæk 30 cm, Sletten 28 cm, Trekroner (Copenhagen) 20 cm, Dragør 8 cm, These specimens were all collected near the low-water mark. A length of over 50 cm has been met with in specimens from Lb, Sf (70 cm) and Sb. In the other waters the following maximal lengths have been recorded: Sk 37, Lf 28, K over 30, Sa 40, Su 47 cm.

The species has been found with erect fronds at all seasons, but only abundantly in the first half of the year, from the middle or the end of the winter to the beginning of the summer. Most of the specimens die in June or July; only single, rare specimens are therefore met with in the more advanced summer and in autumn. As the spores germinate easily immediately after having been shed, the species must be supposed to endure the summer in a crustaceous form, originating for the most part from the spores shed in the last spring but partly also of older date. The sexual organs have been met with in winter and spring and in September, ripe cystocarps in May to July, ripe tetrasporangia in May to July, once even in August (Sk). Sexual organs and tetrasporangia occur always in distinct specimens. The same is the case with the antheridia and the carpogonia; I have found, however, some few specimens which seemed to be monoecious, but the supposed antheridia were not fully developed.

Localities. Sk: Lønstrup (loose on the shore); Hirshals, mole and reef. — Lf: Oddesund; Nykøbing (Th. Mort., F. Børg. !); Glyngøre; Agersund (Th. M.); Aalborg (Th. M.); Hals (F. Børg.). — Kn: Hirsholm; Kølpen; Frederikshavn; Nordre Rønner. — Km: Anholt, harbour. — Ks: Harbour of Grenaa; Hesselø; Isefjord: Lynæs, harbour. — Sa: Coast below Ris Skov; Aarhus, harbour; Odense Fjord: inner side of Enebærodden; Hofmansgave (Lyngbye, Hofm. Bang, C. Rosenb.). — Lb: Bogense; Fredericia; Middelfart; Kongebro; Snoghøj; Fænø Sound; Assens; Faaborg; Dyreborg. — Sf: CT west of Taasinge; Svendborg; Marštal, specimens up to 70 cm long, among Zostera in shallow water, frequently on Littorina; Skaarupør; Lohals. — Sb: South side of Refsnæs; Kerteminde; Korsør; Nyborg, harbour and Avernakhage; Vresen; Spodsbjerg, harbour; DQ, 5,5 meters; UR, 7,5 meters. — Sm: VC, Venegrund 4—4,5 meters. — Su: Hellebæk; Helsingør (Liebman, C. Rosenb., !); Humlebæk; Sletten; TF<sup>1</sup>, Staffans Flak, 12—13 meters. OG<sup>1</sup>, between Trekroner and Middelgrund, c. 9,5 m; Trekroner (Liebman, Ørsted a. o.); RH, Knollen, 9,5 m; Dragør; PR, off Dragør, 7,5—9,5 m. — Bw: KU, Schönhevders Pulle, 6,5 m.

#### Dilsea Stackhouse.

#### 1. Dilsea edulis Stackhouse.

Stackhouse, Mém. soc. Mosc. II, p. 55,71 (non vidi).

Fucus edulis Stackhouse, Ner. Brit. 1. ed. p. 57 (non vidi), II. edit. 1816 p. 22, tab. 12 (good).

Halymenia edulis (Stackh.) Agardh; Flora Danica tab. 2258, 1839.

Iridæa edulis (Stackh.) Bory; Harvey, Phyc. Brit. pl. 97; Areschoug Phyc. scand. p. 89; Kützing, Tab. phyc. 17. Band, tab. 3a.

Schizymenia edulis (Stackh.) J. Agardh, Sp. g. o. II, 1851, p. 172.

Sarcophyllis edulis (Stackh.) J. Agardh, Sp. g. o. III, 1876, p. 265.

From a basal disc a number of flat fronds arise. Their number may be considerable, but when they are numerous they are for the greatest part feebly developed. They attain not seldom a length of about 30 cm; the largest specimen I have measured was 61 cm long in a dried state. As to the anatomy of the frond, reference may be made to the papers of WILLE (Bidrag til Algernes physiologiske Anatomi. K. sv. Vet. Ak. Handl. Bd. 21, 1885, p. 71. tafl. V fig. 61-67, and Beiträge zur Entwickl. d. physiolog. Gewebesyst. Nov. Act. Leop. Car. Ak. Bd. LII Nr. 2, 1887, p. 83, Taf. 5 fig. 72-74 and Taf. 6 fig. 75).

In summer the species is always sterile. It is evidently fructiferous in winter, just as on the British coasts. Tetraspores were found in specimens collected in February to April; they were confined to round or oblong patches measuring at the most 1 cm in diameter. In a specimen collected in May the spots were still visible, but the sporangia were emptied. The sporangia are more or less deeply immersed in the cortex. They arise directly from cells of the inner cortex, and are thus intercalary, being outwardly connected through pits with filaments of the cortex (fig. 76). The ripe sporangium is surrounded by a double sporangial wall. The spores are paired, decussately or cruciately, the dividing walls are often inclined. The spores contain a number of small chromatophores.

The cystocarps are situated in the inner cortex, or at the limit between it and

the medulla. The carpogonial branch is five-celled, the auxiliary-cell branches are curved, and composed of a great number of short cells (fig. 77). Ripe cystocarps have been met with in March. — Antheridia have not been met with.

The species is distributed in the Skagerak, in the northern and eastern Kattegat and in the northern part of the Sound. In the Skagerak it does not attain the same dimensions as in the Kattegat, its length scarcely exceeding 30 cm, probably owing to the more agitated water. It has here only been met with at comparatively slight depths, viz. 4 to 9,4 m. In the Kattegat it is mainly distributed in the eastern part, where it has been met with almost only at depths of 16 m or



Dilsea edulis. A, six sporangia showing various forms and modes of division. 220:1. B, transverse section of cortex with a sporangium. 390:1.

Fig. 77. Dilsea edulis. A, carpogonial branch. B auxiliary-cell branch. 390:1.

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deeper, where the salinity is high and little variable and the variations of temperature are also relatively small; it attains here its greatest size. — In most localities it is taken only in small quantities in the dredge; I have found it most abundantly at Hanstholm (Sk), where it was dominant in some places at 7,5 meters depth. LVNGBVE found it off Gilleleje on the North coast of Sealand, 12 miles from land at 26 meters depth, abundantly in places where other algæ are not met with, but only *Mytili* and other molluscs, barnacles etc. It was here often fixed to the mytili and attained a size of up to 63 cm; the fishermen called it here "røde Klude" (red rags).

Localities. Sk: YT off Hanstholm lighthouse, 7,5 met., rather abundantly; Thorup Strand, washed ashore (C. M. Poulsen); Løkken, washed ashore, FK Kongshøj Grund off Lønstrup, 8,5 met.; NW of Hirshals, 30 met., some fragments (A. C. Johansen); west side of Hirshals mole, 4 met., washed ashore by Lønstrup and Hirshals, Tværsted (V. Schmidt) and Skagen. — Kn: Herthas Flak, 20—22 met., 6 cm long; Hirsholmene, 5,5—7,5 m, 6 cm long; North of Læsø (Edv. Bay), 29 cm long; IX, 11 m; TR near Trindelen, 23,5 m. — Ke: Fladen, ZF, 22,5 m, and IQ, 22—30 m; south side of Groves Flak (Børgesen);

D. K. D. Vidensk, Selsk, Skr., 7. Række, naturvidensk, og mathem. Afd. VII. 2.

IK Lille Middelgrund, 17-19 m, 61 cm; IH, south side of Lille Middelgrund, 20-28 m; ER, Fyrbanken east of Anholt, 23 m, 28 cm; IA, Store Middelgrund, 16,5 m; same locality (Børgesen); off Gilleleje, 12 miles from land (Lyngbye); Nakkehoved (Lyngbye). — Su: Washed ashore at Hellebæk (Rasch, Børgesen), 29 cm, and north of Helsingør (Steenberg, C. Rosenberg, !) 26 cm, bM, south of Hveen, 22,5 m, loose, 40 cm.

#### Fam. 5. Nemastomataceæ.

#### Platoma (Schousboe) Schmitz.

#### 1. Platoma Bairdii (Farlow) Kuckuck.

P. KUCKUCK, Beiträge zur Kenntn. d. Meeresalgen. 12. Ueber Platoma Bairdii (Farl.) Kck. — Wissensch. Meeresuntersuch. Neue Folge. V. Bd. Abt. Helgoland, Heft 3. 1912, p. 187—203. Taf. IX—XI.

Nemastoma (?) Bairdii Farlow, Proceed. Amer. Acad. Arts and Sciences, 1875, p. 351; Mar. Algæ of New England, 1881, p. 142; BATTERS, Cat. Brit. Mar. Alg., 1902, p. 94.

Helminthocladia Hudsoni Batters, Journ. of Bot. 1900, p. 377, Tab. 414 fig. 15-16, non J. Agardh.

In July 1915 I found by dredging in Lille Belt some small specimens of this interesting Alga, hitherto only recorded from three widely remote places (coast of Massachusetts, coast of Northumberland and Helgoland). As the structure and development of the species have recently been exhaustively treated by Prof. KUCKUCK, I shall only make some few remarks upon the Danish specimens, referring for the rest to KUCKUCK's excellent description.

The plant forms small bundles on a granitic pebble, each given off from a well developed basal disc, and reaching only a length of 1 cm. The upright fronds are more or less branched, rarely unbranched, terete, or the thickest fronds somewhat flattened. As shown by KUCKUCK, the frond branches by dichotomy<sup>1</sup>, but one of the shoots produced by the division often becomes more vigorous than the other, and the ramification then seems to be lateral. Hyaline hairs were not met with; according to KUCKUCK their occurrence is variable.

The plants bore either tetrasporangia or carpogonia and cystocarps, while antheridia were not met with either here or at Helgoland. The two kinds of individuals were quite distinct; no carpogonia were observed in the tetrasporiferous specimens or vice versa (comp. KUCKUCK l. c. p. 192). The emptied sporangia were frequently replaced by a sporangium produced from the subjacent cell. "Prospory"  $\mathfrak{d}$ : production of sporangia from the basal disc, was not met with in the Danish specimens.

Locality. Lb: At Lyngs Odde, right opposite Middelfart, stony bottom, about 20 meters depth.

<sup>1</sup> KUCKUCK thinks (l. c. p. 190) that the dichotomy in this plant is only apparent, as it cannot be derived from a longitudinal division of the apical cell. This, however, must be considered a too narrow definition of the conception of dichotomy. In my opinion, dichotomy exists in all cases where the growing point divides into two equal parts by a vertical dividing plane or furrow, the two parts at first diverging equally from the original direction of growth, no matter whether the growing point consists of a single cell (*Dictyola*) or of several cells (*Furcellaria, Lycopodium, Selaginella*, roots of *Isoëtes* etc.) or is a part of a coenocytic organism (*Thamnidium, Piptocephalis*).

#### Halarachnion Kützing.

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#### 1. Halarachnion ligulatum (Woodw.) Kützing.

Kützing, Phycol. gener. p. 394, Taf. 74. I; Berthold, Cryptonem. d. Golfes von Neapel, Leipzig, (1884) p. 22 (an eadem species ?); T. H. Buffham, On the Antheridia etc. of some Florideæ. Journ. of the Quekett microscop. Club, Vol. V, ser. II p. 299, tab. 14 fig. 37-39.

Ulva ligulata Woodward, Linn. Trans. III p. 54.

Halymenia ligulata (Woodw.) Agardh, Spec. Alg., 1821, p. 210; Flora Danica tab. 2199 (1836) from Helgoland; Harvey, Phyc. Brit. vol. I pl. 112, 1846; J. Agardh, Spec. g. o. Alg. II,<sub>2</sub> 1851 p. 201; Bornet et Thuret, Notes algologiques, fasc. 1, Paris 1876, p. 44 pl. XIV, XV.

I have only found a few small specimens of this species and have not submitted them to closer examination As to the structure of the frond, reference may be made to the descriptive works and the quoted figures of HARVEY, KÜTZING, BORNET and THURET, which show that the inner part of the compressed frond consists

of a slimy substance through which run widely spread medullary filaments, while the cortex is composed of two or three layers of cells. Colourless, rather thin hairs proceeding from peripheral cells were observed in specimens from Hirshals, but none in the other examined specimens. BERTHOLD (l. c. p. 7) did not observe them.

In a small specimen from Herthas Flak I found in slender shoots two filaments running to the very end of the shoot, with the two apical cells at the same level and higher than those of the other filaments (fig. 78 B). In thicker shoots such structure is not to be found; the end of the shoot seems to be composed of a greater number of equal filaments.

Sporangia have never been found in this species.

The antheridia occur in the same specimens as the carpogonia (comp. BORNET et THURET, l. c. p. 45; BERTHOLD, l. c. p. 9). They have been briefly described and figured by BUFFHAM (l. c.). According to this author they arise from "a cell which produces four male cells above, and these emit the pollinoids, which are minute." I found their arrangement less regular, their number, seen from the face, varying from 1 to 4 (fig. 78 C). As I had not occasion to examine them in transverse sections, I am not able to decide whether the small cells shown in the figure are really the antheridia (spermatangia) or possibly partly antheridia-producing cells (spermatangial mother cells after SVEDELIUS), as BUFFHAM's fig. 39 may suggest.

The carpogonial branches are 4-celled, situated on the inner side of the cortex, and bent outwards (BORNET and THURET I. c. fig. 1). According to BERTHOLD and SCHMITZ, the fertilized carpogonium gives off in various directions a number of

 $\begin{array}{c|c}
\hline \\
A \\
\hline \\
Fig. 78.
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Halarachnion ligalatum, from XJ. A and B, tips of slender shoots showing two filaments reaching the top. -C, surface of male plant. 630:1.

sporogenous filaments which fuse with the auxiliary cells occurring in great numbers on the inner side of the cortex. After the fusion the auxiliary cell produces on its inner side the gonimoblast (BORNET and THURET l. c. fig. 2—5). The ripe cystocarp is globular or somewhat lobed; it projects in the slimy medullary space (KÜTZING l. c., BORNET and THURET fig. 2—4).

The species has only been found in three localities in the northern Danish waters. The largest specimen (from TQ) is 4,5 cm long, 3 mm large. It has been found with antheridia and carpogonia in July, with cystocarps in August and September. It occurs on stony or gravelly bottom. — At Helgoland it has been found in well developed specimens, and it has been met with at Väderöarne, Bohulän.

Localities. Sk: 1 mile NW of Hirshals, 15 m. - Kn: XI, Herthas Flak, 20-22,5 m; TQ, at Trindelen light-ship.

#### Furcellaria Lamouroux.

#### 1. Furcellaria fastigiata (Hudson) Lamouroux.

- LAMOUROUX, Ann. du Mus. XX. 1813, p. 46; GREVILLE, Alg. Brit. 1830, p. 67, tab. XI; KÜTZING, Phyc. gener. 1843, p. 402, Taf. 71 (habit and anatomy); HARVEY, Phyc. Brit. I, 1846, pl. 94, III, 1851, pl. 357 (cystocarps and tetraspores); 'ARESCHOUG, Phyc. Scand. mar. 1850, p. 88, Tab. IV A; CASPARY, Observations on Furcellaria fastigiata, Huds. and Polyides rotundus Gmel. Ann. & Mag. N. Hist. Ser. 2, Vol. VI, 1850; J. AGARDH, Spec. I, 1851, p. 196; THURET, Rech. s. l. fécondation des Fucacées et des anthéridies des Algues. II. Ann. d. sc. nat. 4e sér. tome 3, 1855, p. 42 pl. 3 fig. 6-7; KÜTZING, Tab. phyc. Bd. 17, tab. 99, 1867.
- REINKE, Allgem. Botanik, 1880, p. 134 fig. 97 (longitudinal section of extremity of frond), Algenflora w. Ostsee, 1889, p. 26 (f. aegagropila); WILLE, Alg. physiolog. Anatomi, 1885, p. 55, 63, 84 ex parte, not Tafl. VIII fig. 14, Beitr. physiol. Gewebesyst., 1887, p. 86, Taf. 6 (VIII) fig. 76-78; KOLKWITZ, Beitr. z. Biol. der Florideen. Wiss. Meeresunters. N. Folge. 4. Bd. Abt. Helgoland Heft 1. 1900, p. 31, 46, fig. 4; SVEDELIUS, Stud. Östersj. hafsalgfl., 1901, p. 130; OLTMANNS, Morph. u. Biol. d. Alg. I, 1904, p. 545, fig. 329 (longitudinal section of upper end of frond and transverse section of frond); DENYS, Untersuch. an Polyides rotundus Gmel. und Furcellaria fastigiata Lamour., Beih. z. Jahrb. d. Hamburg. wissensch. Anstalten. 1910.
- Fucus fastigiatus Hudson Fl. angl. ed. 1. 1762, p. 588; Oeder, Flora Danica tab. 393, 1768 (with adventitious shoots).

Fucus furcellatus Oeder Fl. Dan. tab. 419, 1768.

Fucus lumbricalis Gmel., Hornemann, Flora Dan. tab. 1544, fig. 6, 1816 (tetrasporangia).

Furcellaria lumbricalis Lyngbye, Tent. Hydr. p. 40, tab. 40 A, 1-4.

Fastigiaria furcellata (L.) Stackhouse, Le Jolis, Liste Alg. Cherbourg, 1864, p. 124.

The mode of growth, ramification and structure of this common alga has so often been described and figured that it may be sufficient to refer to other works, adding only some supplementing remarks.

The apex of the frond consists of a great number of densely joined cell-filaments which are parallel and vertical in the middle, becoming gradually more divergent towards the periphery. ("Springbrunnentypus" of OLTMANNS). The central filaments continue downwards in long longitudinal filaments, which constitute an essential part of the medulla, while the more peripheral ones gradually develop into the cortex, which consists of radiating, dichotomously branched filaments. The outer small cells form an assimilatory tissue; the cells of the inner cortex are much larger, containing also several bandlike and ramified chromatophores, but the total mass of these bodies is small compared with the volume of the cell. WILLE mentions these cells as store-cells, "Speicherzellen" (1887 p. 87), as floridean starch is stored in great quantity in them. These cells are connected with each other by small pits.

The cell-rows of the cortex depart from the longitudinal filaments of the central tissue, which consists not only of these filaments but also of irregular hyphæ origi-

nating as outgrowths from the barrel-shaped cells of the inner cortex (fig. 79). The difference between these two kinds of filaments in the medulla has already been remarked by older authors as **KÜTZING and CASPARY:** WILLE on the other hand (1885 and 1887) only refers to the secondary hyphæ but not to the primary longitudinal filaments<sup>1</sup>. The difference is conspicuous, the longitudinal filaments running very regularly and consisting of long cylindrical cells connected with large pits, while



Fig. 79.

*Furcellaria fastigiata.* A, transverse section of frond, at the limit between the medulla and the inner cortex. B, longitudinal section of the same. c, inner cortical cells; l, longitudinal filaments; h, hyphæ. After living material, April. (190:1).

the hyphæ run irregularly, though chiefly in a transversal direction, and are composed of more heterogenous cells, those of the proximal part being more or less inflated, while the cells of the distal part are cylindrical. The cells of the hyphæ contain narrow, partly branched chromatophores. In the longitudinal filaments I did not observe any chromatophores, but DENYS (l. c. p. 10) states that their cells contain colourless ones. This author states that the hyphæ are given off from the longitudinal filaments<sup>2</sup>; it is possible that they may also be produced by these.

<sup>1</sup> For illustration of the anatomical structure of this species WILLE gives only a copy of a figure by KÜTZING (Phycol. gener. tab. 72 fig. 6; WILLE Taf. VIII fig. 14), representing *Furcellaria lumbrialis*; but this is identical with *Polyides rotundus*, which differs from Furcellaria just in the structure of the medulla. OLTMANNS makes the same error (1904 p. 546 fig. 330).

<sup>2</sup> DENYS calls the longitudinal filaments "Längshyphen," but incorrectly, as these filaments have not the active apical growth combined with slipping growth ("gleitendesWachsthum") characteristic of the hyphæ.



Fig. 80. Furcellaria fastigiata. Adventitious shoot in longitudinal section. 95:1.

though I have not observed it, but when DENYS says that they "schliessen nach kürzerem oder längerem Verlauf an die inneren Zellen der mittleren Rinde" (l. c. p. 10) he must have misinterpreted the facts observed. WILLE's statement (1887, p. 87) that these cells "mit einander sowohl als auch mit den Speicherungszellen durch Poren in Verbindung treten" might be understood as if the pits were secondary, whereas in reality they are primary. Whether secondary pits may be formed between the hyphæ, or between these and other cells, I have not observed. — In late summer, autumn and winter these cells are rich in starch. As to the starch compare for the rest Kolkwitz (l. c.). All the vegetative cells contain a single nucleus. Hairs are never produced.

As to the stolons reference may be made to the descriptive works and to KOLKWITZ (l. c. p. 46) and DENYS (l. c. p. 8).

The erect fronds are, as is well known, branched by dichotomy, but besides this normal ramification adventitious branches sometimes occur, especially in the inner Danish waters (Sa, Sf, Sb, Su, Bw) (Flor. Dan. tab. 393). They originate from a little group of superficial cells. In developing they increase early in thickness so that their basal plane is much larger than their plane of insertion (fig. 80). They may be very mumerous, as for instance in some specimens dredged in January in Store Belt (NU, no. 4250) at 11 meters depth, the shoots of which were, for a length of one to three cm or longer, more or less densely beset with very short adven-

titious shoots; some older shoots of this kind had again produced adventitious buds. The cause determining the appearance of these shoots is unknown; the plants producing them may be fertile. Another sort of adventitions shoots develop from the scars arising from the decaying and falling off of the fructifying parts of the shoots (fig. 81, comp. HARVEY,



Fig. 81. Furcellaria fastigiala. Adventitious shoots growing out from scars. Hirshals June. 1,5:1.

Phyc. Brit. Plate 94). As shown by CASPARY (l. c. p. 93, fig. 10) this regeneration can be once or twice repeated.

The reproductive organs are produced in the upper part of the fronds; their development begins at the end of the summer or in the beginning of the autumn. In August very young sporangia may be found



*Furcellaria fastigiata*. *A*, young sporangia in transverse section of frond, August. 220:1. *B*, ripe sporangium. 230:1. in the inflated ends of the frond. They appear as small cells cut off from the outer end of the large cells of the inner cortex, and differ from these by the want of starch, by the higher staining power in presence of hæmatoxyline, and in containing a large, intensily staining nucleus (fig. 82 A). The sporangia increase in September and October; in November specimens with undivided and divided sporangia may be met with. In December the sporangia are always ripe; at the end of



Fig. 83.

Furcellaria fastigiata. A, part of frond with emptied tetrasporangia, December. B and C, parts of fronds with ripe cystocarps, December. D, part of frond with antheridia, March. Nat. size.

December and in January they are often emptied, but in February many sporangia containing spores are still to be found. As is well known, the sporangia are oblong and "zonate"  $\mathfrak{d}$ : divided by parallel walls; the spores contain numerous small chromatophores (fig. 82 B). The parts of the frond producing tetrasporangia are somewhat inflated, fusiform; after the exhaustion of the spores they are a little more inflated, soft and green, while the other parts of the frond in winter are dark red-brown. The upper tip of the frond sometimes remains sterile and therefore retains its dark colour. Downwards the fertile part is sharply marked off from the sterile frond and loosens here in decaying during the winter (fig. 83 A).

The antheridia cover the surface of small terminal inflated segments of the frond; which are about 1 cm long, of a pale rose colour (fig. 83 D). They are given off



Fig. 84. Furcellaria fastigiata. Transverse sections of antheridiabearing fronds, Decemb. 835:1. from small cells, not infrequently smaller than themselves. In a transverse section of the frond these androphorecells, which seem to contain chromatophores, are seen bearing two antheridial cells of different age. Probably they may sometimes bear more than two, and the production of antheridia may possibly be continued after the first has been exhausted. The antheridia always occur in particular male plants; they were first described

and figured by THURET in 1855. Fully developed antheridia have been met with in December, but they may probably occur much earlier. Antheridia containing ripe spermatia have further been found in January to March, and in May I have still found spe-



Furcellaria fastigiata, Carpogonial branches. A and B, two-celled, C and D, 3- and 4-celled. In D, the carpogonium has produced an outgrowth (sporogenous filament?) at the base, although the trichogyne is very short and unfertilized. A, September, 230:1, B-D, August, 390:1.

moblasts may already be met with. The carpogonial branches arise in the inner cortex or at the limit between the cortex and the central tissue; they are frequently placed in small groups, and two or three

cimens with white antheridial branches containing numerous spermatia (no. 5793, UL, Øjet, in Bw, 20 meters depth).

The carpogonia appear at the end of the summer, and in August young goni-



of them may be given off from one of the large storage cells. They are almost always twoor three-celled. The inferior cells of the carpogonial branches are globular or ovate, they contain one or two nuclei, small chromatophores and numerous small starch grains. The carpogonium is much narrowed over the basal part, the narrowing being deepest on one

*Furcellaria fastigiata*, sections of fronds with young cystocarps, August. *a*, auxiliary cell; *s*, sporogenous filaments, *g*, gonimoblast. 210:1.

side (fig. 85 *B*). I cannot give any details about the contents of the carpogonium, as on staining with hæmatoxyline it was in a great part very dark and intransparent. In the specimens collected in August and September numerous carpogonia with short trichogynes were found; other carpogonia had long trichogynes making their way outwards through the cortex, and tips of trichogynes protruding through the surface of the frond were also met with, but I have not yet seen spermatia fixed to them, and it remains thus to state whether fertilization takes place normally or the cystocarp may develop parthenogenetically, as in *Platoma Bairdii*. The car-



Furcellaria fastigiata. Sections of frond with young cystocarps. c, carpogonia; a, auxiliary cells; g, gominoblasts. September. A 180:1. B 190:1.

pogonium shown in fig. 85 D seems to agree with the latter assumption, as an outgrowth is given off from the base of the carpogonium, while the trichogyne is very short and unfertilized.

The auxiliary cells (a in the figs.) arise, as stated by SCHMITZ (Engler u. Prantl, p. 526), from single cells in the inner cortex which seem to be at first but little different from the vegetative cells. They fuse with the long sporogenous filaments produced by the carpogonia and growing widely between the inner cortical cells and the medullary filaments. The fusion takes place at the inner end of the cell. After the fusion the auxiliary cell soon begins to produce gonimoblast cells laterally and at the inner side, and thus young cystocarps may occur already in August (fig. 86). The auxiliary cell after fertilization contains a number of nuclei, four or more, some of which certainly derive from the original nucleus of the cell, while the others are sporogenous (fig. 86 A, 87). The cell increases in volume and takes a more irregular outline. Fusions between neighbouring cortical cells seem to occur (fig. 87).

D. K. D. Vidensk. Selsk. Skr., 7. Række, naturvidensk. og mathem. Afd. VII. 2.

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Furcellaria fastigiala. Section of young cystocarp. At right several carpogonia. s, sporogenous filaments. The cells of the young cystocarp contain minute starch grains while those of the surrounding cells are much larger. August. (200 : 1).

I have also in the same specimens observed the production of small cells at the under end of the large cells of the inner cortex, resembling the formation of secondary pits in the Rhodomelaceæ, but what their significance may be I do not know. The cortical cells situated outside the auxiliary cells have richer contents and stain deeper with hæmatoxyline than the others, forming thus a darker stripe towards the surface (fig. 86 B). The ripe cystocarp appears as a globular heap of carpospore cells, grouped around the auxiliary cell or containing in the centre also a few other sterile cells. The particular gonimolobes are usually not distinguishable. At the periphery of the cystocarp some long cells are frequently found forming an incomplete envelope around it, as shown by ARE-SCHOUG and CASPARY, Il. cc. At the time of ripening a pore is formed in the cortex through which the spores are exhausted. This pore arises by

destruction of the cells of the darker stripe mentioned above. The fructiferous part of the female fronds is more or less inflated, almost as in the sporangia-bearing ones, but the upper part of the fronds frequently remains sterile; this part may be 1 to 2 cm long and branched (fig. 83 C).

Germinating spores of what must be supposed to be *Furcellaria fastigiata* are frequently met with on various Algæ, as *Delesseria*, *Phyllophora* a. o. They are at first hemispherical, and are divided by rather regular anticlinal and periclinal walls



Furcellaria fastigiata. A, germinating spores, seen from above and from the side. B, older stage showing a cylindric shoot growing out from the hemispherial body. without changing form, but increasing in size (fig. 89 A). Later on, a cylindric upright shoot of the typical structure is produced from this hemispherical body, the shoot being a little narrower as the basal part (fig. 89 B). These shoots later branch and produce rhizomes at their base.

This Alga is one of the commonest and most widely distributed in the Danish waters. It attains its highest degree of development in the Kattegat and the Belts, where it becomes up to 28 cm high. In the western Baltic it attains a length of 24,5 cm, whereas at Bornholm I have not found it higher than 9 cm. In the inner Baltic Sea Svedelius found it scarcely more than 10 cm high. He refers the plants here found to f. minor

Agardh, a form differing only by smaller dimensions, in citing Fl. Dan. tab. 393 and ARESCHOUG, Alg. Scand. exs. No. 257. In the most feebly developed specimens the erect shoots are not branched, or but little so (fig. 90). — Furcellaria grows usually on stones or pebbles, but may also be found fixed on other Algæ, as Phyllophora, Chondrus. In some places north of Fyn (especially aZ, near Fyns Hoved) it was found growing in company with other, mostly loose, Algæ forming a dense cover over the bottom, which consisted of coarse sand.

I am not certain whether these specimens were at



Furcellaria fastigiata. Plants from the Baltic Sea off Gudhjem, Bornholm. Nat. size.

first loose or originally fixed at this stationary bottom. In other places detached specimens lying loose on the bottom are met with, often in great quantities, particularly in fjords, as Limfjorden, but also in the Kattegat, e. g. around Anholt. It is apparently able to live long in this condition, for plants in which the under part is in a state of disorganization are often met with. Some of these plants are not much different from the normal ones; in other cases they are more branched, and form globular bushes corresponding to those mentioned by REINKE (1889) and SVEDELIUS as f. *æqaqropila* (fig. 91).

The species has been found in depths from 2 to 28 meters and once in 38 m depth (near Bornholm). It is often a predominant element of the vegetation, particularly in depths of 4 to 15 m. It is perennial, but the fructifying shoots are shed in winter. In sunny localities the upper parts of the fronds are green in summer.

Localities. Ns: Only found at ZQ, jydske Rev, 24,5 m and at



Fig. 91. Furcellaria fastigiata ægagropila. From Guldborgsund. Nat. size.

Ørhage by Klitmøller inside the point at 2 meters depth, farther from land off Klitmøller only a few small specimens. - Sk: Collected at various places (Hanstholm; Bragerne; washed ashore by Svinkløv and Blokhus; Lønstrup; Hirshals; Skagen) in 2 to 13 m depth, in most of the places only in small and scarce specimens. Found in greatest number and best developed at Hirshals, near land in 5 m depth, in company with Polyides. Greatest length observed 15 cm. - Lf: Widely distributed, down to a depth of 6,5 m, but in most places loose, often in abundance on soft bottom (f. ægagropila). Reaches a length of 8-14 cm. - Kattegat: Common and often abundant everywhere on stony bottom in depths down to 15 cm. It reaches here a length of up to 28 cm and is very often over 20 cm high. It has also been dredged in several places in greater depths, down to 30 m (e. g. ZB, Trindelen, about 30 m; ZS, Fladen, 26,5 m; HZ, Store Middelgrund, 25,5 m), but it is more frequently missing than present in these greater depths, and, at all events, it occurs only in small quantities. In Herthas Flak in Kn, where I have dredged several times in 20 to 24,5 meters depth, it has never been met with. In Isefjord it has been recorded in various places, in Holbæk Fjord it occurs abundantly in a loose condition. — Sa and Lb: Common in depths down to 24 m; at aZ growing gregariously over coarse sand (see above). - Sf: Several places. - Sb: Common in depths down to 20 m, greatest length observed 27 cm; generally well developed specimens. - Sm: Several places down to 12 m depth; greatest length observed 10,5 cm -Su: North of Helsingør up to 25 cm high, south of Helsingør in depths down to 13 m, up to 16 cm high. — Bw: Found in depths down to 20 m; greatest length observed 24,5 cm. — Bm: Greatest length observed 12 cm. - Bb: Found in depths from one to 38 m (YA, east of Bornholm) in several places, but reaching only 9 cm in length.

#### Fam. 6. Rhizophyllidaceæ.

#### Polyides Agardh.

#### 1. Polyides rotundus (Gmel.) Grev.

Greville, Algæ Britann., 1830, p. 70, Tab. XI. Harvey, Phycol. Brit. pl. 95, 1840. Caspary, Ann. and Mag. N. Hist. Ser. 2, Vol. VI, 1850, p. 93. Thuret in Le Jolis Liste des Alg. mar. de Cherbourg, 1864, p. 140. Thuret et Bornet, Etudes phycologiques, 1878, p. 73-80, pl. 37-39. Guignard, Développ. et const. des anthérozoïdes. Revue gén. de Botanique. I, 1889, extrait p. 44, pl. 6 fig. 10-12. Fr. Schmitz, Kleinere Beitr. z. Kenntn. d. Florideen. II. La Nuova Notarisia. Ser. IV. 1893, Estratto p. 8. Kolkwitz, Beitr. z. Kenntn. d. Florideen. Wiss. Meeresunters. N. F. 4. Bd. Abt. Helgoland. Heft 1, 1900. Denys, Anatom. Untersuch. an Polyides rotundus Gmel. und Furcellaria fastigiata Lamour. Beih. z. Jahrb. d. Hamburg. wissensch. Anstalten 1910.

Fucus rotundus Gmelin, Hist. Fucor., 1768, p. 110 tab. VI fig. 3. Flora Danica tab. 1544 a (Hornemann 1816). Furcellaria rotunda Lyngbye, Tent. Hydr., 1819, p. 49.

Polyides lumbricalis C. Agardh, Spec. Alg., 1822, p. 392, J. Agardh, Sp. g. o. II, 1863, p. 721.

Furcellaria lumbricalis Kützing, Phycol. gener., 1843, p. 402, Taf. 72, Tab. phycol., Bd. 17, 1867, pl. 100.

The external resemblance between this Alga and *Furcellaria* is well known and has often been mentioned, as well as the difference of the basal part being a disc in *Polyides*, while in *Furcellaria* it consists of branched rhizomes. The structure of the erect frond has already been thoroughly studied by  $K\"umute{u}$ TZING (1843)<sup>1</sup> and CASPARY (1850). The structure of the upper end of the frond is that of the fountain type (Oltmanns' "Springbrunnentypus") as plainly shown by  $K\"umute{u}$ TZING (l. c.). As to the structure of the erect fronds, reference may be made to the papers of

<sup>1</sup> The troublesome synonymy of this Alga is responsible for the fact that WILLE (Bidr. t. Alg. phys. Anat. K. Svenska Vetensk. Ak. Handl. Bd. 21. 1885, tafl. VIII fig. 14) and OLTMANNS (1904, p. 546, fig. 330) have used copies of KÜTZING's figures of it to demonstrate the anatomy of *Furcellaria fastigiata* (comp. p. 165).

KÜTZING, CASPARY, THURET (1878, p. 75, pl. 37, fig. 6) and DENYS. The outer cortex consists of a greater number of layers of small cells (up to 4 or 5) than in Furcellaria. The longitudinal filaments of the central tissue are mostly thicker at the ends than in the middle "so that they have the form of a femur" (CASPARY, p. 94). The cells which form the connection between these filaments and the cortical ones are arranged in regular feebly curved rows running obliquely upwards, while secondary hyphæ are wanting<sup>1</sup>. Hyaline hairs produced by superficial cortical cells may occur, according to THURET (1878, p. 75, pl. 37, fig. 6). I have not observed these hairs, but in specimens collected in April I found that some of the peripheral cells were colourless, narrower and longer than the others; probably they were about to develop into such hairs. As to the cell-structure, reference may be made to the paper of DENYS. The pit in the transverse wall between the cortical cells is very narrow, while that of the longitudinal filaments is broad, and provided with a double plate. Secondary pits do not occur. The structure of the basal disc has been figured by KÜTZING (1843); according to KOLKWITZ (1900, p. 51) older discs are stratified.

The tetrasporangia arise at about the limit between the outer and inner cortex (comp. CASPARY, 1850, fig. 21, THURET, 1878, pl. 36, fig. 6 and 7). As shown by THURET, an issue is formed outwards to each sporangium by removal of the cells from each other, through which issue the contents of the sporangium is emptied. Specimens with undivided sporangia have been met with in October, with ripe sporangia in January and with emptied sporangia in April.

The antheridia arise, as shown by THURET, in nemathecia in particular individuals. According to GUIGNARD (1889, p. 44, pl. 6, fig. 10—12) they are placed in tetrads directly on the nemathecial filaments, while SCHMITZ asserts (1893, p. 8) that they are situated on short cells given off from the filaments. I cannot give any information on this point, as I have not met with male plants in the Danish waters.

As to the structure and development of the female nemathecia, reference may be made to the classical researches of THURET and BORNET (1878, p. 77-80, pl. 38-39). These bodies begin to develop in the Danish waters in August or September. In specimens dredged at the entrance to Vejle Fjord, August 20<sup>th</sup>, nemathecia with well developed but unfertilized carpogonia were found. Similar carpogonia but also others with fertilized carpogonia are frequently met with in September. Ripe cystocarpia were found in December and January. After the exhaustion of the carpospores, the nemathecia are thrown off, while the fronds which have produced them possibly may continue growing. — The germination of the carpospores has been observed by THURET et BORNET (1878, p. 79, pl. 39, fig. 32); they obtained hemispherical bodies producing rhizoids from their under face.

<sup>1</sup> DENYS speaks (l. c. p. 7) of "Querhyphen, welche die Masse der längs verlaufenden durchflechten und seltener auch zwischen die Elemente der grosszelligen Rinde eindringen". But as he designates the longitudinal filaments also as "Hyphen". it is not clear if it is a case of real hyphæ or only of the above named connecting filaments. As he says, on p. 18, that they occur only "ganz vereinzelt", it seems that he has really observed secondary hyphæ, although in very small number. This species is only little variable in shape and size. It often reaches a length of 14 cm, even in the Baltic, almost to the limit of its distribution. The largest specimens, 18 cm high, were found in the Skagerak and the South Fyen waters. The depth has no influence on its size, save that when growing at low-water mark it does not become longer than 6 cm. The greatest length is reached in 5,5 to 9,5 meters depth. Adventitious shoots from scars left by decayed ends of frond frequently occur, as in *Furcellaria*, but rarely developing from the surface of the frond.

The species grows on stones, but is frequently met with loose on the bottom, particularly in the Zostera formation, but also on bare sandy bottom, as for instance around Anholt, where it occurs in great quantities together with *Furcellaria fastigiata*. It occurs in all the Danish waters, with exception of the eastern Kattegat and the Baltic around Bornholm, from a little below low-water mark to about 11 meters depth. In greater depths it occurs more rarely; certainly it has been found in several places down to 23,5 m depth, but in most cases it was certainly or probably loose. As sure deeper localities may be named, in the Skagerak: off Hanstholm and Lønstrup, 13 m; and in the Kattegat: Tønneberg Banke, 16 m. It does not thrive in fjords; in the Limfjord it has however been found in one locality.

Specimens with tetraspores seem to occur much more rarely than sexual specimens in the Danish waters; I have met them only in one locality in the Skagerak and in two in the northern Kattegat, while female specimens have been found in several places from the Skagerak to the Baltic.

Localities. Ns: Ørhage, 2 m. — Sk: Hanstholm, 5,5 to 13 m, abundantly in 13 m depth; washed ashore by Blokhus and Svinekløv (P. Petersen); off Lønstrup 8,5-13 m, most well developed in 8,5 m depth; Hirshals, near land 1-4,5 m, in some places dominant. — Lf: Only found on the mole of Lemvig, 6 cm long. — Kn: Harbour of Skagen; Hirsholmene; Krageskovs Rev; Frederikshavn; N. Rønner 1-5,5 m; several places north of Læsø, 2-9,5 m; Trindelen, about 18,5 m; Tønneberg Banke, 16 m. — Km: NE, NW of Fornæs; around Anholt, abundantly loose. — Ks: Hesselø (Lyngbye). — Sa: PN (Kaløvig); PE (Refsnæs); Hofmansgave (Hofman Bang, J. Vahl, C. Rosenberg): OA (Æbelø). — Lb: AX (Bjørnsknude), 9,5 m; Middelfart (Rasch, !); Fænø Sund, 1 m; DF; CC; DB; UX. At several places it reaches a length of 18 cm. — Sf: CU. — Sb: GQ; harbour of Kerteminde; DO; Y; UR. — Su: North of Helsingør (Liebman, Joh. Lange, !); Taarbæk Rev; RK; PS, off Charlottenlund. — Bw: UY<sup>1</sup>, 18 m, probably loose. LC (Gulstav); South of Nysted. — Bm: QM (Juels Grund); washed ashore at Stevns.

#### Fam. 7. Squamariaceæ.

#### Petrocelis J. Agardh,

#### 1. Petrocelis Hennedyi (Harvey) Batters.

Batters in Holmes Alg. Brit. Exsice. No. 89 (non vidi), Mar. Alg. Berw. Tweed, 1889, p. 94, tab. XI, fig. 3-4.

Actinococcus Hennedyi Harvey, Natural History Review, Vol. 4, 1857, p. 202, pl. 13A, fig. 1 (non vidi). Cruoria pellita Lyngbye Hydroph. 1819, p. 193, tab. 66 ex parte, teste specim.

Chætophora pellita Flora Dan. tab. 1728, 1821.

Petrocelis Ruprechtii Hauck Meeresalg. 1883, p. 30.

The species forms dark-red fleshy crusts, in a dried state glossy, 1-3 cm in diameter. The basal layer is a monostromatic disc composed of radiating filaments.

The margin is somewhat lobed, and the filaments of the basal layer radiate towards the border of the lobes (fig. 92 A). When the surface of the substratum is uneven, small rudimentary rhizoid cells may be given off from the basal layer (fig. 92 C). Fusions between the cells of this layer have not been met with. The upright filaments which are given off from the acroscopic end of the cells in the basal layer are decumbent at the base, so that there often seem to be more than one layer of basal cells. At the border the filaments are directed obliquely forwards. The upright filaments have almost the same thickness in the upper and the lower part



Petrocelis Hennedyi. A, basal layer seen from the under face (230:1). B, vertical section of border of frond. C, vertical section of older part of frond. B and C 330:1.

of the crust; in the upper part they are  $4-6 \mu$  thick. They are imbedded in a glutinous intercellular substance which swells greatly in fresh water, whereby the filaments are separated. The upper end of the filaments is nearly always a little attenuated, the uppermost cell usually being narrower than the other, and more or less conical, or the upper part of the filament is gradually tapering (fig. 95). In some cases, however, particularly in thin crusts, I found the filaments of the same thickness to the very end (fig. 96). The cells are usually twice or thrice as long as broad, they contain a nucleus and a cap-shaped chromatophore with more or less lobed border; in a specimen examined in July the cells contained numerous small starch grains. The upright filaments are simple or little branched. The ramification is lateral, subdichotomous or sometimes sympodial; the latter reminds one of the false ramification of the Cyanophyceæ, the penultimate cell growing out and throwing aside the apical cell, which does not usually develop further. In fig. 93 *B* the wall of the outgrowing cell is seen to have been burst. Hyaline

hairs are sometimes found given off from intercalary cells in the vertical filaments. The cells producing them are usually more or less projecting, but the hairs are feebly developed; they do not ordinarily reach the surface of the frond, and soon



Fig. 93. Petrocelis Hennedyi, from the Limfjord (ZY), showing peculiar ramifications of vertical filaments. 390:1. decay. Once only have I seen a few such hairs projecting over the surface, as in fig. 94 E where the hair, however, is terminal on a one-celled branchlet<sup>1</sup>. — The crusts may certainly reach an age of more than one year. In crusts growing on stems of *Laminaria hyperborea* a stratification is often visible which seems to be due to the cessation of the growth in winter; in the part of the crust beneath the limitating line empty or abortive fructifications may be found, while new fructifications have not yet been produced in the upper part of the frond apparently formed after the hibernal rest.

Characteristic of the genus are the intercalary sporangia. In this species there are as a rule several consecutively in the same filament, in Danish specimens frequently six at least in a row, but there may be up to nine. The row is never interrupted by sterile cells. The sporangia are situated in the upper part of the vertical filaments, only the (1-) 2-5 uppermost cells being sterile. The sporangiferous vertical filaments are usually unbranched, but sometimes a branch is given off, rarely from the articles transformed into sporangia, more frequently from the cell subjacent to the sporangial series (fig. 95). The sporangia are first divided by an inclined transverse wall and then by two walls perpendicular to the wall first formed. The latter are frequently parallel, but the lines of intersection with the transverse wall do not coincide. These seriate sporangia



Petrocelis Hennedyi. Vertical filaments with hyaline hairs. A-C from Begtrup Vig; in C the hairs have been thrown off, the chromatophore of the cells is visible. D-Efrom Hellebæk, E after a living plant with a well developed hair at the top of a unicellular branchlet. A-D, 400:1; E, c. 200:1. are of about the same height as breadth, 14–17  $\mu$  broad, 16–23  $\mu$  high.

In most of the crusts only seriate sporangia are present; but in some cases the sporangia were single or at most two in a series. These sporangia are more lengthened than the seriate ones. A transitional case is shown in fig. 95 D, where the series contains only two sporangia. But in fig. 95 G and H single, terminal or subterminal sporangia are represented. In fig. 95 H the sporangium seems to be terminal, but I cannot assert that there has not been one or more sterile cells which may be decayed or possibly removed by the preparation. Similar sporangia were found in a thin crust with the ends of the filaments truncate; fig. 96 shows

<sup>1</sup> Comp. L. KOLDERUP ROSENVINGE, Hyaline hairs (Biol. Arbejder, tilegn. E. Warming, 1911, p. 206).

at left a sporangium with a single small sterile cell at the top and at right an apparently terminal sporangium. There is no doubt that the sporangia here mentioned are transformed cells of the filaments in which they are situated; this is

more doubtful in the case represented in fig. 95 I, where the sporangium has the appearance of being lateral, but as it has been found in the same crust as those figured in fig. 95 F-H, it must be supposed that it has really been terminal. The single sporangia are 2 to 3 times as long as broad,  $26-50 \mu$  long,  $11-14 \mu$ broad. Their great length depends probably on their terminal or subterminal place, which permits them to develop unhindered by sporangia or sterile cells lying above. In some crusts only such lengthened sporangia, singly or in pairs, are found; in others they are found in company with the ordinary seriate ones, as a rule, however, in different parts of the frond. By this fact it is shown that the two kinds of sporangia really belong to the same species. Single sporangia have been met with in three places in spring (Ks: Hastens Grund; Sa: Rønnen in Begtrup Vig and Lb: off Middelfart).

There is no resemblance between the single sporangia of this species and those of *Petrocelis cruenta* J. Ag., which are strictly intercalary and globular (comp. LE JOLIS Alg. mar. Cherb. pl. III, fig. 4).

In specimens gathered in November in the Great Belt I have found spores germinating in the seriate sporangia (fig. 95 E). The spores were divided by variously orientated walls and some of the uppermost resulting cells were growing out upwards into filaments.

The antheridia arise in the upper part of the vertical filaments, where they form small lateral bushes, rather similar



Petrocelis Hennedyi. Vertical filaments with tetrasporangia. A, six still undivided sporangia, November B and C, ripe sporangia, July. D, filament with two sporangia only, April. E, tetraspores germinating in the sporangia, April. F-I, from Begtrup Vig, May, F with seriate sporangia, G with subterminal, H and I apparently with terminal sporangia (in I possibly lateral?). A, D, E, G, H 390:1 B, C, F, I, 300:1.

form small lateral bushes, rather similar to those of *Cruoria*. They are borne on the upper end of small, usually unicellular, more rarely bicellular, branchlets, two

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Fig. 96. Petrocelis Hennedyi, thin crust from Lillebelt, March. Vertical filaments with truncate end-cell. Sporangia subterminal or terminal.

▶ 390.:1.].

or three on the same stalk (fig. 97). Sometimes they appear to be produced directly from a cell of the vertical filament.

The carpogonial branches are situated laterally on the vertical filaments. They are somewhat variable in shape and number of cells. Usually they are two-celled, and the undermost cell then frequently projects considerably downwards beyond the insertion point (fig. 99 A).

Fig. 97. Petrocelis Hennedyi, from the North Sea (Klitmøller), August. Vertical filaments with antheridia. 390:1.

More rarely the carpogonial filament is 3-(or 4-)celled. A carpogonium situated directly on the vertical filament was also met with, but the cell from which it was given off had in this case the character of the cells of carpogonial branches (fig. 98 *A*), its contents being more homogenous and staining more intensely by



Petrocelis Hennedyi, from Bornholm, July. A, carpogonium situated directly on the vertical filament. B-D, two-celled carpogonial branches; in B and D the supporting cell has the same character as those of the carpogonial branch. E, carpogonial branch with short sporogenous filaments given off from the carpogonium and the subjacent cell. F, carpogonial branch producing (sporogenous?) filaments. G, vertical filament with two larger cells, one of which bears a hyaline hair. H, vertical filament with a presumed auxiliary cell with scar after a decayed hair. I and K, auxiliary cells in contact with sporogenous filaments. L, probably young gonimoblast. A-E and L, 630:1 F-K 390;1. hæmatoxyline than the ordinary cells. This may also sometimes be the case with the cell bearing 2-celled carpogonial branches (fig. 98 B). The cell bearing a carpogonial branch is frequently swollen, resembling the auxiliary cells.

The auxiliary cells arise from single cells in the vertical filaments. which become somewhat swollen and more susceptible to colouring matter. They appear to arise in some cases from cells having produced a hair (fig. 98 G, H). The development of the cystocarps has not been followed; I have only observed a few stages succeeding the presumed

fertilization<sup>1</sup>. Sporogenous filaments are found given off not only from the carpogonium but also from other cells in the carpogonial branch; in the latter case, however, fusion between these cells and the carpogonium could not always be discerned, as for instance in fig. 98 E, where two young sporogenous filaments are seen projecting from the carpogonium and the subjacent cell. Older stages are shown in fig. 99 C and E; in C the filaments causing the fusion between the cells

of the carpogonial branch are easily visible. The sporogenous filaments are here seen growing out in a horizontal direction from the carpogonial branches. Fig. 98 I, K show auxiliary cells in contact with sporogenous filaments, and fig. 99 G represents probably the same after the fusion. The stages shown in figs. 99 D and 98 L are probably young gonimoblasts, though sporogenous filaments are not visible. Ripe cystocarps are shown in figs. 99 H, I; they consist, as shown by Batters (l. c. pl. XI, fig. 4), of an almost spindle-shaped heap of carpospores which easily segregate on preparation. The spores are 14 to 17 µ in diameter.

The species has been found in almost all the Danish waters, in depths of 1 to 19 meters. It grows on stones and shells of *Mytilus edulis* and *Littorina littorea*, often in company with incrusting *Lithothamnia* and growing over them. In the North Sea and Skagerak it has principally been found growing on the stem of *Laminaria* 



#### Fig. 99.

Petrocelis Hennedyı. A, two-celled carpogonial branch, January. B-D, Begtrup Vig, May. B, three-celled carpogonial branch, unfertilized. C, carpogonial branch after fertilization (?), giving off sporogenous filaments. D, young gonimoblast arising from an auxiliary cell (?). E, carpogonial branch giving off three sporogenous filaments (Skagerak, April). F-G, Hellebæk, July. F, carpogonial branch giving off sporogenous filaments. G, presumed auxiliary cell fused with a sporogenous filament. H, cystocarp, not fully developed, Lysegrund, May. I, ripe cystocarp, Storebelt, January. A, H 300:1. B-G 390:1. I 230:1.

hyperborea. The sporangia begin their development as a rule in the autumn; they were found undivided in September and November, ripe in January to July, emptied or abortive in June to September and November. But young sporangia

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<sup>&</sup>lt;sup>1</sup> Spermatia have not been found adhering to the trichogynes, and in some cases carpogonia having produced sporogenous filaments show no interruption of the protoplasm over the ventral part (fig. 98 E, 99 E) which might suggest a parthenogenetic development of the cystocarp.

were also met with in July. The antheridia have only been met with in particular male specimens from the North Sea and the Limfjord, collected in August, and a cystocarp-bearing specimen from Lillebelt collected in July also appeared to bear emptied antheridia. The cystocarps develop, as it seems, at about the same seasons as the tetrasporangia. They have been found ripe in January, May and June, emptied or degenerated in August. The carpogonia seem to arise at various seasons. In specimens collected in November I have found very young carpogonia still without trichogynes, but in crusts collected at Bornholm in July carpogonia with long trichogynes, partly also with sporogenous filaments, were met with (fig. 98), and unfertilized and fertilized carpogonia (at all events producing sporogenous filaments) have also been found in spring. In some cases sporangia and cystocarps have been found in the same crust.

Localities. Ns: Klitmøller, on the stem of Laminaria hyperborea washed ashore; Hanstholm (YU), 2 meters. — Sk: 4 miles N<sup>1</sup>/4E of Svinkløv beacon (A. C. Johansen); Løkken, on Lam. hyp. on the shore; off Lønstrup, about 9 m; off Hirshals, on Lam. hyp. — Lf: Nissum Bredning off Helligsø, 6 m (C. H. Ostenfeld); at Mullerne (ZY), 4,5 m; Søndre Røn near Lemvig; Holmtunge Tange (MK). — Kn: Krageskov Rev (TV). — Ke: JO, Fladen; OO, Søborghoved Grund, 8,5 m. — Km: XC, NW of Anholt. — Ks: OS, OS<sup>1</sup>, Hastens Grund, 14—16 m; HQ, Lysegrund; EJ, entrance to Isefjord. — Sa: GD, near Sejerø; FS, Vejrø Sund; Rønnen in Begtrup Vig, 1 m; North side of Refsnæs Reef, 13 m, (Ostenfeld); DK, Bolsaxen; MQ, South of Paludans Flak, 12 m; Halsgab near Hofmansgave, "in saxis maris Hindsholm" (Lyngbye, Hofman Bang); DJ, east of Æbelø. — Lb: FZ, Kasserodde, 6,5 m; North of Fænø Kalv; off Middelfart, about 15 m. — Sb: Stavreshoved; GP, Halskov Reef; NN, SW of Sprogø, 19 m; Avernakhage near Nyborg, 2 m; GZ, north of Egholm; DN, Vengeance Grund; near Vresen (Ostenfeld); DP, north of Onsevig. — Su: BQ, off Ellekilde, Ellekilde Hage, 11 m; North of Lappegrund, about 20 m (H. E. Petersen). — Bw: DU, off Dimesodde, 11 m. — Bm: QQ, off Rødvig. — Bb: YG, Arnager Rev, 7 m.

#### Cruoria (Fries).

#### 1. Cruoria pellita (Lyngb.) Fries, Areschoug.

El. Fries, Corpus florar. prov. Suec. I. 1835, p. 317; J. E. Areschoug, Algarum pug. sec. Linnæa, Vol. 17, p. 267, tab. IX fig, 6-8, 1843, ex parte, Phyceæ scand. mar., 1850, p. 157; Alg. scand. exsice, No. 309 (1872); J. Agardh, Sp. II, 1852, p. 491, III, 1876, p. 377; Le Jolis, Liste alg. Cherbourg p. 108, pl. IV, fig. 1-3; Batters, Mar. Alg. Berw. 1889, p. 95, pl. XI fig. 5.

Chætophora pellita Lyngbye Hydr., 1819, p. 193, pl. 66 B, ex parte (quoad specim. færoëns.). Cruoria adhærens Crouan in J. Agardh Sp. II, p. 491, III, p. 377, (comp. Le Jolis, Liste, p. 108).

An examination of the specimens of *Chætophora pellita* in Lyngbye's herbarium has shown that this name includes two distinct species, the specimens from the Færøes belonging to *Cruoria pellita*, while those from Denmark belong to *Petrocelis Hennedyi* (comp. p. 174). The description and the figures, which treat only of sterile specimens, agree tolerably well with both species; it appears most probable, however, that they have been worked out after the Danish specimens, as the filaments in the fig. 2 are not thicker towards the base, and as they are described as "æqualia, apice parum attenuata" (l. c. p. 194), which agrees best with the last named species. The genus *Cruoria*, to which the species of LYNGBYE was referred in 1835 by FRIES, was also very ill defined. ARESCHOUG and the later authors, however, have applied the name of LYNGBYE and FRIES to the species here treated of, and it must be used in the future in the same sense, as the specific name of LYNGBYE in fact comprises both species.

This species, in habit quite resembling *Petrocelis Hennedyi*, forms crusts on the stems of *Laminaria hyperborea*, stones, shells of *Mytilus* and barnacles, more



rarely on *Fucus servatus* and the basal part of *Halidrys siliquosa*, from 1 to 12 cm in diameter or more. The crust has at first a basal layer consisting of one layer of cells from which the vertical filaments are given off. The fila-



Cruoria pellita. A, border of frond seen from above. B, vertical section of under part af frond showing basal layer and sub-basal layer. C, similar, older crust. A, B 390:1. C 230:1.

Fig. 101. Cruoria pellita. Basal layer of frond seen from the under face, showing creeping rhizoidal filaments. 390:1.

ments of the basal layer are radiating towards the margin (fig. 100 A). According to SCHMITZ and HAUPTFLEISCH (1897, p. 535) the thallus is quite coalesced with the substratum and without root-hairs (Wurzelhaare); the first is true, but the latter assertion is not quite correct. As shown in figs. 100 and 101, short filaments are here and there given off from the under side of the basal layer; these filaments have first the character of unicellular rhizoids, but increase in length and form long septate filaments running under the primary basal layer, and in older crusts they may form a continuous layer consisting of one to more layers of variously disposed cells, the undermost of which may have the character of rhizoids penetrating into the unevennesses of the substratum, while the upper cells in thicker fronds resemble those of the primary basal layer. According to SCHMITZ and HAUPT-FLEISCH (l. c.), rhizoids are frequently produced in the undermost part of the cortical layer. The vertical filaments are ascendent at the base; they are thicker near the base than in the upper part, and consist there of somewhat swollen cells, about 12,5–14  $\mu$ 



Fig. 102.
Cruoria pellita. A, vertical filament with branch, above a carpogonium (?); the cells contain a, chromatophore and starch grains. B, vertical filament with young sporangium. 300:1.

thick, while the cells of the upper part are  $6-11 \mu$ , frequently 7,5-9  $\mu$  thick.

The lower part of the filaments tapers gradually upwards, while the upper part is usually of equal thickness. The ultimate cell is truncate or rounded, but never pointed. The cells contain a nucleus and a single calotte-shaped chromatophore, the border of which seems to be more or less lobed. The cells, particularly those of the undermost part of the filaments, are usually filled with starch grains. The filaments are sparingly branched, by lateral ramification (fig. 102 A). Hyaline hairs were not observed, but I some-



Fig. 103. Cruoria pellita. Branches consisting of narrower cells with refringent contents. 300:1.

times found septate branches thinner than the filaments and with more refringent contents, reaching the same level as the ordinary filaments (fig. 103).

The tetrasporangia and the sexual organs occur as a rule in distinct individuals; carpogonia have, however, been met with in tetrasporangia-bearing crusts. The tetrasporangia are lateral on the vertical filaments. As shown in the figure published in Le Jolis' Liste (l. c.) they are attached in such a manner that their under part projects below the point of attachment. They are very large and divided by three horizontal walls. In specimens from Frederikshavn they were  $250-283 \mu$ long,  $45-60 \mu$  broad. A young sporangium is shown in fig. 102 *B*. In one case the spores seemed to contain several nuclei, but the observation was not certain, owing to the numerous starch grains contained in the spores.

The antheridia form small lateral tufts at the upper end of the vertical filaments, as shown by THURET (LE JOLIS l. c. pl. IV fig. 3). They are usually produced in small numbers on the upper end of a unicellular branchlet (fig. 104). The antheridia are linear, but the liberated spermatia, according to THURET (l. c.) are globular. I have only once observed antheridia, in a specimen collected at Frederikshavn in July, having also carpogonia and cystocarpia.



Fig. 104. Cruoria pellita. Upper ends of filaments with antheridia, mostly emptied. 390:1. The development of the cystocarps has only been incompletely followed. The carpogonial filaments are lateral on the vertical filaments. Their number of cells may be variable, at most four (fig. 105 A), more frequently less, e. g. two in fig. 105 B, and in fig. 106 A, where the trichogyne reached over the surface of the frond. Most of the carpogonial filaments observed had short trichogynes, and were probably young or abortive. Carpogonia sitting directly on the vertical filaments also occur, but in such cases it was often difficult to decide whether they were really carpogonia. Such dubious cases are shown in fig. 105 C, D; I have been inclined to interpret them as carpogonia, since they had the same refringent and colourless contents as the others. In some cases the supporting cell in the vertical filament had a similar appearance (fig. 105 C, D) (Comp. *Petrocelis Hennedyi*, p. 178). The undermost cell in the carpogonial filament is sometimes connate in its whole length with the supporting filament. Sporogenous filaments were not seen in connection with the carpogonium, but they were found fusing with the auxiliary cells. These cells are intercalary in the vertical filaments and differ but little from



#### Fig. 105.

Cruoria pellita. Carpogonia A, four-celled carpogonial branch. B, two-celled carpogonial branch. C, presumed carpogonium sitting directly on the vertical filament; the supporting cell and the next following have the same homogenous and refringent contents as the carpogonium. D, Carpogonia given off directly from the vertical filament. A, D 300: 1; B, C 390: 1.

the other cells, possibly sometimes swollen before fusion. The sporogenous filaments run principally in a horizontal direction, but sometimes give off upward branchlets,



Fig. 106.

Cruoria pellita. A, two-celled carpogonial branch. B, filament with a somewhat swollen cell \*, possibly an auxihary cell. C, auxiliary cell fused with sporogenous filament. D, similar; the sporogenous filament has given off a branchlet upwards. E, auxiliary cell fused with a sporogenous filament which has given off two upwards directed branchlets. F, auxiliary cell in connection with an incompletely developed cystocarp. G, ripe cystocarp; the pits connecting the auxiliary cell with the neighbouring cells in the vertical filament are marked with a  $\times \cdot$  c, carpogonium; a, auxiliary cell; s, sporogenous filament. A-F 390:1. G 300:1.

the signification of which is unknown (fig. 106 D, E). An incompletely developed cystocarp is shown in fig. 106 F, it consists of a very small number of upwardly directed filaments, which have been somewhat displaced by pressure; the auxiliary cell has produced a lateral outgrowth, but is otherwise not swollen. Fig. 106 G shows a ripe cystocarp; the auxiliary cell, or better, the fusion cell, is here seen as a large cell connected by pits with the neighbouring cells of the vertical filament. All the cells of the cystocarp seem to produce a very large carpospore. The ripe cystocarp consists of a spindle-shaped heap of large cells, few in number, reaching downwards considerably beyond the insertion of the auxiliary cell; it has earlier been shortly described and figured by Batters (l. c.).

The species occurs from low-water mark down to 30 meters depth. In some places in the eastern Kattegat it occurs abundantly, covering the stones with extensive crusts, forming an association. The sporangia arise in autumn; they are found ripe in winter and spring, emptied in spring and summer. Carpogonia were met with at all seasons, often abortive however; cystocarps have only been met with once in July.

Localities. Sk: Off Lønstrup (ZK<sup>2</sup>), on Laminaria hyperborea. — Kn: Herthas Flak (!, Børgesen); TX, at Hirsholmene; Krageskovs Rev; Busserev at Frederikshavn; harbour of Frederikshavn; VU, east of Nordre Rønner, 15 m; TO, TP, Tønneberg Banke, 16—18 m; FF, TR, Trindelen, — Ke: IR, IT and VZ, Groves Flak, 24,5 m; IQ, ZE<sup>1</sup>, Fladen; II, IK, Lille Middelgrund; Store Middelgrund (Børgesen), 30 m; IA, Store Middelgrund, 16 m; OO, Søborghoved Grund. — Km: XC, NW of Anholt, 11 m, on the base of Halidrys; D, north of Isefjord, on Fucus serratus, 11 m. — Sa: BF, off Sletterhage, 14 m; PH, Lindholms Dyb, 20,5 m; Northside of Refsnæs (C. H. Ostenfeld), 19 m; DK, Bolsaxen, 14 m. — Lb: CC, South side of Hornenæs, on Mytilus, 7,5 m. — Sb: NN, Southwest of Sprogø, 19 m. — Su: bM, South of Hveen.

#### Cruoriopsis Dufour.

Dufour, Elenco delle Alghe della Liguria, Genova 1864, p. 35 (non vidi), Schmitz and Hauptfleisch in Engler u. Prantl. I., p. 535.

#### 1. Cruoriopsis danica sp. nov.

Crusta sanguinea, diametro c. 2–3 mm, ad 74  $\mu$  crassa. Stratum basale unistratosum, substrato arcte adnatum, e filis radiantibus compositum, cellulis 4–9  $\mu$ plerumque c. 6–9  $\mu$  latis, c. 6–7  $\mu$  altis, latitudine plerumque c. duplo longioribus, nonnunquam lateraliter confluentibus. Fila erecta 4–7-cellularia, æqualia vel in inferiore parte nonnunquam sursum paulo attenuata, 5–11  $\mu$  lata, cellulis longitudine vario, inferioribus nonnunquam non nisi dimidiam partem latitudinis attingentibus, superioribus latitudine sæpe duplo longioribus, chromatophorum singulum continentibus. Pili hyalini terminales nonnunquam sparse occurrunt. Sporangia in filis erectis terminalia, solitaria, rarius bina, ellipsoidea, 23–30  $\mu$  longa, 14–18  $\mu$ lata, oblique cruciatim divisa. Organa sexualia ignota. Cellulæ auxiliariæ (?) brevissimæ in parte media vel superiori filorum seriatæ.

The cells of the basal layer form regularly radiating filaments of varying breadth. Lateral fusions may be wanting in some cases, while in others they occur in great numbers (figs. 107 *I*, 108 *A*). More than two cells may sometimes fuse together. The cells of the basal layer are low, and the same may also be the case with the undermost cells in the erect filaments, while those of the middle and the upper part of the filaments may reach a length of up to 2,5 times the breadth. The erect filaments have almost the same breadth in their whole length, frequently, however, they are a little thicker towards the base, and the uppermost cell may be a little thicker than the second from the top. The filaments are rather firmly connected, but not or only to a slight degree united by a gelatinous collode. In the undermost

part of the frond fusions may sometimes take place between contiguouscells of different filaments, as in the following species. The surface is covered with a rather firm outer wall. Each cell contains a calotte - shaped chromatophore and a small nucleus, little



Cruoriopsis danica. A-H from M. A-D, vertical sections of frond, in B a young hair, in C, a more developed hair, in D, fully developed erect filaments, a little swollen at the top, E, unripe sporangium. F, new sporangia formed within emptied sporangial walls. G, H, ripe sporangia. I, K from MK. I, basal layer from the face showing fusions. K, erect filament ending in hair. 390:1.

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susceptible to staining reagents. The frond is, at all events in some cases, polystromatic to the border (fig. 108 F).

Here and there some of the erect filaments terminate in hyaline hairs; these occur in varying quantity, usually solitary. They are fairly rich in protoplasm. The subjacent cell is somewhat lengthened, conical (fig. 107).

The sporangia arise from the terminal cell of erect filaments. They reach the surface of the frond and are originally, like the vegetative cells, covered with a thick outer wall (fig. 108). The first wall is inclined, the two following perpendicular to it (figs. 107 G, 108 E). After evacuation of the sporangium a new one may sometimes be formed from the subjacent cell within the emptied sporangial wall (fig. 107 F).

In specimens dredged in the Little Belt in July 1915 I found very short-celled filaments which were supposed to be auxiliary-cell filaments, though carpogonia were not found. They arose from erect filaments, which in a smaller or greater extent of their length consisted of low, disc-shaped cells, the undermost and one, or more rarely two or three, of the uppermost cells showing the ordinary length. The short cells were of a feebler colour than the other cells; they resembled the auxiliary-

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cell-rows of several other Cryptonemiales, but they seem to be different from those found in *Cruoriopsis cruciata* Dufour, which, according to SCHMITZ (Sitzungsber. d.



Fig. 108.

*Cruoriopsis danica.* A-E from Groves Flak. *A*, basal layer from the face. *B*, vertical section of frond; at left probably two young sporangia. *C*, two emptied sporangia on the end of a filament. *D*, *E*, ripe sporangia. *F*-*H*, from Lille Belt; *F*, vertical section of the margin. *G*, *H*, supposed auxiliary-cell filaments. A-E 390:1. *F*-*H*625:1.

wards the apices of longer and narrower cells, three or four times as long as broad and only 4 or  $5\mu$  in diameter, while at the base of the filaments the cells are  $10-15\mu$ in diameter. Nevertheless I should perhaps have referred my plants to the named

species, had I not, through the kindness of the late Mr. BATTERS, received from him a microscopical preparation with two sections of a plant designed as *Cruoriopsis Hauckii* Batt. Plymouth 24<sup>th</sup>





Cruoriopsis Hauckii Batt., after preparation sent from Batters. A, basal layer from the face. B, vertical filaments. C, sporangium. 390:1.



#### Fig. 110.

Cruoriella armorica Hauck, after specimen from Naples, from Hauck's collection. A, basal layer from the face. B, vertical section, showing unripe sporangium within an emptied sporangial wall. C, ripe sporangium. 390:1.

niederrhein. Ges. für Natur- u. Heilk. zu Bonn. 1879) are lateral and 3- to 5-celled.

As may be judged from the above description, our species much resembles Cruoriopsis Hauckii BATTERS, according to the description given in the Journ. of Botany 1896 p. 387 (New or critical Brit. mar. Algæ), and I have indeed been much in doubt, whether it might not be identical with it. **BATTERS'** species differs however, by the erect filaments consisting toJanuary 1896, thus apparently a type specimen, but differing from the author's description in the dimensions of the erect filaments and the sporangia, the first being thin in their whole length,  $3,5-5 \mu$  in diameter, not broader at the base, thus much thinner than in our species, and consisting of much more lengthened cells (fig. 109). Further, the crust appeared to have another consistency than the Danish plant, the filaments being connected by a gelatinous substance, while the special membranes of the cells were not distinct. The sporangia were smaller, more lengthened,  $18-25 \mu \log$ ,  $7-11 \mu$  broad. Hyaline hairs were not present. I think it therefore best to consider the Danish alga as representing a distinct species.

According to BATTERS (l. c.), *Cr. Hanckii* is identical with *Cruoriella armorica* Hauck, Meeresalg. p. 31 (non Crouan). An examination, through the kindness of Mrs. WEBER-VAN BOSSE, of a microscopical preparation of this species from HAUCK'S collection, labelled Neapel 1878, has shown me that this plant is different from the Danish, and also from BATTERS' species. The crust is thicker, up to 164  $\mu$ , the basal layer consisting of much larger cells, the erect filaments are thinner, more loosely united, sometimes dichotomous above, the sporangia regularly cruciate and much larger,  $46-56 \mu \log$ ,  $26-28 \mu broad$  (fig. 110)<sup>1</sup>.

Cr. danica reminds one not a little of Cr. arctica K. Rosenv. (1910, p. 102); it forms, like this, small, thin, blood-red crusts on stones. It differs by lower cells in the basal layer, occasionally fusing with the neighbouring cells, by the presence of hairs, by the oblique division of the sporangia, and by the fact that the sporangia are always terminal, never lateral. It must be admitted that two sporangia may sometimes be found at the end of an erect filament, one of which must possibly be regarded as lateral, but they are in fact both placed terminally on the filament (fig. 108 C), while in Cr. arctica, true lateral sporangia occur. Finally, the sporangia are somewhat larger.

The species grows on stones in 1 to 17 meters depth; it has been found with ripe sporangia in April (Groves Flak) and September (Søndre Røn by Lemvig).

Localities. Lf: M, Søndre Røn by Lemvig, c. 1 m; MK, Holmtunge Tange, 1-2 m. - Ke: North end of Groves Flak (Børgesen). - Lb: At Lyngsodde off Middelfart, 15-19 m.

#### 2. Cruoriopsis gracilis (Kuckuck) Batters.

E. A. L. BATTERS, Catal. of the Brit. Mar. Algæ (Suppl. to the Journ. of Botany 1902), p. 95.

Plagiospora gracilis Kuckuck, Bemerk. z. mar. Algenveg. v. Helgoland II. Wiss. Meeresunters. N. F. II. Bd. Heft 1, 1897, p. 393.

Cruoriopsis cruciata Batters, New or critical Brit. Mar. Algæ. Journ. Bot. 1896, p. 388.

In July 1915 I found by dredging in the Little Belt near Middelfart a few crusts on stones, agreeing perfectly with the plant described by KUCKUCK under the name of *Plagiospora gracilis*. A few additional remarks may be given here to KUCKUCK's rather short description.

<sup>1</sup> Another specimen in HAUCK's herbarium, labelled *Cruoriel la armorica*, from Rovigno was sterile, and evidently belonged to another species, possibly a species of *Cruoria*.

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The crusts are thin, bright purple, up to 1,5 cm in diameter. The basal layer consists of isodiametrical cells. The erect filaments are  $4,5-5,5 \mu$  thick. Not unfrequently transversal fusions between contiguous cells in different erect filaments occur (fig. 111 *B*). The sporangia are normally lateral on the erect filaments and





Cruoriopsis gracilis. A, erect filament with two-celled sporangium. 430:1. B, fusion between cells of two different filaments. C and D, filaments with sporangia on one-celled stipe. B-D, 730:1. sessile. In some cases however I found them pedicellate, on a one-celled stipe, as shown in fig. 111 *C*, *D*. The sporangia are first divided by an oblique transversal wall (fig. 111 *A*) and later by two walls perpendicular to the first; at maturity they are  $21-22 \mu$  long,  $11-14 \mu$  broad.

KUCKUCK has established the genus Plagiospora on the oblique division of the tetrasporangia. As such divisions occur not only in *Hildenbrandia*, as mentioned by KUCKUCK, but also in *Cruori*opsis (and further in *Petrocelis*), and as

in the genus *Cruoriopsis* both terminal and lateral sporangia occur, even in the same species (*Cr. hyperborea*), it is justified to refer the species here mentioned to the genus *Cruoriopsis*.

Locality. Lb: At Lyngsodde, right opposite to Middelfart, about 15 meters, with sporangia in July.

#### Cruoriella Crouan.

#### 1. Cruoriella codana sp. n.

Thallus tota superficie inferiori paulum calcaria substrato adhærens, rhizinis unicellularibus affixus, diametro 2-5 (?) cm latus, purpureus. Stratum basilare (hypothallium) e lobis lateraliter conjunctis e filis flabellatim ramosis compositis formatum, cellulis 14—33  $\mu$  longis, 9—14  $\mu$  latis, 9—11  $\mu$  altis. Thallus adultus e pluribus frondibus superpositis compositus. Fila verticalia frondium singularum plerumque e cellulis 3—10 formata. — Paranemata nematheciorum sexualium sursum attenuata, e 4—5 cellulis composita, basi 7—8 $\mu$ , superne 2—3(—4) $\mu$  lata. Antheridia, in nematheciis specialibus aut in iisdem ac carpogonia, divisionibus transversalibus et longitudinalibus filorum orta, diametro 2 $\mu$ . — Carpogonia in ramulis specialibus 4—5-cellularibus terminalia, membrana obliqua curvata a cellula penultima limitata. Cellulæ auxiliariæ in filis aliis intercalariæ. Cystocarpia e filis erectis paucis parce ramosis composita. Carposporæ 11—12 $\mu$  diametro.

The specimens on the base of which this species has been described were for a long time referred by me to *Cruoriella armorica* Crouan<sup>1</sup>, a species which has

<sup>1</sup> Ann. d. scienc. nat. 4e sér. t. 12, 1859, p. 289.
often been confounded with other species. It was only by becoming acquainted with the recently published description of *Peyssonnelia* (*Cruoriella*) Nordstedtii Webervan Bosse<sup>1</sup> and by the final revision of my material that I arrived at the conclusion that it was not identical with the former, but more resembled the last named species. As it proved to be different also from this and did not appear to agree with any other well known species. I describe it here as a new species.

Cruoriella codana has only been met with once on a calcareous stone much bored by worms. It forms thin crusts of a bright purple colour, brighter than in Cr. Dubyi, and is adherent to the substratum in its whole extent, being fixed to it by unicellular rhizoids. The greatest crust is more than 5 cm in diameter, but it has probably arisen by coalescence of several distinct crusts; the other were at most 1 cm broad. When seen from the underside, the young basal layer appears composed of distinct lobes, which coalesce laterally. The lobes have a flabellate structure. Even when having a continuous outline, the margin is composed of very distinct lobes (fig, 112 A), and the same structure is found in the older parts of the hypothallium, where there are no principal rows of larger cells, as found in P. Boergesenii and P. Nordstedtii by Mrs. WEBER-VAN BOSSE (l. c. p. 138 and 140). The cells of the basal layer are  $14-33 \mu \log_2 9-14 \mu$  broad and  $9-11 \mu$  high. Unicellular rhizoids, bounded by a cell wall, are given off from its under face. The marginal cells of the frond divide by vertical cell-walls, and the segments divide immediately by a horizontal wall, the hypothallic cell becoming thus lower than the marginal cell (fig. 114). The monostromatic basal layer or hypothallium is only little distinct from the "perithallium" consisting of the vertical filaments given off from it. These filaments are vertical in their whole extent or slightly ascending; they are only rarely branched. The cells are of almost equal breadth in the same filament,  $9-12 \mu$ , or the undermost may be a little broader. Their height is as a rule a little less than the breadth, near the surface sometimes much less, more rarely the same or a little greater. The number of cells in the erect filaments usually varies from 3 to 10.

Old crusts are composed of two or more fronds growing one over the other. At first observation these superposed fronds might be supposed to come into existence in the same way as recently described by Mrs. WEBER-VAN Bosse in *Peys*sonnelia (*Cruoriella*) Nordstedtii (l. c. p. 141, fig. 146), by the formation of a horizontal split in the frond and following constitution of the part situated over the split as a new crust with a new-formed hypothallium. I have seen several cases which were favorable to this interpretation, in particular some apparently young cases and such where the under face of the upper crust was very irregular, and I might suppose that the new upper frond may really arise in this manner. But in other cases it is without doubt that the upper frond arises from horizontal outgrowths from certain parts of the crust which have preserved their growing power, while the covered

<sup>1</sup> Rhizophyllidaceæ in F. Børgesen, Rhodophyceæ of the Danish West Indies. Dansk Botan. Arkiv, Bd. 3. Nr. 1, 1916, p. 140. parts have lost it by formation of nemathecia or from other causes. The meeting point between the overlapping frond with another similar one or with the forthgrowing old frond is usually easily found (fig. 112  $B^*$ ). The places from which the new fronds are given off are frequently inverted conical, being upwardly enlarged and composed of filaments slightly diverging upwards. The number of these



Fig. 112.

Cruoriella codana. A, marginal part of frond seen from below. 195:1. B and C, vertical sections of frond showing the overlapping of the frond by a new lobe; at \* the point of concretion of this lobe with another part of the frond; in C the basal layer of the new lobe is not normally developed. In C auxiliary-cell filaments and sporogenous filaments are visible 205:1. D, vertical section of frond with antheridial nemathecium 350:1.

points of departure is variable; sometimes they are very close, in other places they are more distant. The new-formed fronds coalesce laterally and form together a uniform plain surface. The cells of the basal layer of the overlapping fronds were frequently found connected with pits, a fact which supports the here proposed explanation of their development. As the new fronds were evidently not produced at the season when the specimens were collected, I have not been able to follow their development, but must content myself with examining the advanced stages. A further fact confirming my view is that nemathecia are frequently found on the surface of the covered crust (fig. 112 C). The under face of the frond is often

irregular; in some places the frond projects downward sand, consists there of larger cells, which may here be up to  $17 \mu$  high.

The cells of the frond contain, as far as could be judged from the examination of dried specimens, a vaulted chromatophore in the upper part of the cell. Numerous starch grains often fill the cells, particularly in the under part of the frond.

The under face of the frond is covered with chalk, but the frond itself does not appear to be incrusted.

The sexual organs are always situated in nemathecia on the upper side of the frond. The nemathecial filaments consist of4 or 5 cells, the undermost of which have the same breadth as the upper cells of the crust, or about 7-8 µ, while the thickness of the filaments tapers towards the midd-



Fig. 113.

Cruoriella codana. A and B, young carpogonia. C, more developed carpogonium with short, thick trichogyne. D, carpogonium showing disjunction of the trichogyne but no other signs of fecundation. E-H, auxiliary-cell filaments; a, auxiliary cell; s, sporogenous filament. I, not fully developed cystocarp; a, auxiliary cell or fusion cell. A-D 630:1. E-I 400:1.

le and in the upper part it is only  $2-3(-4)\mu$ , without considering the gelatinous outer wall (fig. 112 C). The upper cells are 3 or 4 times as long as broad or even longer.

The antheridia arise from the nemathecial filaments by division of all the cells or with the exception of the undermost one or two cells. The cells are divided by transversal walls or at the same time by longitudinal walls in small antheridial cells (spermatangia), which are about  $2 \mu$  in diameter; in a longitudinal section each filament appears as composed of one or two longitudinal series of cells (fig. 112 D). The antheridia occur in particular male nemathecia or in the same nemathecia as the carpogonia.

The carpogonia are terminal on 4- or 5-celled branches given off from the lower part of the nemathecial filaments. They are cut off by an oblique curved wall going from the middle of the longitudinal to the border of the basal wall of the mother-cell. Two young stages are shown in fig. 113 A, B. The carpogonium shown in fig. 113 C is a little more developed, though yet unfertilized; the trichogyne is short and thick, the carpogonium encloses completely the right side of the hypogynous cell. The carpogonium represented in fig. 113 D has the appearance of being fertilized, the continuity of the trichogyne with the ventral part being





Fig. 114. Cruoriella codana. A. vertical section of margin of frond. B, vertical section of sporangial nemathecium 350:1. interrupted, but the carpogonium has not reached the surface of the frond, and no spermatia adhere to it, nor have any sporogenous filaments been formed. Later stages of the carpogonia I have not observed.

The auxiliary cells are more numerous than the carpogonia; they occur in particular branches given off at the base of ordinary nemathecial filaments and are shorter than these (fig. 113 E - H). The cells of these filaments have a dense protoplasm and are somewhat swollen, particularly the two uppermost cells, while the third cell from the top (more rarely the fourth) is not swollen. This latter cell is the auxiliary cell, which may be concluded from the fact that it is sometimes found in connection with thin sporogenous filaments running in a horizontal direction between the nemathecial filaments. Over the auxiliary-cell filament a space containing a hyaline substance and provided with a membrane open above is visible; it resembles an abortive hair (fig. 113). The development of the cystocarps has not been followed, but a cystocarp, not quite ripe it is true, but apparently not far from ripeness, is shown in fig. 113 *I*. It consists of a few upward directed, slightly branched

filaments, the cells of which each produce a carpospore. In the most developed cystocarp I have seen the carposporal cells were  $11-12 \mu$  in diameter.

The sporangial nemathecia, of which I have only observed one, much resemble those of *P. Nordstedtii* (Mrs. Weber-van Bosse I. c. p. 142). The nemathecium had a height of 88  $\mu$ , the paraphyses were less tapering than those of the sexual nemathecia, the upper cells being  $4 \mu$  broad; the undermost cells were usually 2—3 times as long as broad. The tetrasporangia, fixed at the base of the nemathecium, are certainly cruciately divided, but the ripe sporangia were disturbed by the preparation. Some were divided by a transverse or slightly oblique wall, but the direction of the following walls could not be stated (fig. 114). The almost ripe sporangia are about  $50 \mu$  long, 18  $\mu$  broad.

As mentioned above, I at first referred the specimens here described to *Cruoriella armorica* Crouan, and I maintained this determination also after having examined, through the kindness of Prof. NORDSTEDT, a type specimen of this species from CROUAN in J. AGARDH'S herbarium at Lund (Nr. 27630), having in one specimen found a still sterile nemathecium with thin upwardly tapering nemathecial filaments as in the sexual nemathecia of the Danish species. The sporangial nemathecia, which at that time were unknown to me in *Cr. codana*, present, however, such differences that it is impossible to identify our species with that of CROUAN, the nemathecial filaments of the latter being forked, fastigiate, and the sporangia being terminal on undivided erect filaments and reaching the surface of the nemathecium, in which respect I found the specimens of CROUAN corresponding to his description and figures.

Our species is apparently related to Cr. Nordstedtii, which shows resemblances in the structure of the frond and of the sporangial nemathecia, but there seems to be a difference in the superposed fronds arising only by splitting of the frond in Cr. Nordstedtii, while in C. codana they seem to arise principally as excressences from the surface of the frond. The first-named differs further, according to Mrs. WEBER-VAN BOSSE, by the want of principal rows of cells thicker than the others in the basal layer and by the presence of pluricellular rhizoids besides the unicellular ones. The sexual nemathecia are unknown in C. Nordstedtii.

It is highly probable that this species has been met with earlier, but confounded with *Cr. armorica*; this, however, cannot be stated without examination of the corresponding specimens.

Locality. Kn: TR, near Trindelen, 23,5 meters, September.

### 2. Cruoriella Dubyi (Crouan) Schmitz.

Fr. Schmitz, Syst. Übersicht, Flora 1889, p. 20; id. in Kolderup Rosenvinge, Grønl. Havalger, 1893 p. 783; Fr. Schmitz und P. Hauptfleisch in Engler u. Prantl, 1897, p. 536.

Peyssonnelia Dubyi Crouan, Ann. sc. nat. IIIe sér. t. 2. 1844, p. 367, pl. 11; id., Alg. mar. du Finistère (Exsicc.) 2º vol. no. 236, Brest 1852; id. Florule du Finistère, 1867, p. 148, pl. 19; HARVEY, Phycol. brit. I, 1846, plate 71; J. AGARDH, Sp. II, 1852, p. 501; III, 1876, p. 384; HAUCK, Meeresalg., p. 35; BATTERS, Mar. Alg. Berw., 1889, p. 90; KUCKUCK, Bemerkungen, II, 1897, p. 393, fig. 18 (antheridia).

The purple-coloured crusts are 1 to 3 (4) cm in diameter. In a dried state they show characteristic radial folds. The outline of the frond is undulate; the course of the cell-filaments in the marginal part is not regularly radiating, owing to its composition of coalescing lobes, the growth being usually arrested in one of the meeting lobes (fig. 115 C). From the underside of the frond, which is covered with a layer of chalk, a varying number of rhizoids are given off; when fully developed they are separated by a wall from the producing cell (fig. 115 A).

The thickness of the frond is variable. As shown in a vertical section, it is divided immediately behind or at a small distance from the border by horizontal walls (fig. 115 A). The cells of the undermost layer, which produces the rhizoids, are usually somewhat lengthened in the radial direction. Two erect cell-rows are frequently given off from one cell in the basal layer or the subbasal layer (fig. 115 B); the cells are therefore greater in the under part of the frond than in the upper. Each cell contains a nucleus and apparently a vaulted chromatophore in the upper part of the cell. To judge from the figure given by KUCKUCK (l. c. p. 394, Fig. 18 B) the chromatophore is either divided into ribbonlike branches or there are several bandlike chromatophores; they are not mentioned in the text. The cells, particu-

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D. K. D. Vidensk. Selsk. Skr., 7. Række, naturvidensk. og mathem. Afd. VII. 2,

larly those of the undermost part of the frond, often contain a great quantity of starch grains taking a brownish colour on treatment with iodine.

Old crusts are often composed of several crusts growing one over the other. This is principally caused, as in the foregoing species, by the cessation of growth of great parts of the fronds, particularly those which have produced nemathecia, while in other parts the erect filaments continue growing in the next season, giving rise to a new frond growing in a horizontal direction over the old frond, and this may be repeated several times, so that old fronds may be composed of 6 or more



Fig. 115.

Cruoriella Dubyi. A, marginal part of frond in vertical section. B, inner part of frond in vertical section. C, marginal part of frond seen from above. A and B, 295:1; C, 215:1.

distinct crusts. The under side of fronds or lobes thus produced is usually rather irregular (fig. 115 A). Overlapping, though in a smaller degree, may also take place in the border of the frond, where the lobes sometimes grow over one another, and the same may occur on the meeting of two of the fronds produced in the manner first described. A formation of superposed fronds by horizontal splitting, as described for Cr. Nordstedtii by Mrs. WEBER-VAN BOSSE may also occur (see above p. 189).

The sexual nemathecia are cushion-shaped, of various extent. The antheridia occur in particular nemathecia or interspersed in the female ones. As shown by KUCKUCK (l. c. fig. 18) the spermatangia arise by transverse and longitudinal divisions of the cells of the nemathecial filaments (fig. 116 A).

The nemathecial filaments of the female nemathecia are of equal thickness in their whole length, and consist at the stage of fertilization of about 5 cells, which are a little longer than broad; up to twice as long. When the cystocarps are ripe, the cushion is thicker, the filaments somewhat longer, the constituting cells more numerous and sometimes longer. The carpogonia are terminal on particular (3-)4-5-celled branches given off from one of the undermost cells in a nemathecial filament or from one of the bottom cells of the nemathecium (fig. 116). As in the foregoing species, the carpogonium encloses one side of the subterminal



Fig. 116.

*Cruoriella Dubyi.* A, antheridia, upper part of male nemathecial filament. B-E, vertical sections of nemathecia with carpogonia (c), trichogynes (t), sporogenous filaments (s) and auxiliary-cell filaments (af). A, E 630:1; B-D 390:1.

cell, giving off a production reaching beyond the under face of this cell. In some cases no such lateral production was found, but these carpogonia were doubtless abnormally developed, abortive (fig. 116  $C^*$ ). The auxiliary-cell branches which are given off from the lowest part of the nemathecial filaments consist of about four low seemingly equal cells. In fig. 116 E two fertilized carpogonia are shown, from which sporogenous filaments growing in a horizontal direction are given off. A similar filament in connection with an auxiliary-cell filament is shown in fig. 116 D. The development of the cystocarp has not been followed. At maturity the cystocarpial nemathecium contains numerous rows of carpospores, each row consisting of up to five almost globular carpospores, each surrounded by a thick hyaline wall.

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The carpospores are  $19-29 \mu$  in diameter, with the envelope  $35-40 \mu$ ; a nucleus is seen in the centre. How many such rows belong to each cystocarp I cannot say; according to BATTERS (l. c. p. 91) each cystocarp consists of one, two or three rows.

Sporangia were only met with in two specimens after evacuation. According to CROUAN, HARVEY and others they are regularly cruciate<sup>1</sup>.

The species has been met with in several places from Skagerak to the Samsø waters and the Sound, usually in considerable depths viz. from 13 to 25 meters, in



Fig. 117. Cruoriella Dubyi. Vertical section of nemathecium with ripe cystocarps. 200:1.

2 m and in the Limfjord in 6 meters depth. It grows on stones (granite and flint) and old shells of bivalves (Cyprina, Mytilus modiola a. o.) and gastropods, and Serpula, frequently in company with Cruoria pellita. It is perennial, but has only been collected in the months of April to September. Most of the specimens were sterile, but two specimens with emptied sporangia were found in the eastern Kattegat in April and May, and some

Skagerak however also in

collected in the Samsø waters in August had antheridia and carpogonia, partly fertilized, and long sporogenous filaments. Specimens with ripe cystocarpia were collected in August off Lønstrup in Skagerak. According to BATTERS it is fructifying in January to June at England's east coast.

Localities. Sk: At Roshage, Hanstholm, near land, 2 m; ZK<sup>0</sup> and ZK<sup>6</sup> off Lønstrup, 7–13 m. – Lf: Nissum Bredning, off Helligsø, 5,5 m. – Kn: Herthas Flak; Böchers Banke, 29 m; TO, Tønneberg Banke; ZB, east of Trindelen, about 30 m; TR, FF and TQ near Trindelen; VU, east of Nordre Rønner, 15 m; N.E. of Hirsholmene, 9,5 m (Henn. Petersen). – Ke: IL, IP, IQ, ZE<sup>1</sup> Fladen, 21–25 m; ZJ, IR, IS, VZ, Groves Flak, 22,5–26,5 m; Groves Flak (Børgesen); IK, IH, Lille Middelgrund; Store Middelgrund, IA, 16,5 m (l) and 30 m (Børgesen). – Sa: KI, south of Hjelm, 13 m; BF, off Sletterhage, 14 m. – Su: bM, South of Hveen, 22,5 m.

<sup>1</sup> The above was written long before I received V. SCHIFFNER's Studien über Algen des adriatischen Meeres (Wiss. Meeresuntersuch. N. F. 11. Bd. Abt. Helgoland, Heft 2, 1916). The author describes here (l. c. p. 148) a species named *Cruoriella Dubyi*, which he supposes is identical with the Atlantic species of the same name. This supposition, however, seems to be doubtful, the Adriatic plants apparently differing, in the structure of the frond and of the nemathecia as well. Thus, the frond is said to be rarely more than 6 cells thick; nothing is said as to the complex structure of older fronds described above; and the rhizoids seem to be much more numerous. Further, the paraphyses are said to be attenuated upwards. The author says, p. 148, that the species has been wrongly referred by DE TONI to *Cruoriella*, but p. 501 he approves that SCHMITZ has made the same determination.

# Rhododermis Crouan.

Crouan in J. Agardh, Sp. Vol. II, pars 2, 1852, p. 504.

### 1. Rhododermis elegans Crouan.

Crouan in J. Agardh, Sp. Vol. II, pars 2, p. 505. Crouan, Florule de Finistère, 1867, p. 148, pl. 19, fig. 130, Batters, Mar. Alg. Berw., 1889, p. 91, pl. XI fig. 1 (forma *polystromatica* Batters). Kolderup Rosenvinge, Deux. mém., 1898, p. 18, id., Mar. Alg. N. E. Greenl. 1910, p. 104.

This small arctic and north-atlantic species has been collected in several places in the Danish waters. It forms small, thin crusts of a lilac-rose colour with an irregular outline, the diameter of which scarcely exceeds 5 mm. It resembles in many respects *Rh. parasitica* of which KUCKUCK has given an exhaustive description and splendid figures (Beitr. z. Kenntn. d. Meeresalg. 1. Wissensch. Meeresunters. N. F. II, Heft 1. 1897). According to BATTERS, one of the principal differences is that the cells of the frond in *Rh. elegans* are broader than long, while in *Rh. parasitica* they are longer than broad. This difference is in reality general though not absolute, as may be judged from the figures of KUCKUCK and from the fact that cells may be found in *Rh. elegans*, which are at least as high as broad. *Rh. parasitica* differs further by its greater diameter, greater thickness and darker colour. A difference exists also in the structure of the border of the frond, this consisting in *Rh. parasitica* of distinct filaments (KUCKUCK, l. c. p. 7, Taf. VIII fig. 10) while it is continuous in *Rh. elegans* (fig. 118 A).

The basal layer consists of radiating cell-rows, the cells of which are more or less lengthened in a radial direction. In the marginal part of the frond the cellrows are frequently flabellately radiating towards the irregularly lobed border, here and there showing lateral ramifications (fig. 118 A). The cells are usually  $5,5-7 \mu$ broad,  $1^{1/2}$  to 3 times as long as broad. In the basal layer lateral fusions between cells belonging to different cell-rows frequently occur, the cells corresponding through a broad open canal. Such fusions may occur at the very margin of the frond. More than two cells may sometimes fuse together (fig. 118 A, B).

The crust is at first monostromatic, and a rather broad monostromatic marginal part may often be found. The inner part of the frond was always found to be from 2 to at least 5 cells thick. I have never found it distromatic in a greater extent, and I must therefore suppose that it is only accidentally that CROUAN has attributed a distromatic frond to this species, and that there is no reason to maintain the var. *polystromatica* Batters. The cells contain several chromatophores as in *R. parasitica*. In the upper part of the crust the cells are  $8-11 \mu$  broad. In several specimens I found, projecting from the surface, scattered hyaline hairs (fig. 118 *C*). Their number varied; they were placed between the paraphyses or in the sterile parts of the crust.

The sori form irregular spots on the surface of the frond; they consist of feebly curved paraphyses, usually 4- or 5-celled,  $40-50 \mu$  long, at the base  $5-9 \mu$  broad, and between them the sporangia, which are terminal on the vertical filaments of the crust, the upper cell of which has often the character of an upward slightly

broader stalk-cell. In some specimens from the Little Belt (Middelfart) the paraphyses were but few in number, in some cases almost wanting; the plant had then a certain resemblance with *Rhododiscus pulcherrimus*.

The sporangia are first divided by a transverse wall; the vertical walls occur at a later moment, for which reason sori containing only bipartite and undivided sporangia are not infrequently met with (comp. KUCKUCK l. c. p. 7 and BATTERS l. c. pl. XI fig. 1*a*). The ripe sporangia are usually  $24-33 \mu$  long,  $16-20(24) \mu$  broad.



Fig. 118.

Rhododermis elegans. A, marginal part of frond seen from above. B, basal layer of fructifying frond seen from below. C, vertical section of fertile part of frond with paraphyses, a bipartite sporangium and a hyaline hair. D, vertical section of frond with sorus; sporangia bipartite. E, almost globular ripe sporangium from Hornenæs. F, ripe sporangium. G, regeneration of sporangium. 385:1.

The greatest sporangium was found in a specimen from Refsnæs; it measured  $33 \mu$  in length and  $24 \mu$  in breadth. In the southernmost place in the Danish waters (at Hornenæs in the Little Belt) I found almost globular sporangia,  $20-21 \mu$  long,  $18 \mu$  broad (fig. 118 *E*). After evacuation a new sporangium may be produced from the stalk-cell within the empty sporangium wall (fig. 118 *G*).

Sexual organs were not met with. Antheridia are only known in specimens from North-East Greenland (K. Rosenvinge 1910).

As to the time of fructification only incomplete information can be given. In winter (October to February) the species has not been met with, but it must be supposed from observations from the coasts of England and of Greenland, that it will be found fructifying in winter with us, and this supposition is in accordance with the fact that it has been found with ripe sporangia in March (Lille Belt) and with empty sporangia in April (Limfjord, Samsø waters). On the other hand it has also been found with ripe sporangia in June, July and September, and it seems thus that it may produce ripe sporangia at all seasons.

The species occurs on stones (flint, limestone, granite), shells and carapaces of animals (*Mytilus, Serpula, Hyas*) and Algæ (*Polysiphonia elongata, Chondrus crispus*, hapters of Laminaria digitata), in 5,5-19 meters depth.

Localities. Sk:  $YN^2$ , S.E. of Bragerne, 10,5 m. – Lf: XX in Nissum Bredning, 5,5 m. – Kn: TG, north of Læsø, 9,5 m. – Ke: VY, Fladen, 18 m. – Ks: OP, Lysegrund, 6 m. – Sa: Northside of Refsnæs, 19 m. – Lb: NV and XQ, near Middelfart, 15–19 m; CC, south side of Hornenæs, 7,5 m.

# 2. Rhododermis Georgii (Batters) Collins.

F. S. Collins in Phycotheca Bor. Amer. Nº 1299; id., Notes on Algae, III, Rhodora, August 1906, p. 160. Rhodophysema Georgii Batters, New or critical Brit. mar. Algæ. Journ. of Botany, Vol. 38, 1900, p. 377. Kylin, Algenfi. schwed. Westk., 1907, p. 194-196, fig. 41.

Rhododermis Van Heurckii Heydrich, Über Rhododermis Crouan, Beihefte z. Botan. Centralblatt, Bd. 14, 1903, p. 243, Taf. 17.

Strange to say this characteristic little species was first described in 1900, though it has later proved to be widely distributed. It has also been recorded in several places in the Danish waters, always growing, as elsewhere, on *Zostera*-leaves, but it has further been found growing on uncovered roots of *Zostera*.

The plant begins as a thin monostromatic crust much resembling that of *Rho-dodermis elegans*, and with the same marginal growth. The marginal part is usually continuous with an irregularly undulating outline, and consisting of radiating filaments which are  $4-6\mu$  broad; more rarely the ends of the filaments are free, not laterally connate. Lateral fusions between cells of these cell-rows not unfrequently occur (fig. 119 A). The crust is early divided by horizontal divisions, which advance from the centre towards the periphery, with the result that the crust usually becomes polystromatic to the margin. The radial growth has meanwhile ceased, so that the diameter of the crust rarely exceeds  $300 \mu$ .

As shown by HEYDRICH, COLLINS and KYLIN, the species occurs in two forms, a disc-shaped and a globose or pear-shaped or irregularly lobed. In the disc-shaped form, the frond is usually 4 to 5, at most 7 cells thick, when fully developed and fructiferous. The cells of the erect cell-rows are  $4-6\mu$  thick. As shown by HEYDRICH and KYLIN, some of the superficial cells may produce long, vigorous hyaline hairs of the usual type in the Florideæ; they are  $5-7\mu$  thick near the base, and contain a nucleus near the top. The cells of the frond contain a nucleus and several chromatophores.

In the disc-shaped specimens the sorus often originates shortly after the formation of the first horizontal walls. The upper cell produced by these divisions in the central part of the frond develops then in a paraphyse or in a sporangium with its stalk cell, and there is only one layer of vegetative cells under the sorus. When the surrounding cells now continue growing in a vertical direction and dividing by horizontal walls, the sorus will finally be placed in a groove in the frond (fig. 119 C, comp. HEYDRICH l. c. Fig. 3). When rising later it takes a more superficial position.

The other specimens arise from disc-shaped ones by very strong enlargment of the under cells of the frond with the exception of the peripheral ones. The figures of BATTERS and HEYDRICH show a great number of large hyaline cells in the interior of the frond, suggesting that the erect cell-rows from which they arose consisted of about 10 cells. Such figures represent, according to my observations,



#### Fig. 119.

Rhododermis Georgii. A, basal layer seen from below, showing the border and lateral fusions. B, marginal part of frond in vertical section, showing a young hair. C, vertical section of disc-shaped frond showing a sorus sunk in a groove. 350:1.

early period, and there seems to be ordinarily no question of protruding of these cells between those of the second layer. But the cells increasing not only in length but also in breadth, there is no room for all the cells of the basal layer when enlarging their volume, and a number of them must therefore remain unchanged in size. Connected with the growth of the inner cells is the enlargment of the surface of the frond which makes its appearance in the lateral branching of the cell-rows in the periphery of the frond (fig. 120 C). — In the large vesicular cells a number of small chromatophores are easily visible; in some cases these cells were poor in cell-contents, in others they contained small starch grains.

basal layer remain often unchanged,

but in typical specimens of the in-

flated form they are enlarged at an

The simultaneous occurrence of the two forms of the species on the same leaf of Zostera is very curious. As a rule, the specimens growing on the faces of the leaves are disc-shaped or low cushion-shaped, while those placed on the margins are inflated. Cushion-shaped specimens may, however, be found on the margins and inflated on the faces, thus the two forms of specimens may occur side by side apparently under equal external conditions; this may perhaps be caused by a different

moment of development. The possibility that there might be two distinct forms is quite precluded by the fact that transitional forms are everywhere met with, and by their accordance in all other respects. Specimens are sometimes found which are partly cushion-shaped, partly inflated and bearing sori in both parts of the frond. It cannot be doubted that the inflated specimens arise under certain conditions which are usually only realised on the margins of the Zostera-leaves. It



Fig. 120.

Rhododermis Georgii, vertical sections of the inflated form. A, sterile plant. B, plant with sorus with unripe sporangia. C, part of sorus with ripe and emptied sporangia, the latter becoming filled with new sporangia from the stalk-cells. A, B 200:1; C 350:1.

might be supposed that the causa efficiens must be sought in the movements of the water which are much greater at the margins than on the faces of the undulating leaves. It must be left to experimental studies to decide this and to determine whether it is the friction against the water, or the better conditions for nutrition caused by the stronger movements which induce the increased growth of the inner cells of the frond.

The sorus occupies the central part of the frond. Usually there is only one, but sometimes two (or more?) are met with, which perhaps fuse together. As mentioned above, the sorus may sometimes be sunk in a groove. The paraphyses are

D. K. D. Vidensk. Selsk. Skr, 7. Række., naturvidensk. og mathem. Afd. VII, 2.

curved towards the centre of the sorus; they are 3-5-celled,  $6\mu$  broad at the base, upwards a little thinner. The sporangia are born of a stalk cell as in the other species; they are 26-32  $\mu$  long, 21-24  $\mu$  broad. After the evacuation, a new sporangial cell is cut off from the stalk cell within the empty sporangial wall.

I agree with HEYDRICH and COLLINS in retaining the species in the genus *Rhododermis*. When occurring in its disc-shaped form it resembles *R. elegans* so much that it differs only in the dimensions of the cells of the frond, and there but slightly.

The species grows on the leaves of Zostera produced in the foregoing year, but also in shed leaves. It has been met with in the months of April to August, in all these months in disc-shaped and inflated specimens and with sori. In April the sporangia were yet undivided; in May and June unripe and ripe sporangia were met with, in July and August ripe sporangia were found, but also emptied and regenerated ones. The species has also elsewhere been found with sporangia in spring and summer.

Localities. Lf: Repeatedly at Nykøbing (!, C. H. Ostenfeld). — Kn: In several places at Hirsholmene (!, Ostenfeld, Henn. Petersen); Frederikshavn, Busserev, and between Borrebjergs Rev and Marens Rev; ZL, S.E. of Nordre Rønner, 6,5 m and 11 m. — Sa: Off Risskov at Aarhus.

# Fam. 8. Hildenbrandiaceæ.

The family of the Hildenbrandiaceæ, established long since (Comp. RABEN-HORST, Fl. eur. Alg. III, 1868, p. 408) and still maintained by SCHMITZ in 1882 (Hauck, Meeresalgen, p. 37), was later abandoned by this author as the presumed cystocarpia of the genus *Hildenbrandia* had proved to be conceptacles of tetrasporangia, and he therefore ranged this genus under genera incertæ sedis in 1889 (Flora, p. 22). In 1897 SCHMITZ and HAUPTFLEISCH range it as a dubious *Corallinacea*. On the other hand DE TONI places it under the *Squamariaceæ* in a subfam. *Hildenbrandtieæ* (Sylloge Alg. Vol. IV, sect. IV 1905, p. 1713). I think it better to consider the genus as a representative of a particular family intermediary between the *Squamariaceæ* and the *Corallinaceæ*. Although the sexual reproduction is unknown, the family is sufficiently characterized by the want of incrustation with lime of the frond, by the presence of immersed conceptacles of sporangia, and by the oblique divisions of the sporangia. The conceptacles resemble those of the *Corallinaceæ* but develop in another way, as will be mentioned below. Oblique divisions of the sporangia do not occur in the *Corallinaceæ*, but are characteristic of several *Squamariaceæ*.

# Hildenbrandia Nardo.

### 1. Hildenbrandia prototypus Nardo.

Nardo, De novo genere Algarum cui nomen est Hildbrandtia prototypus. Oken's Isis 1843, p. 675; Hauck, Meeresalg. p. 38.

Zonaria deusta Lyngbye, Hydr., 1819, p. 19 ex parte; cfr. notula.

*Erythroclathrus pellitus* Liebman in Flora Danica, tab. 2317, fig. 2, 1840 (sterile). *Hildenbrandtia rosea* Kützing, Phycol. generalis, 1843, p. 384; J. Agardh, Spec., II, pars 2, 1852, p. 495. *Hildenbrandtia sanguinea* Kützing, Phycol. generalis, 1843, p. 384, tab. 78, V. *Hildenbrandia Nardi* Zanardini, Synops. Alg. in mar. Adriat., p. 238; J. Agardh, Spec. II, p. 494.

When young, the crusts are nearly orbicular, or with a more or less lobed margin. A number of such young crusts frequently fuse together into a large crust, leaving no traces of the limits between the particular crusts. On the other hand, older crusts may, when meeting, be separated by a very distinct limiting line.

The margin is composed of radiating filaments, the ultimate cells of which are long and almost colourless, frequently swollen at the end. Not only the outer-

most cell, but also the second cell from the border may be several times as long as broad, longer than the next inward following cells of the basal layer, from which it must be concluded that intercalary divisions may occur. Now and then the number of the cell-rows is increased by ramification. The fig. 121 A suggests that the cell-rows may branch by dichotomy; but a closer examination showed that their ramification is really lateral (fig. 121 B. The crust represented in this figure showed numerous lateral branches, some of which penetrated between and under the pri-





mary filaments, in the latter case causing irregularities in the structure of the basal layer. In other cases this layer showed a very regular structure; it is densely appressed to the substratum, without rhizoids.

Horizontal divisions occur at a small distance from the margin. The adult frond is composed of regular vertical rows of nearly cubical cells, which are 4 to  $6.5 \mu$  broad. The cell-walls are firm, not swelling at the death of the cells. There is a single calotte-shaped chromatophore situated in the upper part of the cell (fig. 123 C).

The tetrasporangia occur in immersed conceptacles, which often occupy the whole crust except the marginal part and are uniformly spread over it, but may also be arranged in groups. In a fully developed state, the nemathecia are nearly globular or a little depressed, about  $100 \mu$  in diameter. The sporangia are situated on the bottom and the sides, and even on the under side of the peripheral part of the roof, the thickness of which diminishes towards the aperture. The conceptacle is not prominent; on the contrary, the surface is often a little sunk towards the aperture.

The conceptacles arise from a small group of superficial cells which produce tetrasporangia, while the contiguous cells remain vegetative and continue dividing by horizontal walls, with the result that the sporangia are placed in a low cavity.

26\*



Fig. 122.

Hildenbrandia prototypus, vertical section of old crust showing two conceptacles and limiting lines between the productions of three years. 195:1.

usually apparently a year (or more ?), while the crust grows gradually in thickness. When the sporangia have been emptied, new ones are produced on the same place from the cells forming the bottom of the cavity, within the emptied sporangial walls or between them, and at the same time the formation of sporangia extends

at the sides and upwards on the lateral walls of the cavity, the cells of the vertical cell-rows limiting the cavity at the sides producing sporangia directed obliquely or horizontally towards the centre of the cavity, which gradually takes a nearly orbicular outline. The sporangia-producing cells divide into a small stalk-cell and a greater outer cell, the sporangium. The stalk-cells of the lateral sporangia seem usually to decay, and the replacing sporangia must therefore be produced by the cells of cell-rows situated within the stalk-cells. In such a manner the conceptacle increases in transversal outline, new vertical cell-rows being gradually engaged in the production of sporangia. The parts of the cell-rows which are active in this manner are consumed by this production, and the continuity between the upper part forming the roof of the conceptacle and the under part is thus abolished. The upper part of these cell-rows therefore finally decays, at least in those situated nearest the aperture, where the regular arrangement of the cells is disturbed; the cell-walls swell, and the contents become discoloured and degenerate (fig. 125 A). In the peripheral part of the roof, the undermost cells of the interrupted vertical cell-rows often undergo a growth in a transversal direction, in consequence of which the cell-rows become bent inward below (fig. 122). The above

In specimens collected in June I found such cavities about 6 cells in diameter and not so deep but that the sporangia reached the border of the aperture (fig. 123 A). The sporangia in these young conceptacles are of different age. Besides fully developed or two-parted sporangia young ones are found, but also aborted sporangia occur, having sometimes the character of paraphyses (fig. 123 A, B), The production of sporangia continues a very long time,



Hildenbrandia prototypus, vertical sections of young conceptacles. A and B from specimen collected in June (near Refsnæs), C, from spec. collected in January (Store Belt). 560 : 1. described development of the conceptacles has evidently been known to SCHMITZ, as can be seen from the diagnosis of the genus *Hildenbrandia* in SCHMITZ and HAUPT-

FLEISCH Corallinaceæ in ENGLER u. Prantl, Nat. Pflanzenfam. I,<sup>3</sup>, p. 544. It is here said that the conceptacles are "anfangs sehr klein, unter allmählich fortschreitendem Verbrauch des nächst angrenzenden Gewebes allmählich an Grösse zunehmen", and that they frequently fuse laterally together. The development is designed as "lysigen" though it is not lysigenous in the usual significance of the word.

The sporangia are somewhat variable in shape and dimensions; they are now ovoid or obovate, e. gr.  $21 \mu$  long,  $14 \mu$  broad, now long, nearly cylindric, e. gr.  $30 \mu$  long,  $9.5 \mu$  broad. The length varies between (16-)21 and  $30 \mu$ , the breadth between 9 and  $12 (14) \mu$ . No relation between the dimensions of the sporangia and the locality has been found. The dividing



Fig. 124. Hildenbrandia prototypus. Vertical section of conceptacle with undivided and empty sporangia. Above a ripe sporangium. 560:1.

walls are always oblique. The first wall is much inclined to one side, the two following to the opposite side and often parallel to each other. But the first wall is often broken where it meets the following walls, in such a manner that the succession of the walls is not always easily discernible. The upper part of the first wall is often bent downwards so that it goes in continuation of the upper secondary wall, and the sporangium thus presents the appearance of having been divided first



Fig. 125.

Hildenbrandia prototypus. A, left side of conceptacle in vertical section. B-K, ripe sporangia. A-F from Karrebæksfjord, G-K, from Guldborg. 560:1.

into three by two parallel walls and afterwards by a wall dividing the middlemost cell into two (fig. 125 J, B, E, F). The secondary walls nearly always intersect the primary one, but usually near its border; this is true particularly of the undermost wall, which may also meet it at the very border or even intersect the outer wall under the border (fig. 125 C). An extreme case is shown in fig. 125 K where the sporangium has the appearance of having been divided by nearly parallel walls; but on regarding only the insertions and not the curvatures of the walls, it

will be seen that the middlemost (primary) wall is inclined to the left, the two others to the right; the walls, however, do not intersect, in accordance with the unusually narrow shape of the sporangium.

After the evacuation of the tetraspores, the sporangial walls are kept for a long time; they swell and fill the conceptacle. They have been considered as paraphyses by KÜTZING and others, but such organs do not occur in the adult conceptacles (comp. SCHMITZ and HAUPTFLEISCH l. c.). Small Sarcina-like bacteria sometimes form strings between the empty sporangial walls.

Conceptacles are met with at all seasons, and ripe sporangia have been found in all the months of the year, most frequently, however, in summer. As a rule empty, ripe and unripe sporangia are found simultaneously, from which it must be concluded that the formation of sporangia continues during the whole year, in the winter only with diminished activity. At what moment the development of the conceptacles begins I cannot say with certainty as I have seen but a small number of young stages. The youngest of the observed stages (fig. 123 A, B) were met with in June, which might suggest that the development of the conceptacles begins in spring, when the growth of the crust must be supposed to be active.

In older crusts the periodicity of the growth is marked by distinct limiting lines between the layers of the successive years. The upper line in fig. 121 probably represents the surface of the frond at the end of the foregoing season, but the lower, more irregular line does not represent an old surface; the deepenings are the bottoms of emptied conceptacles, and the higher parts between them represent the limit of the crust after disorganisation of its upper parts. It really frequently happens that the outer cell-layers die in winter over a greater or lesser part of the crust, and the faculty of growth is then often restricted to limited portions of the frond, which then become higher, and provided with conceptacles, while the other parts are low and sterile.

The species is widely spread in the Danish waters, particularly in shallow water, also over the low-water mark, and in sheltered places, where it is often a characteristic element of the vegetation, covering the stones with a red crust in company with *Ralfsia* etc., frequently under *Fucus*. But it is also common in deeper water, even in the greatest depths where vegetation has been met with, e. g. in the North Sea at 31 meters depth, in the Little Belt at 26,4 m and near Bornholm at 38 m, but it seems to be less abundant at greater depths. It has repeatedly been met with in a fructiferous state at about 19 meters depth, at Bornholm even at 29 m. In very insolated localities in shallow water it takes a yellowish colour during summer.

Localities. Ns: aF, off Thyborøn, 31 meters, small sterile specimens; groin at Thyborøn. — Sk: YU, Roshage, Hanstholm, 2 m, small sterile spec.; washed ashore near Bulbjerg, sterile; Hirshals, on stones adhering to the hapters of Laminariæ washed ashore after storm, sterile. — Lf: Rønnen near Lemvig, 3 m, MA, off Jestrup, 5 m; Oddesund, stone slope, fr.; Nykøbing and otherwhere in Sallingsund; aT<sup>1</sup>, Draaby Vig; Livø Bredning (C. H. Ostenfeld); west side of Feggeklit. — Kn: Herthas Flak, 21—25 m, ster.; Hirsholmene; Deget; Busserev; Frederikshavn; Nordre Rønner. — Km: Mariager Fjord, at Hobro; ND, off Fornæs, 11,5-13 m. - Ks: HR south of Hesselø; shore at Gilleleje; D, off the entrance to Isefjord; Ourø, near Roskilde and Boserup in Isefjord. -- Sa: FS, Vejrø Sund; PG, west of Hatter Rev; north end of Besser Rev; north-side of Revsnæs (Ostenfeld); shore by Koldby Kaas; Bolsaxen; Hindsholm (Lyngbye); NZ, off Tørresø; Odense Fjord, inner side of Enebærodden (!) and shore at Hofmansgave (Car. Rosenberg); Juelsminde. - Lb: OB, off Stavrshoved; Snoghøj, Middelfart, Fænø a. o. places from 0 to 19 meters; CE, south of Helnæs, 26 meters. - Sf: UV, north of Ærø; Birkholm. - Sb: Refsnæs; Romsø Sund (Ostenfeld); NU, off Strandskoven near Bogense; stone reef at Korsør; GP, Halskov Rev; near Sprogø, 10-15 m (Ostenfeld); AC, off Knudshoved, 17 m; DN, Vengeance Grund; Nyborg Fjord, shallow water; near Vresen, 23-24 m (Ostenfeld). UT and US<sup>1</sup> in Langelandsbelt, about 19 m. - Sm: Karrebæksfjord off Skraverup (Warming); Guldborg (C. Christensen); HF, west of Farø. --Su: bM south of Hveen, 22,5 m; Hvidøre; off Charlottenlund; south end of Middelgrund; Trekroner (Rützou); QC, QD, Saltholms Flak; PR<sup>1</sup> off Dragør, 4 m. - Bw: DV, south of Marstal; LC, near Gulstav, 11 m; UP off Kramnisse Gab; UM, Kadetrenden. - Bm: HG, Præstebjerg Rev, 7 m; QS, N. of Møens Klint 21 m; at Møens Klint; VD, Bøgestrømmen; QQ off Rødvig; RG, N.W. of Falsterbo; QN, off Køge Søhuse 6,5 m. - Bb: SF, Adler Grund; SH, Rønne Banke; Off Rønne, 13 and 38 m (Børgesen, !), reef at Rønne; Davids Banke, 29 m; off Gudhjem; YA, east of Dueodde lighthouse 38 m; Christiansø.

### 1. Hildenbrandia Crouani J. Agardh.

J. Agardh, Spec. G. O. II, 1852, p. 495, III, 1876, p. 379; Batters in Journal of Botany 1897, p. 438. Hildenbrandtia rosea Crouan, Florule de Finistère, 1867, p. 148, pl. 19 fig. 126, non Kützing.

In the Little Belt I found by dredging in depths of 15 to 19 meters a stone covered with crusts of a *Hildenbrandia* which in hanit scarcely differs from *H. prototypus*. It forms pretty blood-red crusts with similar conceptacles. In the structure of the frond and the shape and dimensions of the conceptacles it agrees also with the named species. The cells are  $6-7\mu$  broad and contain a calotte-shaped chromatophore, the conceptacles are up to  $100 \mu$  in transverse diameter. On the other hand, it differs decidedly by its cylindric sporangia divided by parallel oblique walls, in which respect it agrees with *Hildenbrandia Crouani* J. Agardh.

This species was first described on the basis of specimens sent from CROUAN, but, as shown by AGARDH and BATTERS, the brothers CROUAN have confounded it both with *H. rosea* Kütz. (*H. prototypus*) and with *Hæmatocelis rubens* J. AGARDH (BATTERS 1. c. p. 438). I have had an opportunity of comparing my specimens with those in AGARDH's herbarium sent from CROUAN (herb. AGARDH nº 27613 "roches de l'anse du Corsens, environs de Brest") upon which his description is founded, and I have found them fully agreeing. I found also accordance with microscopical preparations from BATTERS in AGARDH's Herbarium.

The conceptacles are similar in structure and development to those of *H. pro*totypus. The cell-rows in the peripheral part of the roof are much bent inward below, in consequence of the transverse growth of the undermost cells, as sometimes also occurs in *H. prototypus* (comp. p. 204), while the cell-rows in the inner part of the roof decay. The sporangia are produced, as in *H. prototypus*, from the bottom and the sides, and also from the peripheral part of the roof. A little stalkcell is present; J. AGARDH has already perceived that the sporangia are pedicellate, but he wrongly indicates that the stalk is articulated (Sp. III, p. 379). The sporangia were found to be  $19-30 \mu$  long,  $6-7 \mu$  broad; the normal length of the fully ripe sporangia is probably nearest the upper limit indicated. The sporangia have thus the same length as those of *H. prolotypus*, but are narrower.

Zonate sporangia, divided by transverse walls, were described and figured in *Hildenbrandia rubra* Harvey in Phycol. Brit. pl. 250, 1851; but it is rather probable that this figure really represents *H. prototypus*, as it shows the same shape of the



Fig. 126. Hildenbrandia Crouani. Vertical sections of conceptacles. 560:1.

sporangia as in this species, and the pretended zonate division might then be due to an inexact observation of the irregularly divided sporangia.

Zonate sporangia have further been described in *H. prototypus* var. kerguelensis ASKENASY (Forschungsreise S. M. S. Gazelle. Botanik, Berlin 1888 p. 30), the sporangia of which are said to be cylindric and divided by exactly parallel walls in 4 parts. As nothing is said with regard to the direction of the walls it must be presumed that they are transverse. It otherwise differs from *H. Crouani* by its conceptacles being up to  $200 \mu$  high but only half as broad, while those of *H. Crouani* are broader than high.

Locality. Lb: Opposite to Middelfart, 15-19 m, July 1900.

# Fam. 9. Corallinaceæ.

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H. F. G. STRÖMFELT (1886), Om algvegetationen vid Islands kuster. Göteborg.

N. SVEDELIUS (1911), Corallinaceae. Engler u. Prantl, Nat. Pflanzenfam. Nachtr. zu I. Teil, Abt. 2. Leipzig. G. THURET (1878), Études phycologiques. Publ. par les soins de M. le dr. E Bornet. Paris.

When carrying out my systematic investigations in the Danish waters, I arranged with M. Foslie, the well-known authority on calcareous alge, that he should deal with the Melobesieæ-group of the family of Corallinaceæ, and forwarded to him accordingly, from time to time, such material as I had collected of these algae, which he also mentioned in various publications. Unfortunately, M. FOSLIE'S energetic work in this field was brought to a close by his unexpected and premature decease in 1909. Since then, I have collected but few calcareous algæ, and nearly all the present specimens from Danish waters have thus been determined by Foslie. As we know, this writer repeatedly altered his view concerning the limitation of these difficult species, and his last great work on Northern Melobesieæ (Remarks 1905) bears evident witness to his indecision on this point. When, after his demise, I myself took up the task of dealing with this group, I considered it necessary to investigate all species by means of microtome sections, in order to obtain closer knowledge as to the structure of the frond and reproductive organs, being also further instigated hereto by the newly published works of PILGER, Mme LEMOINE and MINDER. In many cases, the results attained were disproportionate to the amount of time involved, partly owing to the fact that the great bulk of the material had only been preserved in a dried state, and also because suitable developmental stages of the various sorts of conceptacles were in many cases lacking. With regard to distinction of species, for the Lithothamnia I have in the main followed Foslie in his valuable work above-mentioned; on the other hand, closer investigation has led me to distinguish several new Melobesia species.

With regard to structure and development of the frond and reproductive organs, I may refer to the works above quoted by ROSANOFF, SOLMS, PILGER, Mme LEMOINE, MINDER and SVEDELIUS, as also to what is stated below with regard to the various species. It will here suffice to mention certain particular features.

The frond is in all cases composed of branched cell filaments, the cells of which are connected up by pits of the structure characteristic in Florideæ, in the middle of the transverse walls. These pits are however, very thin, and are often

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not distinctly visible in the dried material; they are therefore in many cases not shown in the illustrations, or if so, only in small numbers, though as a matter of fact, they are always present, or have at any rate been so. I mention this point, as Mme LEMOINE states that the cells are in some cases connected by open channels, (Struct. p. 35) and that in other instances, neither pits nor channels were found (l. c. p. 37). As illustrations of the latter, the writer in question cites *Lithothamnion læve* and *L. norvegicum*; I can here refer to my figs. 129 and 143, where the pits are shown.

Pits between cells belonging to different filaments are found in the Danish species only within the genus *Lithophyllum*, where the cells in the perithallium form transverse layers, in which they lie at equal height, and are then connected by pits with all the cells in the same layer, with which they are in contact. This has, it is true, been known before, but the importance of the fact as a systematic character has not been sufficiently emphasized. The character in question would in particular seem to afford an excellent means of distinguishing between the genera *Lithophyllum* and *Melobesia*, which otherwise closely resemble each other. Unfortunately, I have not been able to ascertain how these pits arise; they are formed at an early stage, and I must presume that they originate in a similar manner to the secondary pits in the *Rhodomelaceæ* etc., though I have not been able to demonstrate the co-operation of nuclei in the process, probably owing to insufficient fixing and staining of the material.

In all other genera (where, as we have seen, no such transverse pits are found) the cells possess another means of entering into connection with cells in other filaments, viz. by forming an open communication between them, the separating wall being partially dissolved. These fusions, which were first described by Ro-SANOFF, are of common occurrence in the Danish species of the family which do not belong to the genus *Lithophyllum*<sup>1</sup>.

Where the cells lie densely packed and the walls are thin, the fusions make themselves apparent merely by the fact that the longitudinal walls are partially dissolved (*Lith. Lenormandi* fig. 133 D); where the cell walls are thicker, on the other hand, a distinct connecting channel of varying length is seen. These appear both in the hypothallium and in the perithallium, and may very often take place between more than two cells. They are particularly easy to distinguish in the basal layer of *Melobesia* and in the central tissue of the upright, branched *Lithothamnia*. In the latter, they often form characteristically curving partially branched bodies, which may embrace almost all the cells in the central tissue (fig. 139). In the perithallium also, however, of the mentioned *Lithothamnia*, they may be extraordinarily frequent (*Lith. calcareum*, fig. 144, etc.). Fr. SCHMITZ, who has investigated these fusions with regard to the behaviour of the nuclei, found in 1880 (Untersuch. über die Zellkerne der Thallophyten. Sitzungsber. der niederrhein. Gesellsch. f. Natur- u.

<sup>1</sup> Of the species mentioned below, they appear to be lacking only in *Choreonema Thureti*, where the vegetation organs are highly reduced (cf. Minder l. c.) and in *M. minutula* (fig. 172).

Heilkunde zu Bonn 1880) that the nuclei, in two fusing cells of Jania rubens did not fuse together. I came to a different result on investigating this point in several

other species, especially Corallina officinalis. In a tetraspore-bearing plant of this species I found the fusions followed by a fusion of the nuclei. The process was studied in the central tissue under a young conceptacle where numerous fusing cells were found, partly in pairs, partly a greater number fusing together. As shown in fig. 127, the two nuclei of a fusing pair of cells are frequently found lying near each other at the place where the two cells have fused together, and there is reason to believe that the nuclei have been active in the realisation of the cell-fusion. In some cases the nuclei were found touching, and finally fused cells were found containing only one nucleus situated at the same place and derived from fusion of the two nuclei (fig. 127 D). These fusional nuclei seem to be



Fig. 127. Corallina officinalis. Fused cells from a vertical section of a young joint under a young sporangial conceptacle. 730:1.

able to fuse with other nuclei when fusion takes place between more than two cells. In fig. 127 D is shown a syncytium produced by fusion of four cells and containing at left two nuclei in mutual contact and near the middle a nucleus which must be supposed to have arisen from fusion of the nuclei of the two cells at right. This nucleus has approached the middlemost opening, where it would perhaps later on have fused with the other fusional nucleus. Syncytia arising from fusion of four cells but containing only one nucleus, undoubtedly produced by fusion of the nuclei



Fig. 128. Lithothamnion glaciale var. Granii. Syncytia produced by fusion of from two to four cells, all showing only one nucleus; at right a cell containing starch grains. 650:1.

of the cells, I have observed in Lithothamnion glaciale var. Granii (fig. 128). Also in Melobesia uninucleated syncytia produced by fusion of two cells were observed. It must therefore be supposed that fusion of nuclei generally occur in the fusing cells.

That SCHMITZ has not observed them may be due to the fact that the process was not so far advanced in the plant investigated by him; it might also be imagined, however, that fusion does not take place in all cases, since multinucleate syncytia are found even in older tissue. It is not unlikely that the nuclei may themselves co-operate in the process of fusion, the nuclei of the two cells placing themselves opposite each other in the two cells and bringing about a

dissolution of the cell wall. The reason of their taking up such a position would then be, that a mutual attraction exists between them, in which case it would be natural to suppose that such attraction should continue to exist after the fusing of

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the cells, finally resulting in a fusion of the nuclei themselves. If this were so, then the fusion of the nuclei would be of no particular importance in itself, but merely a consequence of the cell-fusion. Such supposed co-operation of the nuclei in effecting the fusion of cells is, however, purely hypothetical; I have not with certainty observed the nuclei immediately prior to commencement of the fusions, and it must be admitted that certain cases where cell fusions took place between four cells (fig. 127 D) do not tend to support the theory. Fusion of nuclei in vegetative cells of higher plants has recently been observed in several cases, where cells have, for some reason or other, proved to contain more than one nucleus (cf. for instance Schürhoff, Kernverschmelzungen in der Sprossspitze von Asparagus officinalis. Flora, N. F. 8. Bd. 1916, p. 55).

The cells always contain, fusions apart, a single nucleus. The only exception is the female plant of *Corallina officinalis*, where the cells of the central tissue contained from two to four nuclei. The chromatophores are small, disc-shaped; there is often a rather small number in each cell (figs. 130, 143 E; comp. Pilger l. c. p. 253).

Starch-grains occur in all the species. They are often very numerous, particularly in the older tissues. Mme LEMOINE distinguishes between single and compound (coalescents) starch grains. According to my observations, this distinction appears to depend exclusively on whether the cells are more or less densely filled with starch grains, in the first case the grains may be applanated on the faces where they meet, as also stated by PILGER (l. c. p. 254), but they are not really connate. In *Lithothamnion glaciale* var. *Granii*, which is said by Mme LEMOINE to possess compound starch grains, I found distinct single grains (fig. 128). The starch-grains frequently contain a small air-bubble in the centre in the preparations from dried specimens (comp. figs. 130 B, 143 F, 174).

The well known transversal limiting lines which undoubtedly indicate periods of stand-still in the growth occur in all the species of *Lithothamnion*, except those with thin crust, but they are also met with in *Lithophyllum orbicalatum* (fig. 180 A), whereas Mme LEMOINE did not find them in any species of this genus (l. c. p. 28). As shown by this author they are very intensely stained by hæmatoxyline; they may pass between the cells, coinciding with the middle-lamella, but more frequently they meet the longitudinal walls of the cells without bending under them (figs. 136, 138, 143, 144, 145). Mme LEMOINE describes further alternating zones with varying power of staining with hæmatoxyline. Such zones, not limited by a blue line, were met with in *Lithophyllum norvegicum* where the ordinary limiting lines were otherwise also present (fig, 143 B, C).

In some genera (*Melobesia*, *Lithophyllum*, *Corallina*) unicellular, hyaline hairs occur. They resemble those occurring in numerous other Florideæ (com. L. KOLDERUP ROSENVINGE, Remarks on hyal. unic. hairs; Biolog. Arb. tilegn. E. Warming, 1911, p. 203) but differ, however, in not being limited from the cell producing them by a transversal wall. The hair-producing cells have been long known in the species of *Melobesia*, particularly *M. farinosa*, where they were given the name of heterocysts by ROSANOFF (1866 p. 70), but as shown by SOLMS (1881, p. 24), they are really hairs or hair-producing cells. They are easily recognizable after the hair has been shed, showing a scar left by the latter; I propose to name them trichocytes or hair-cells.

The sporangia are always divided by one or three transversal walls, dividing the cells into two or four spore-cells. Vertical divisions I have only found as rare exceptions in *Lithothamnion Sonderi* (fig. 137 E, F). The tetrasporic sporangia are first divided by a transversal wall, but the formation of this wall proceeds slowly from the periphery towards the centre, and the formation of the two following walls has frequently begun before that of the first is completed. In *Corallina officinalis* I found that the primary nucleus of the young sporangia divides into four nuclei which arrange themselves in a longitudinal row in the middle of the sporangia, and that these rest for a long time in this stage before the divisions, which take place almost simultaneously (fig. 197). Also in *Epilithon membranaceum* the three divisions are almost simultaneous (fig. 152, comp. otherwise fig. 134). The dividing wall is shown in figs. 131 B and 142.

The number of spores is constant in most of the species, either 4 or 2; but in some species both disporic and tetrasporic sporangia are met with. One of these species is *Lithothamnion læve* which, however, in the Danish waters has only been found with disporic sporangia. The above mentioned fact that the divisions of the tetrasporic sporangia are, at least in several cases observed, almost simultaneous, makes it improbable that the disporic sporangia can here be interpreted as unripe, not fully divided. It is an incontestable fact that some species may, according to circumstances, have tetrasporic or disporic sporangia. This I have also found to be the case in *L. Lenormandi*, in which only tetrasporic sporangia were previously known. In *Melobesia Fosliei* also, and in *M. minutula*, both kinds of sporangia would seem to occur.

In material fixed in Juel's liquid the protoplasm of the tetraspores showed a foamy structure. The central part containing the nucleus was brighter and distinctly marked off from the outer (figs. 132, 142 B and Plate III fig. 1).

The antheridia present considerable differences as to their position and development. In Lithothamnion Lenormandi they have a similar position to that previously described in L. polymorphum, being produced on the surface of great bushes extending from the periphery towards the centre of the conceptacle (Plate III fig. 2). If this structure is to be found in all the species of the genus, we have here an important generic character. In Epilithon membranaceum, referred by some authors to the genus Lithothamnion, the antheridia are, as shown by GUIGNARD (Rev. gén. de Bot. I. 1889, p. 182) seriate in short filaments clothing the bottom of the conceptacle, and in the other genera the antheridia (spermatangia) are also placed on the bottom of the conceptacle, being produced as outgrowths from a layer of small cells, but they are not seriate. The antheridia are more or less lengthened, short cylindrical or upwards somewhat thickened and more or less curved. In Melobesia Lejolisii, the spermatia are produced at the end of long sterigmata, as shown by Mrs. WEBER-VAN BOSSE, and the same was found in Lithophyllum Corallinæ. In the last named species the isolated spermatia found in the conceptacles were seen to contain two nuclei (fig. 189), an interesting fact, as spermatia with two nuclei have formerly only been observed in spermatia fixed to the trichogyne, but not at an earlier term.

Concerning the development of the cystocarp in the Corallinaceæ, diverging statements have been advanced. As I have had no occasion of making thorough researches on this question, I must, in referring to the quoted papers of Solms, SCHMITZ U. HAUPTFLEISCH, PILGER and MINDER, content myself with stating some few facts noted in some of the species in question.

The carpogonial filaments are, at least usually, two-celled, being composed of a terminal carpogonium and a cell situated under it, separated from it by a more or less inclined wall; probably an auxiliary cell (fig. 148 C). A hypogynous cell as that described in Choreonema by MINDER (l. c. p. 12) was in no case observed. As shown by BORNET and THURET (1878) and SOLMS (1881) a large disciform cell, from the border of which the carpospores are produced, arises after the fertilization in the bottom of the female conceptacle. SOLMS and SCHMITZ were of the opinion that in Corallina it arose from fusion of all the auxiliary cells. PILGER showed that in Lithothamnion Philippii the two cell-layers situated below the carpogonial branches in fusing together take part in the formation of the disc-cell. On the other hand, MINDER, by a careful study of Choreonema Thureti, showed that the disc-cell arises in this plant from the fertilized carpogonium, which increases, becomes lobed and gradually fuses with all the auxiliary cells, the contents of which is absorbed by the disc-cell, which is thus no fusion-cell. The statements of MINDER appear to be so well founded that they cannot be doubted and it must be supposed that similar processes also take place in other Corallinaceae, though with various modifications in the different genera, e. g. combined with other cell-fusions. Having in most cases had only insufficiently preserved material of female conceptacles, I can only state, that the carpospores are in most of the species examined produced at the periphery of the cystocarp, as in *Corallina* and others, but that in *Lithothamnion* Lenormandi and Lithothamnion polymorphum they arise also from various points of the bottom of the conceptacle. In these cases a disc cell could not be observed in the dried material and it was impossible to state whether the aberrant position of the carpospores is founded on the fact that the disc-cell is more irregularly lobed or whether it must be otherwise explained. As to HEYDRICH's statement of the development of the carpospores in Lith. polymorphum, reference may be made to the mention of this species below.

# Lithothamnion Philippi.

# Subgenus Eulithothamnion Fosl., char. mut.

Conceptacles of sporangia superficial or more or less immersed; the roof plane or vaulted.

# 1. Lithothamnion læve (Strömf.) Fosl.

FOSLIE in K. Rosenv. Deux. Mém., 1898, p. 14; Rev. Surv., 1898, p. 15; Remarks, 1906, p. 16 and 131;
Algol. Notiser V, 1908, p. 6; K. ROSENVINGE, Mar. Alg. N. E. Greenl., 1910, p. 100, fig. 1; Lemoine, Struct., 1911, p. 74, figs. 36 and 37.

Lithophyllum læve Strömfelt, Isl., 1886, p. 21, tab. I fig. 11-12.

Lithothamnion Lenormandi (Aresch.) Rosanoff, f. læve (Strömf.) Foslie, Contrib. II., 1891, p. 11. Lithothamnion tenue K. Rosenvinge, Grønl. Havalg., 1893, p. 778, figs. 4-7 (Alg. mar. Gr. p. 58). Lithothamnion Strömfeltii Foslie, Norw. Forms, 1895, p. 145.

This species, very common in the Arctic Sea, has been found in two localities in the sea north of Sealand, the most southerly stations known in Europe. The specimens from the Kattegat were mentioned by Foslie in 1906 (Remarks p. 131). I have examined the structure of the specimen from the Sound which was preserved in JUEL's liquid. The species is easily distinguished from *L. Lenormandi* by its smooth surface and the large conceptacles.

The thallus in the Danish specimens is thin. The filaments of the hypothallium are, as pointed out by Mme LEMOINE, loosely connected. When seen from the surface, they show here and there transversal fusions. The cells are  $21-33 \mu \log_{10}, 7, 5-9, 5 \mu$  broad. According to Mme LEMOINE, the undermost cells of the hypothallium form rectangular

cells directed towards the substratum, thus constituting "une rangée de rhizoides obliques". I have not been able to see anything of this kind in the specimen examined. The filaments of the perithallium are composed of a small number of roundish cells,  $7 \mu$  thick or a little more, up to 10 µ. These dimensions, which I found in specimens from both localities. are in accordance with Foslie's statement (Remarks p. 18), while Mme LEMOINE gives the thickness as only  $4-5\mu^1$ . The

<sup>1</sup> This indication is not in accordance with the figures of Mme LEMOINE, in which the cells are thicker.







cells of the hypothallium and the undermost part of the perithallium often contain a number of distinct starch grains. In the cells of the perithallium a nucleus and



Fig. 130. Lithothamnion lawe. A, cells from the perithallium showing chromatophores and nucleus. B, cells from the hypothallium showing starchgrains. 730:1.





Lithothamnion lave. A, vertical section of conceptacle of sporangia. B, part of a similar section. 200:1.

a small number of disc-shaped chromatophores could be distinguished. (fig. 130).

In the Danish specimens, only conceptacles of sporangia were met with. Their diameter is somewhat smaller than in the Greenland specimens; in the plants from Hesselø it is  $500-650 \mu$ , in those from Hellebæk  $600-800 \mu$ . The roof consists of narrow filaments of cells which are longer than in the vegetative frond, and connected

> with numerous transverse fusions, while the cells are only rarely fusing in the perithallium. The sporangia I found always disporic when fully developed,  $126-129 \mu$  long,  $67-72 \mu$  broad, thus somewhat smaller than in the specimens from Greenland. The species has otherwise been found with two and with four spores in the sporangia. Foslie has (1908, p. 7) given all the localities where it has been found with two-cel-

led sporangia only and those where it has been met with only with four-celled sporangia. Both are found in a number of localities in the arctic regions and at the Norwegian coast as well.



Fig. 132, Lithothamnion læve, Tetraspore, 390 : 1.

Localities. Ks: A, S.E. of Hesselø, 28 m on stone and shell. — Su: Hellebæk Aug., on Mylilus Modiola, Henn. Petersen.

# 2. Lithothamnion Lenormandi (Aresch.) Foslie.

Foslie, Norw. Forms, 1895, p. 150; Heydrich, Lithoth. von Helgoland, 1900, p. 78, Taf. II. fig. 23-25; Foslie, Remarks, 1905, p. 12; Mme Paul Lemoine, Struct. anat., 1911, p. 81<sup>-1</sup>; Deux. expéd. antarct. franç. 1913, p. 10.

Melobesia Lenormandi Aresch. in J. Agardh. Sp. G. o. II p. 514.

<sup>1</sup> Mme LEMOINE cites the fig. 7 of my paper, "Grønlands Havalger" as representing Lith. Lenormandi; however, it does not represent this species but L. tenue Rosenv. (= L. læve Strömf.). Lithophyllum Lenormandi (Aresch.) Rosanoff, Rech. anat. p. 85, pl. V, fig. 16 et 17, pl. VI, fig. 1, 2, 3, 5. (Fig. 5 is said in the text to represent L. Lenormandi, while in the explanation of plates it is attributed to L. lichenoides). Hauck, Meeresalg. p. 267, Taf. III fig. 4; Strömfelt, Algveg. Isl. kuster, p. 21, tab. I, fig. 9-10.

Lithothamnion squamulosum Foslie, Norw. Forms of Lithoth p. 155, Tab. 19 fig. 24-26.

Squamolithon Lenormandi (Aresch.) Heydrich, Die Lithoth. von Roscoff. Ber. deut. bot. Ges. 1911, p. 26, Taf. II.

This widely spread species has been met with in almost all the Danish waters. It is particularly characterized by its thin reddish-violet crust with a lobed, whitish border, by its hypothallium composed of densely joined filaments, and at all events in the typical species, by the

densely crowded conceptacles.

As pointed out by Mme LEMOINE, the hypothallium is composed of more densely joined filaments than in the other crustaceous species. According to this author, the number of horizontal filaments in a vertical section is usually 7—8; in thicker crusts it may be greater (fig. 133 *B*), in thinner it may be only 3—4 (fig. 133 *A*, *C*). In horizontal sections through the hypothallium transverse fusions are frequently seen





(fig. 133 D). Mme LEMOINE states that the filaments of the hypothallium "se relèvent d'une façon très brusque pour constituer les files du périthalle". This, however, is, in my opinion, not characteristic of the species, as will be seen in my fig. 133. The cells of the hypothallium which, according to Mme LEMOINE, are  $3-4\mu$  thick, I generally found somewhat thicker,  $3,5-6\mu$ , in specimens from the Limfjord  $5-6\mu$ , the length  $12-18,5\mu$ . The cells of the perithallium I found  $4-6\mu$  thick,  $4-13\mu$ long. In the perithallium also numerous transverse fusions occur, but as the cells are closely joined, the fusion canals are very short.

The sporangial conceptacles are very crowded, in particular in f. typica; they measure  $200-300 \mu$  in diameter. The flat roof is, according to FOSLIE, intersected by 25 to 35 muciferous canals, which is in accordance with my observations; I have, however, met with up to 45 canals. Transverse fusions between the cells of the roof are frequently met with. The sporangia which are otherwise always tetrasporic, are also normally so in the Danish waters. Conceptacles with disporic sporangia only, however, not infrequently occur (fig. 134 A). It might be suggested

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that the sporangia in such cases were not quite ripe, and would later on have been divided into four spores, but as in other cases the divisions have shown to be al-



Fig. 134.

Lithothamnion Lenormandi. A, vertical section of crust with sporangial conceptacles. B, tetrasporangium in two consecutive sections. C, tetrasporangium in three consecutive sections. A 63:1. B 200:1. most simultaneous (fig. 134 C) it seems most probable that disporic sporangia occur besides tetrasporic ones, as in several other species. Sporangia with 4 spores found in the Limfjord and in the Kattegat were  $100-112 \mu$  long,  $34-48 \mu$  broad; in specimens collected in Bramsnæs Vig (Ise Fjord) they were only  $53-91 \mu$ long,  $14-25 \mu$  broad.

Antheridial conceptacles were found in specimens from Staffans Flak in the Sound and from Bramsnæs Fjord. In both cases they were  $300-350 \mu$  in diameter, thus much larger than stated by FOSLIE (150

-200  $\mu$ ). In the specimens from the first named locality collected in September they were fully developed and showed a rather complicated structure, the spermatia being produced on the ultimate ramifications of dendroid systems of filaments given off from several points of the inner surface of the conceptacle, from the bottom and from the upper side as well (Plate III fig. 2). The structure of the antheridial conceptacles is thus rather similar to those of *Lith. polymorphum* described by HEYDRICH (Lith. Helg. p. 65, Taf. II fig. 1-3). The dimensions of the spermatia seem to be  $3 \times 4 \mu$ .

The cystocarpic conceptacles are hemispheric to conical,  $320-350 \mu$  in diameter. It is remarkable that the carpospores are not only produced at the periphery of the bottom of the conceptacle but from the whole face of the floor, a fact by which our species differs, as it appears, from the type not only of the genus but also of the family. The carpospores are  $50-63 \mu \log_2 21-32 \mu \operatorname{broad}^1$ .

<sup>1</sup> HEYDRICH has in 1911 (l. c.) established a new genus, Squamolithon, founded on Lithothamnion Lenormandi,



Fig. 135. Lithothamnion Lenormandi. Vertical section of cystocarpic conceptacle. 200:1.

This species occurs on stones and rocks, and on shells of molluscs (*Mytilus*, *Modiola, Trochus, Littorina*), from ordinary water-mark to 19 meters depth. Almost all the specimens belong to f. *typica*, a few only have been referred by FosLie to f. *sublævis*, which differs by smoother surface and less crowded sporangial conceptacles. It was rather surprising to me to find the species growing at low-water mark on the granitic rocks of Bornholm, where the salinity of the water is about  $7-8^{0/00}$  only. It was here fairly typical though sterile, and with numerous adventitious fronds, and occurred in fairly great numbers. In the other locality in the Baltic (RG), only sterile but rather large crusts were found.

Ripe sporangia have been met with in July (partly together with undivided) and September. Antheridial conceptacles with spermatia were found in July and September, and ripe cystocarpic conceptacles in July.

Localities. Ns: Thyborøn, groin no. 58, stunted specimens. — Lf: Søndre Røn by Lemvig; Thisted harbour (!, C. H. Ostenfeld); Sallingsund (Th. Mortensen); LS<sup>1</sup>, off Bjørndrup, east of Mors, 5,5 m. — Kn: Frederikshavn, at low-water mark; Trindelen, 15 m (small spec.). — Ke: EU, Lille Middelgrund, 14 m (small specim.); IA, Store Middelgrund, 16 m. — Ks: Ourø Sund; Bramsnæs Fjord. — Lb: At Lyngsodde off Middelfart, 15—19 m, large fertile crusts. — Sb: GP, at Halskov Rev, 9,5—11,5 m; Avernakhage by Nyborg, low water. — Sm: VC, Venegrund, 3—5,5 m. — Su: TF<sup>1</sup>, Staffans Flak, 11—13 m; PS, off Charlottenlund, 5,5 m. — Bm: RG, 6 miles N.N.W. of Falsterbo lighthouse, 11,5 m. — Bb: Helligdomsklipperne, Rø, Bornholm.

### 3. Lithothamnion Sonderi Hauck.

Hauck, Meeresalgen, p. 273, Taf. III, fig. 5; Foslie, Norweg. Forms, 1895, p. 127; Heydrich, Lithoth. Helgol., 1900, p. 77, Taf. II fig. 20-22; Foslie, Remarks, 1906, p. 23; Lemoine, Structure, 1911, p. 96.

Though this species has been met with in a number of different localities in the Danish waters, it has in most cases been found only in small quantities together with other species. I have therefore only little to communicate with regard to it, but must refer to the descriptions of HAUCK, FOSLIE and Mme LEMOINE.

As pointed out by FOSLIE and Mme LEMOINE, the hypothallium is feebly developed. According to the last-named author it consists only of a single layer of cells; "les autres se relèvent très rapidement pour former le périthalle". The ascending filaments may, however, rise more gradually, and the hypothallium may then consist of two or three cell-layers (fig. 136 B). The hypothallic cells measured  $5-7 \mu$ broad,  $15-21 \mu$  long; those of the vertical filaments I found to be  $3,5-7 \mu$  broad,  $5,5-11 \mu$  long. These measurements are somewhat smaller than those of Foslie and Mme LEMOINE. Transverse fusions between the cells are very frequent in the perithallium. In sections stained with hæmatoxyline the middle lamellæ are very distinct. In the same sections the horizontal limiting lines are intensely stained; their course is somewhat irregular (fig. 136). Older crusts may have a considerable number of layers. The cells of the under part of the frond are often filled with

and characterized principally by cytological statements relating to the development of the cystocarp. These statements are, however, very insufficiently supported, and I have had no opportunity of verifying them.



Lithothamnion Sonderi. A, vertical section of frond with a single-layered hypothallium. B, thinner crust with two or three layers of cells in the hypothallium, containing starch grains. C, upper part of a thick frond with an uneven surface. 350:1.

les, but seems otherwise to agree with this species. The conceptacles of sporangia were however a little smaller than usual,  $260-280\mu$  in diameter (inner diameter about  $200\mu$ ). The sporangia were tetrasporous, in some cases showing vertical divisions (fig. 137).



Fig. 137.

Lithothamnion Sonderi (?), from Halskov reef (no. 3171). A, vertical section through a crust with overgrown conceptacles.
63:1. B, part of a similar section with an overgrown conceptacle, showing the hypothallium. 350:1. C, sporangial conceptacle with sporangium. 205:1. D-F, sporangia with anomalous divisions. 205:1.

starch grains, but in other cases starch is wanting.

Fructiferous specimens I have had no opportunity to submit to closer examination. The sporangial conceptacles are, according to Foslie very little prominent,  $300-500 \mu$  in diameter, not overgrown, the sporangia tetrasporous.

A crust dredged at the beacon of Halskov Rev in Nov. (no. 3171) and referred by FOSLIE to this species, differs by having overgrown sporangial conceptacThe species forms crusts on stones and gravel, in depths from 5 to 24,5 meters. In one case it was found growing on a dead specimen of *Lithothamnion calcareum*. It has been found with sporangial conceptacles and cystocarpic conceptacles in May and September.

Localities. Sk: Off Hirshals, 13 met. (F. Børgesen). — Lf: ZY, Nissum Bredning, 5 met. (determination uncertain). — Kn: Herthas Flak, 20—23 met.; FF and TR, Trindelen, 23,5 and 15 met. — Ke: IP and IL, Fladen, 20,5—24,5 met.; IK, Lille Middelgrund, 17—19 met. — Sb: GP near the lightbuoy at Halskov Rev (no. 3171, see above); Strandby reef, W. side of Langeland (?). — Sm: VC, Venegrund, 4—5,5 met.

### 4. Lithothamnion glaciale Kjellm.

F. R. Kjellman, Norra Ish. algfl. p. 123 (93) tab. 2 and 3. Foslie, Norw. Forms p. 13; Remarks p. 26. Mme P. Lemoine, Struct. p. 92.

Nearly all the rather numerous Danish specimens referred to this species have been determined by FOSLIE, who received them from me at different times and accordingly gave them different names. In 1895 he described and figured Norwegian specimens, corresponding exactly to those mentioned here as var. Granii, under the name of L. flabellatum f. Granii. Later on this variety was referred to L. glaciale, an opinion which has only been expressed in Rev. Surv. (1900, p. 11, where after the name L. Granii, which is here a nomen nudum, is added: "(L. glaciale f. ?)"). As late as in 1905 Foslie referred specimens of these alge to L. glaciale, partly to f. Granii, partly to other forms. But in the same year (Remarks p. 59,<sup>1</sup>) Foslie established L. Granii as a distinct species. That he has been uncertain at the last as to the limitation of the species can be concluded from the fact that the same species, on p. 10 of the same paper, is mentioned as L. glaciale f. Granii. It is easy to understand that it has been difficult to come to a decision as to the delimitation of species when considering that Foslie (Remarks p. 28) "found it almost impossible to draw any line between L. Granii, admitted below, and L. glaciale". L. c. p. 59 is said, as to the relation between L. Granii and L. tophiforme f. divergens, that there are many specimens "which are quite like each other in almost every respect, but that the specimens of one species show a somewhat greater tendency in one direction and the other in a different one". It is however not to be seen in the named paper on which characters the difference between the two species really rests, save that L. Granii has thinner, usually more ramified branches. Some Danish specimens formerly determined as L. glaciale, in part as f. colliculosa, are now (Remarks p. 34) referred to L. colliculosum which is here regarded as a separate species, while he had formerly considered it a form of L. glaciale; a description of it is given, but he does not emphasize how it differs from L. glaciale. As I cannot see any distinct difference between these specimens and some of those referred by Foslie to L. Granii I prefer to adhere to Foslie's somewhat older opinion in regarding L. colliculosum and L. Granii as varieties of L. glaciale.

<sup>1</sup> Foslie's "Remarks" appeard however only in 1906.

#### var. colliculosa (Fosl.)

Lithothamnion colliculosum Foslie, Contrib. II, 1891, p. 8, tab. 3 fig. 1 ex p.; Norw. Forms, 1895, p. 75 ex p.; Remarks, 1905, p. 34.

FOSLIE has referred to *L. colliculosum* specimens from two localities in the western part of the Limfjord. They resemble arctic specimens of *L. glaciale* with not much developed processes which are thicker than in *L. glaciale* f. *Granii* and, as it seems, less closely placed, up to 4 mm high. The crust is well developed, expanded, and contains conceptacles. These specimens were found growing on *My*-tilus and stones.

#### var. Granii (Fosl.)

Lithothamnion flabellatum K. Rosenv. f. Granii Foslie, Norw. Forms (1895) p. 70, tab. 17 fig. 1-7, tab. 22 fig. 1.

L. Granii Foslie, Remarks (1905) p. 59.

All the other Danish specimens belong to this variety. It differs from the typical L. glaciale by more closely placed, thinner and often more ramified branches. The thickness of the branches, however, varies somewhat; it is lesser, for instance in f. reducta Foslie. The crust is usually much developed and may be widely expanded over the substratum. In the latter case the processes are frequently small, wartlike and rather spread, and the crust then frequently contains numerous conceptacles (fig. 138 A). When growing on pebbles on gravelly bottom it often completely encompasses the pebble, and when this is small, branches may project from it at all sides. Usually however, they grow principally to one side, viz. upwards, and these upward growing branches may branch repeatedly. In branching they often have a tendency to take globular form, and such globular branch-systems may at last be loosened, the conjunction with the pebble being given up. On gravelly bottom, loose individuals, "Ægagropila-forms", exactly similar to these branch-systems, are often found (Plate IV figs. 1-4). H. Jónsson assumes that the loose Ægagropila-forms of L. Ungeri and L. tophiforme are produced in the same manner off the shores of Iceland<sup>1</sup>. Probably loose individuals may also arise by division of other loose ones. On gravelly bottom the plurality of the individuals may be loose (e. gr. Lille Middelgrund, Ke). In the inmost localities in the Danish waters (Ks, Sa, Lb, Sb, Su) only specimens with well developed crust but small processes were met with.

The crust contains a hypothallium composed of few cell-layers from which obliquely ascending filaments continuing in the perithallium are given off. The cells of the hypothallium were in the specimen examined  $20-22 \mu \log_{2} 5-7 \mu$  broad. Mme LEMOINE states the dimensions for L. glaciale to be  $12-18 \times 2 \mu$ . The latter figure, however, must be presumed to be exceptionally low. Mme LEMOINE further states that the hypothallium gives off a layer of rhizoids or rectangular cells inclining against the substratum; this I have not found in the Danish specimens

<sup>1</sup> H. Jónsson, Om Algevegetationen ved Islands Kyster. Botan. Tidsskrift **30**. 1910 p. 322. — The Marine Alg. Veg. of Iceland. The Botany of Iceland, Part  $I_{11}$  1912 p. 154.

(comp. fig. 138). The same author finally states that the filaments of the hypothallium are "formées de cellules arrondies, très serrées les unes contre les autres, de sorte

sue they

qu'il est impossible de suivre le trajet de chaque file". As will be seen in my fig. 138, the filaments of the hypothallium are very distinct in well developed crusts. The cells of the perithallium are roundish, sometimes almost globular, usually however longer than broad,  $7-10,5 \mu$  long,  $4-8 \mu$ broad. They are often fused together two or three in a horizontal direction. The crust is divided in zones by horizontal lines stained intensely by hæmatoxyline.

The branches have a similar structure to the perithallium in the crust. The cells are usually oblong or rectangular with rounded angles. They are sometimes situated more closely together in the outer layer than in the inner, that is to say, the walls are thinner (fig. 139 A). The cells are  $5-7\mu$  broad,  $7-11\mu$  long. Transverse fusions between the cells are frequent, often connecting several cells; in tangential sections they are often especially numerous and appear as irregular, curved, partly ramified formations (fig. 139 C). In transverse sections of the central tis-



Fig. 139.

Lithothamnion glaciale var. Granii. A, longitudinal section of upper end of a branch. B, transverse section of branch, from the centre. C, tangential section of branch. 400:1.



Fig. 138. Lithothamnion glaciale var. Granii. A, vertical

section of crustaceous frond with sporangial conceptacles. 65:1. *B*, part of the same section, showing the hypothallium and a peripheral part of a conceptacle. 350:1.

cell-fusions contain, at least usually, only one nucleus (comp. p. 211, fig. 128). Starch grains appear very irregularly, without relation to the layers. The cells may contain a greater or smaller number of them, and they may consequently be placed closely together; but composed grains (comp. Mme LEMOINE, l. c. p. 94) do not seem to occur.

Conceptacles are frequently found, but only sporangial conceptacles were observed. They are usually placed on the branches, especially on the upper part of them, but they may also occur in the crusts when these are much developed. They are slightly prominent, about  $260-350 \mu$  in diameter. The conceptacles in the crusts show the same aspect as those of the branches (figs. 138, 140). By proportionally few countings I found 30-60 muciferous canals in the roof. The conceptacles are usually gradually overgrown and immersed in the tissue of the branch, and this is also the case with those of the crusts. In such immersed conceptacles the septa between the sporangia are frequently visible for some time (Plate III fig. 4). Slime-strings may also remain distinct after the im-



Fig. 140.

Lithothamnion glaciale var. Granii. Transverse sections of branches with tetrasporangial conceptacles. In A an immersed conceptacle filled out by tissue from the bottom. 65:1. mersion. Conceptacles filled out by tissue produced from the bottom of the cavity frequently occur (fig. 140 A). The sporangia are always two-parted,  $70-110 \mu$  long,  $39-50 \mu$  broad.

As mentioned above, the var. colliculosa has only been found in two localities in the Limfjord while a specimen found in a third locality of the same fjord seems to belong to the var. Granii. The specimens from the other localities were all referred to this variety, which is best developed in the eastern Kattegat where it was found in most of the localities in rather great quantities as branched specimens, partly loose. In the inner water it occurs only in the form of crustaceous specimens with short, often densely placed wartlike processes. The species has been found growing on stones,

gravel and shells, in the Limfjord in 5,5 meters' depth, in the Kattegat in 17-30 m, in the Samsø waters in 9,5--19 m, in the Great Belt in 19 m and in the Sound in 34 meters' depth. Ripe sporangia have been found in April-May.

#### Localities.

var. colliculosa. Lf: north of Rønnen by Lemvig (6874); Nissum Bredning off Helligsø tile-kiln, 5,5 m (C. H. Ostenfeld).

var. Granii. Lf: western Limfjord, on an oyster-bed, brought up by a diver; form with rather long unbranched branches. — Kn: FG, Herthas Flak; off Frederikshavn; TR, Trindelen. — Ke: IR and ZI, Groves Flak; IL and IQ, Fladen; IH and IK, Lille Middelgrund, in quantity, on pebbles and gravel and loose; IA, Store Middelgrund (! and F. Børgesen). — Km: Læsø Rende, a crustaceous specimen with scarce low papillæ, on a piece of coal; ND, N.E. of Fornæs. — Ks: HO, E. of Hesselø; EO, 26,5 m; A, S.E. of Hesselø. — Sa: E. of Samsø (C. Løfting); BE, off Sletterhage, 10 m; KM, E. of Øreflippen; PL, Wulffs Flak; north side of Refsnæs, 19 m (C. H. Ostenfeld); MS, S. of Klophagen by Endelave. — Lb: Middelfart. — Sb: MO, S.W. of Refsnæs (? young specimens); near Sprogø, 19 m (C. H. Ostenfeld). — Su: Øretvisten (Johs. Schmidt); on the beach by Hornbæk (Mrs. M. Fibiger), probably brought by fishermen from the southern Kattegat; bM, 22,5 m, crusts up to 1,5 cm in diameter with small wartlike processes.

#### 5. Lithothamnion norvegicum (Aresch.) Kjellman.

Kjellman, N. Ish. algfl. p. 122 (93), pl. 5 fig. 9-10; Foslie, Remarks 1905, p. 65; Lemoine, Structure, 1911, p. 108 fig. 11 and 48.
Lithothamnion calcareum Ellis et Sol. var. norvegicum Areschoug, Observ. phycolog. III. 1875, p. 4. Lithothamnion coralloides Crouan f. norvegica (Aresch.) Foslie, Norw. Forms 1895, p. 62, tab. 16 fig. 1–11.

According to FOSLIE, this species is almost always freely developed on the bottom (Remarks p. 66). The specimens found in the Danish waters were all loose. FOSLIE has referred them all to f. *pusilla* which, in his opinion, is "perhaps the typical form of the species". He observes however (l. c. p. 64 and 67) that they "partly approach stunted forms of *L. nodulosum* f. *gracilescens*". They give off branches in all directions and become up to 3 cm (more rarely 3,5 cm) in diameter.

The anatomical structure is not very different from that of *L. glaciale*. According to Mme LEMOINE, the cells are in the greater part of the frond rectangular, while



Lithothamnion glaciale var. Granii. Vertical section of sporangial conceptacle with ripe sporangium. 350:1.

Lithothamnion glaciale var. Granii. A, sporangium; the process of division not yet completed. B, ripe spore. 390:1.

near the periphery they are ovoid. This may be so, but it frequently happens that rectangular cells in the inner parts of the frond alternate with ovoid ones (fig. 143 C). The change may take place at the distinctive lines between the zones or independently of them. The zones are limited by somewhat irregular lines staining deeply by hæmatoxyline, and the staining power of the single layers may sometimes be a little different, but the limit between such zones is not always marked as a blue line (fig. 143 C). The irregular course of the distinctive lines is probably in accordance with the irregularity of the increase. Transverse fusions between the cells frequently occur, though not so frequently as in L. Granii, and not uniting so many cells as in that species. The cells are  $8-14 \mu$  long,  $6-9 \mu$  broad; the rectangular ones are  $11-14 \mu$  long,  $6-7 \mu$  broad. The central tissue shows a different aspect in transverse section, according to whether the section has fallen in a zone with rectangular or with roundish cells. The appearance of the starch is variable. It may appear in great quantities in the more deeply stained and in the less stained zones as well, all the cells being filled with starch grains except the outermost ones. In other cases it is entirely or almost entirely wanting.

Conceptacles were found in specimens from most of the localities named below; D. K. D. Vidensk. Selsk. Skr., 7. Række, naturvidensk, og mathem. Afd. VII. 2. 29 they were in all cases, when examined, empty and more or less destroyed. I found sporangial conceptacles  $300 \mu$  or somewhat more in diameter.

On stony bottom in 10-21 meters depth, usually associated with *Corallina* officinalis, in some places abundantly. Only found in the Samsø area.

Localities. Sa: KI, south of Hjelm; PH, Lindholms Dyb; east of Samsø (Løfting); Stenpladen off Sletterhage (G. Winther); BE and BF off Sletterhage.



#### Fig. 143.

Lithothamnion norvegicam. A, axile longitudinal section of branch. B, part of a similar section near the top. C, part of axile longitudinal section of frond. The upper part of the tissue was deeper stained by hæmatoxyline than the under part. The fusion canals with the over-lying cells appear as round figures. D, transverse section of the central tissue of a branch. E, cell-rows from the periphery of a section of a branch. F, cells with starch grains. A 31:1; B-D 350:1; E, F 560:1.

#### 6. Lithothamnion calcareum (Pallas) Aresch.

J. Areschoug in J. Agardh, Sp. g. o. II, 1851, p. 523. Foslie, Lith. Adriat. Meeres u. Marokko, Wiss. Meeresunt. VII. Heft 1, 1904, p. 13 and 32, Tafel II; Remarks, 1905, p. 67; Mme P. Lemoine, Répartition et mode de vie du Maërl (Lithothamnion calcareum) aux environs de Concarneau (Finistère), Annales de l'Institut océanographique, tome I, fasc. 3, 1910; Structure, 1911, p. 102.

Millepora calcarea Pallas, Elench. Zooph. 1766, p. 265.

Lithothamnion coralloides Crouan, Flor. Finist., 1867, p. 151, pl. XX no. 133.

This species has been found in a few localities, in particular in the eastern Kattegat, but always only in loose specimens without or with imperfectly developed conceptacles. It is, as elsewhere, rather variable. The Danish specimens have been referred by Foslie to the following forms.

1. F. squarrulosa Foslie, Lith. Adr. Meer. Taf. II fig. 1-4; Lemoine, Répart. du Maërl fig. 1, 5, 14, Structure pl. I, fig. 5. To this form approaches f. corallioides (Crouan) Foslie, Norw. Lith. p. 62 pl. 16 figs. 24-25, 27-31. — This form has terete branches spreading in all directions.

2. F. compressa (M'Calla) Foslie, On some Lithothamnia, 1897, p. 9, Lith. Adr.

Meer., 1904, p. 32 Taf. II figs. 15–23; Lemoine, Répart. du Maërl pl. I fig. 14. — It is "flabellate, the branch-systems spreading like a fan in all directions from the centre of the frond almost in one plane. Sometimes it forms rather thick and compressed fronds" (Foslie, Remarks p. 69).

3. F. palmatifida Foslie, Some new or crit. Lith., 1898 p. 6, Remarks p. 69; Lemoine, Répart. du Maërl pl. I fig. 3, Structure, p. 104. — "With branches more distant and palmate" (Foslie, 1905).

4. F. subsimplex (Batt.) Foslie, Norw. Lithoth. 1895 p. 62 pl. 16 figs. 38-42; Lemoine, Rép. du Maërl pl. I fig. 10, Structure p. 104. Frond "simple or feebly branching" (Foslie Remarks).

There are no distinct limits between these forms, which occur together at the same locality.

The structure has been mentioned by Mme LEMOINE (Structure p. 105), whose description may here be referred to. It will suffice to add some small remarks.

According to Mme LEMOINE there is always at the periphery a cortex composed by 5 or 6 layers of cells which are rectangular, while the other cells are ovoid. I have certainly observed such a cortex in some cases, but it does not occur normally; the outer tissue, in the sections examined by me, more frequently consisted of cells of the same shape as those of the inner tissues (fig. 144). Transverse fusions between the cells are very frequent. The size of the cells is somewhat variable, generally they are  $9-13 \mu \log_{1} 5-7 \mu$  broad. Starch grains were found in great quantity in all cells except the outermost. On being treated with acetic acid and iodine in potassium iodide the starch grains swelled and filled the cells with a homogenous violet-brown mass.



Fig. 144. Lithothamnion calcaream, Transverse section of frond, at the periphery. Several transverse fusions. 350:1.

In a specimen from Trindelen (ZB, July) empty conceptacles were found, the kind of which could not be determined; they were almost entirely immersed. Possibly they were antheridial conceptacles.

The species has been found in 17 to 30 meters depth, on gravelly or stony bottom, generally associated with other *Lithothamnia*, in particular *Lith. glaciale*, and with *Corallina officinalis*.

Localities. Kn: ZB, near Trindelen, 28-30 meters. - Ke: IL and IP, Fladen; IK, Lille Middelgrund. - Km: Læsø Rende, clayey bottom, small fragments (C. H. Ostenfeld).

## Subgenus Phymatolithon Foslie.

In 1898 FOSLIE (Syst. Surv., p. 4) established the genus *Phymatolithon*, founded on *Lithothamnion polymorphum*, and distinguished from the genus *Lithothamnion* chiefly by immersed conceptacles and the roof of the sporangial ones being depressed or cup-shaped. Later on he has referred *L. lævigatum* and another species to the same genus. I must, however, agree with Mme LEMOINE, who observes (Struct. p. 63) that the characters pointed out by FOSLIE are not sufficient for generic distinction but only for separation of sections beyond the genus. The roof of the sporangial conceptacles is frequently scarcely immersed, and it is often, particularly in L. *lævigatum*, convex within a feebly elevated border.

## 7. Lithothamnion polymorphum (L.) Aresch.

J. E. Areschoug in J. Agardh, Spec. II, pars 2, 1852, p. 524 ex parte; Rosanoff, Mélobés., p. 99; Strömfelt, Algveg. Isl., 1886, p. 19, pl. I, fig. 1-3 (sporangia); Foslie, Norw. Forms, p. 86, pl. 17, fig. 17-23 (f. tuberculata, f. valida and f. papillata); Mme P. Lemoine, Structure, 1911, p. 87, pl. V fig. 2. Phymatolithon polymorphum (L.) Foslie, Syst. Survey, 1898, p. 4, Remarks, 1906, p. 75.

Eleutherospora polymorpha (L.) Heydrich, Lith. Helgol., 1900, p. 65, Taf. II, fig. 1-14.

The species forms more or less irregular crusts extended over larger boulders, of a thickness of up to 6 mm. As to the structure reference may be made to the



Fig. 145.

*Lithothamnion polymorphum. A*, vertical section of frond showing the hypothallium and the lower part of the perithallium. *B*, vertical filaments of another frond with narrower cells. *C*, cells of perithallium with starch grains. 350:1.

papers of Foslie (1906) and Mme LE-MOINE. The hypothallium is shown in fig. 145 A. The cells of the perithallium are somewhat variable in thickness,  $4-7\mu$ , in some specimens proportionally narrow,  $4-5\mu$  (fig. 145 B). Mme Lemoine mentions as an interesting character that the starch grains are single, very small and grouped at the ends of the cells. This is, however, not always so, for I found the starch grains up to  $3\mu$  in diameter, and in some parts, frequently the greater part of the crust, all the cells were filled with starch grains, while they were totally wanting in others, Particularly abundant starch grains were found in the tissue filling out the emptied conceptacles in the inner part of the crusts. Cells con-

taining starch grains at the ends of the cells but not in the middle were indeed observed, but only as exceptions. Transversal fusions between the cells of the perithallium occur here and there.

The increase in thickness of the crust normally takes place by continued growth of the perithallium, which may show several zones limited by horizontal, but somewhat irregularly running lines. In older crusts a more complex structure may be found, the frond being composed of two or more crusts one over the other, each with a particular hypothallium. This arises through cessation of growth in thickness in certain parts of the perithallium, which become overgrown by new crusts developing from other parts of the crust. This structure has been mentioned by Mme LEMOINE (Struct. p. 24 and 88, pl. V fig. 2), who appears to consider it as arising through differentiation of the same crust. In the new overgrowing crusts, the limiting lines between the successive zones of tissue are more or less inclined. This complex structure is not always found even in old fronds. Crusts up to 1,5 mm in thickness showing only one hypothallium are frequently met with,

The muciferous canals of the sporangial conceptacles open outwards in a low hollow surrounded by a slightly elevated border, but it is sometimes very slight or



#### Fig. 146.

Lithothamnion polymorphum, vertical sections of sporangial conceptacles, A, the first division of the sporangium is not accomplished, the following not yet begun. B, with a very long sporangium. C, conceptacle with undivided and fully divided sporangia. D, ripe sporangium. E, empty sporangial conceptacle with covering tissue; below, limiting line of zones and outline of empty conceptacle filled with regenerative tissue. A-D 200:1; E 63:1.

scarcely perceivable, if at all (fig. 146). The sporangia are at least divided into 4 spores. As stated by FOSLIE, the sporangia are  $80-110 \mu \log 25-45 \mu$  broad; the outermost ones, however, reach a greater length (fig. 146). After the evacuation of the sporangia, the conceptacles become sunk in the crust by continuation of the growth in thickness of the frond, but their surroundings may then behave in different manners. 1) The filaments of the roof grow upwards in accordance with those of the surrounding frond, and the conceptacle forms an empty round hole. 2) The roof falls into decay and the conceptacle is filled more or less completely by tissue growing inwards from the tissue which is developed by increase in thickness of the surrounding part of the frond and united over the conceptacle. 3) The conceptacle is completely filled by a tissue produced from the bottom of the conceptacle is completely filled by a tissue produced from the bottom of the conceptacle is completely filled by a tissue produced from the bottom of the conceptacle is completely filled by a tissue produced from the bottom of the conceptacle is completely filled by a tissue produced from the bottom of the conceptacle is completely filled by a tissue produced from the bottom of the conceptacle is completely filled by a tissue produced from the bottom of the conceptacle is completely filled by a tissue produced from the bottom of the conceptacle is completely filled by a tissue produced from the bottom of the conceptacle is completely filled by a tissue produced from the bottom of the conceptacle is completely filled by a tissue produced from the bottom of the conceptacle is completely filled by a tissue produced from the bottom of the conceptacle is completely filled by a tissue produced from the bottom of the conceptacle is completely filled by a tissue produced from the bottom of the conceptacle is completely filled by a tissue produced from the conceptacle is completely filled by a tissue produced from the conceptacle is completely fille



Fig. 147. Lithothamnion polymorphum. Vertical section of emptied sporangial conceptacle, showing two muciferous canals and the covering tissue. About 350:1. ceptacle. The newly evacuated conceptacles are sometimes covered by a peculiar, rather thick tissue, which is sharply marked off from the roof (fig. 146 *E*, 147, Plate III fig. 6). Its cells are frequently broader than those of the roof, (fig. 147). In a living state this covering tissue appears as a white dot. It has been mentioned by FOSLIE (Remarks, p. 78). A similar tissue also occurs over the sexual conceptacles. Its signification is unknown.

Antheridial conceptacles I have not seen; they have been mentioned by HEYDRICH (1900, p. 68, Taf. II fig. 1-3) and Foslie (1905). According to the first named author, the spermatia are produced from branched filaments given off from the inner side of the conceptacle, as it seems, in a similar manner as in L. Lenormandi.

THURET states (Ét. phyc., 1878, p. 91) that the spermatia resemble those of Jania rubens.

The cystocarpic conceptacles are, according to FOSLIE, at first convex, but they are not always so, for fairly young, totally immersed conceptacles may be found (fig. 148). As to the development of the cystocarp more detailed statements are given by HEYDRICH (l. c. p. 70) which are in several respects in discordance with those of SOLMS for other *Corallinaceæ*. They very much need a critical trial, but as I have

had only dried specimens at my disposal I can only throw little light upon the matter. Before fertilization the concave bottom of the conceptacle is covered with numerous procarps which are two-celled, as shown by HEYDRICH (fig. 148, Plate III fig. 5). These filaments are intensely coloured by hæmatoxyline. The lowest cell is probably an auxiliary cell, as maintained by HEYDRICH, and this is also in accordance with the statements of MINDER for Choreonema (Fruchtentw., p. 12). This cell may be rather long (fig. 148 C). The



Fig. 148.

Lithothamnion polymorphum. A, vertical section of female conceptacle with carpogonia. B, similar, with a rather long neck. C, procarps. D, vertical section of the bottom of a female conceptacle, showing fusions between the cells. A, B 200:1. C, D 350:1.

wall between the two cells is more or less oblique, but a hypogynous cell is not cut off from the lowermost end of the carpogonium as in *Choreonema*. I have not been able to follow the development of the carpogonia after fertilization, but it must be said that there is nothing to support the supposition of HEVDRICH that each auxiliary cell becomes a carpospore. The only thing which might favour this view is the fact that the carpospores are produced not only at the periphery but also from the central part of the floor of the conceptacle, as shown by HEVDRICH (l. c. fig. 12), and as I have also observed it (fig. 149). But the carpospores do not arise singly; they are produced in short rows, as shown by earlier authors (SOLMS, PILGER,

MINDER) for other Corallinaceæ. This is shown in fig. 149 where a smaller (vounger) carpospore is situated under the most developed ones; they have undoubtedly been produsuccessively ced by the sporophyte, but the behaviour of the latter could not be stated. The low cells visible



Lithothamnion polymorphum, vertical sections of cystocarpic conceptacles with carpospores. A 200:1. B 350:1.

under the youngest carpospores are probably parts of the sporophyte (or of the fusion cell, if Solms' view is correct); or might there perhaps be more than one sporophyte? The cells situated below the procarps may show lateral fusions (fig. 148 D), but it is doubtful whether these fusions have any relations to those of the sporophyte with the auxiliary cells. The evacuated cystocarpic conceptacles remain empty, or become partly filled with regenerating tissue produced from above.

As mentioned above, this species grows particularly on large boulders; it is therefore probably much commoner than might be supposed from the localities given below, while it does not always become loosened from the stone by the dredge. It occurs in all the three forms quoted by FOSLIE which however, as stated by this author, are "not well defined, as transitions often appear to occur". It seems to be rather common in the Danish waters to the limits of the Baltic Sea, with the exception of the Limfjord and other fjords where it is wanting. It seems most common in the Kattegat. It occurs in depths of 2 to 19 meters. Tetrasporangia have been met with in April, carpogonia in January and May, and carpospores in May.

Localities. Sk: ZK<sup>10</sup> off Lønstrup, 11,3 m; off Hirshals, 11-15 m. – Kn: TX, north of Græsholm (Hirsholmene; on stones picked up by Hirsholmene, about 4,5 m, large crusts; east of Deget; off

Frederikshavn; UC, TO, 18 m and FF (Trindelen) north of Læsø. — Ke: ZE, Fladen; IB, Store Middelgrund. — Km: XB and XC south of Kobbergrund. — Ks: HS, Briseis Grund; OU, Schultz's Grund; OO, Søborghoved Grund. — Sa: KK, Klørgrund, south of Hjelm; FT, Klepperne. — Lb: Middelfart. — Sb: Reef at Korsør harbour, 2 m; NN, south-west of Sprogø, 19 m. — Su: Off Aalsgaarde, 26 m (H. E. Petersen); TF<sup>3</sup>, Staffans Flak, 14-18 m. — (Bm: Stones picked up near Stevns ?).

## 8. Lithothamnion lævigatum Foslie.

Foslie, Norweg. Forms, 1895, p. 139, pl. 19, fig. 21-23; Heydrich, Lithoth. Helgoland, 1900, p. 76. Lithothamnion emboloides Heydrich, Lith. Helgol., p. 74, Taf. II Fig. 15 (teste Foslie). Phymatolithon lavigatum (Fosl.) Foslie, Remarks. 1905, p. 79.

Judging from Danish specimens, this species appears to be quite distinct from L. polymorphum, whereas, according to FosLie (Remarks, p. 79), in more southern localities there is no distinct limit between these two species. L. lævigatum is characterized by a comparatively thin, smooth crust, up to 0,5 mm thick, by the roof of the sporangial conceptacles disappearing after the evacuation of the sporangia, and by the two-parted sporangia. When occurring together with L. polymorphum, the difference between them is evident; the two species are, however, only rarely met with in the same locality, and it must be emphasized that L. polymorphum does not occur in the Limfjord, where L. lævigatum has been met with in several localities. I therefore do not doubt that they are specifically distinct.

The anatomical structure much resembles that of *L. polymorphum*. The hypothallium is similar, but is sometimes more fully developed. Its cells were found to be  $13-21 \mu \log_{2} 4,5-7 \mu$  broad. The cells of the perithallium were less variable



Lithothamnion lævigatum. Vertical sections of crust from Bolsaxen.Sb, showing sporangial conceptacles and limiting lines between the zones, fig. D also the hypothallium. 65:1.

in breadth than those of L. polymorphum; they were almost always  $6-7 \mu$  thick. The length was usually  $6-9\mu$ , most frequently 7–8 $\mu$ , or only little greater than the breadth, and the rounded cells thus approach the spherical form; but cells shorter than broad are also met with (fig. 151 A). Transverse fusions occur here and there, in the hypothallium and the perithallium as well. Starch grains are frequently present as single grains in great numbers in most of the cells, except the uppermost. Only sporangial conceptacles were

met with. They resemble those of *L. polymorphum*, and the hollow containing the roof is, as in that species, sometimes very slight or wanting, and the elevated border may also be wanting, the surface over the conceptacle thus being quite even or with

only a feeble trace of deepening or elevation (fig. 150 C). The roof is sometimes convex, though inserted in the bottom of a hollow. The sporangia are, as stated by FOSLIE, always two-spored. I found them to be  $95-126 \mu \log$ ,  $(18-)37-53 \mu$ broad, thus a little smaller than the dimensions found by FOSLIE, which might

perhaps partly be caused by the fact that my measurements have mostly been made with dehydrated sections. The conceptacles are sometimes covered by a particular tissue similar to that mentioned for L. polymorphum (p. 230). It has also been mentioned by HEYDRICH and FOSLIE (Remarks, p. 80). According to the first named author (l. c. p. 76) it is always present in L. emboloides which, as shown by Foslie, is identical



Lithothamnion lawigatum. A, vertical section of hypothallium and the under part of perithallium. B, vertical section of crust with emptied sporangial conceptacle filled with regenerative tissue, showing the outlines of older filled conceptacles C, vertical section of empty conceptacle with covering tissue. A 350: 1. B-C 65: 1.

with L. lævigatum; it is, however, not suitable for use as a specific character, for in some specimens it covers all or nearly all the conceptacles, while in others it is almost or entirely wanting. I have only seen it on emptied conceptacles which still showed muciferous canals (fig. 151 C). It has a white colour.

After the evacuation of the sporangia, the roof falls into decay. A regenerating tissue, produced from the bottom of the conceptacle, consisting of ascending filaments, may then fill the empty cavity. A new conceptacle is frequently produced at so small distance over the first one that the base of the second is situated within the limit of the first, and the new one is thus partly produced by the regenerating tissue (fig. 150, 151). Overgrown empty conceptacles do not occur.

The species occurs in depths of 2-24,5 m, most frequently 5-20 m, growing on stones and on *Mytilus* and *Ostrea*, often in company with other *Lithothamnia*, as *L. Lenormandi*, *L. glaciale* and *L. polymorphum*. It has been found growing over *L. glaciale*, and in one case on the frond of *Chondrus crispus*. It has been found with ripe sporangia in April and May.

Localities. Ns: aF, N.W. of Thyborøn, 31 m. — Sk: 4 miles N.<sup>1</sup>/<sub>2</sub>E. of Svinkløv beacon, 9 m (A. C. Johansen); SY off Løkken, 13 m; ZK<sup>6</sup>, off Lønstrup, 12 m; off Hirshals (Børgesen). — Lf: Sallingsund near Nykøbing (Th. Mortensen, !); LS<sup>1</sup>, 5,5 m and aT<sup>1</sup>, 4—5 m, east of Mors; Livø Bredning (C. H. Ostenfeld); Lendrup Røn. — Kn: Herthas Flak, 19—22 m; east of Deget near Frederikshavn; Trindelen, near the double broom (Børgesen). — Ke: IL, Fladen, 24,5 m; OO, Søborg Hoved Grund, 8,5 m. — Ks: RL, north of Gilleleje, 15 m; HO, N.W. of Gilleleje, 22,5 m; OS, Hastens Grund, 14 m. — Sa: KM, east of Øreflippen; BE, off Sletterhage; YV, east of Samsø, 15 m; north side of Refsnæs, 19 m (C. H. Ostenfeld);

D. K. D. Vidensk. Selsk. Skr., 7. Række, naturvidensk. og mathem. Afd. VII. 2.

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DK, Bolsaxen, 13-15 m. - Lb: XQ, off Middelfart, north side of Lyngsodde, 19 m; north of Fænø Kalv. - Sb: GT, near the broom at Asnæs; GP off Halskov, 10 m; Avernakhage by Nyborg, shallow water; near Vresen, 7-9 m (Ostenfeld). - Su: At Ellekilde Hage 11,5 m.

### Epilithon Heydrich.

Melobesiae, Ber. deut. bot. Ges. 1897, p. 408.

# 1. Epilithon membranaceum (Esper) Heydrich.

Heydrich, l. c.; Cotton, Mar. Alg. Clare Island, 1912, p. 150.

Corallina membranacea Esper, Pflanzenk. 1786 t. 12, fig. 1-4 (not seen).

Melobesia membranacea Rosanoff, Mélob., 1866, p. 66, pl. II figs. 13-16, pl. III fig. 1; Hauck, Meeresalg., p. 265; Guignard, Dével. et const. des anthéroz., Revue gén. de Botanique. I, 1889, p. 182, pl. VI figs. 22-23.

Melobesia corticiformis Kützing; Rosanoff, Mélob. p. 76, pl. I figs. 14-16; Solms, Corall. p. 11, Taf. III Fig. 25. Lithothamnion membranaceum Foslie, List of spec. of the Lith., 1898, p. 7; Remarks, 1905, p. 72.

As to the morphology of this species reference may be made to the descriptions of ROSANOFF and FOSLIE, to which I have only little to add.

The cells of the basal layer are, as pointed out by ROSANOFF (l. c. p. 67), not arranged in distinct concentric zones; they are often connected through transversal fusions (fig. 152 A). The frond is monostromatic in its marginal part, which may be of greater or lesser extent. Otherwise the frond is often partly distromatic, and near the conceptacles it becomes gradually thicker, the cells dividing by transverse walls. There is thus no distinction between hypothallium and perithallium.

The sporangial conceptacles were often somewhat smaller than stated by Foslie, viz.  $110-140 \mu$  in diameter. Their outline is frequently oval, as mentioned by ROSANOFF (l. c. p. 76) and Mme LEMOINE (in COTTON, Clare Isl. Surv. p. 150). The



#### Fig. 152.

number of the muciferous canals was also often somewhat less than that found by FosLIE, namely 8—27, most frequently 16—21, while FosLIE indicates 20—30. No relation was found between the number of the muciferous canals and the locality.

The sporangia apparently arise from the second cell-layer. The



cells of the basal layer situated at the periphery of the conceptacle lengthen in a vertical direction, fuse laterally two or three together, and are finally disorganized,

the upper part of their membrane being dissolved as far as it meets the cavity of the conceptacle. The cells of the same layer forming the central part of the floor of the conceptacle are disorganized in the same way, their contents finally disappearing, but they do not lengthen. In fig. 152 D the contents of these cells are still visible. In the sexual conceptacles the basal layer is exhausted in a similar way. The formation of the three dividing walls of the sporangia



Fig. 153. Epilithon memb anaceum, vertical, somewhat excentric section of sporangial conceptacle. 345:1.

is almost simultaneous, the walls advancing slowly from the periphery towards the longitudinal axis of the sporangium (fig. 152 B, D).

The antheridial conceptacles were found agreeing with the description and figure of ROSANOFF (l. c. p. 59, pl. II fig. 14). The cells surrounding the orifice are elongated and directed obliquely upwards (fig. 154). The antheridia clothe the bottom of the conceptacle; their development and structure have been followed by GUIGNARD, who found that they are seriate in densely placed short filaments. When the spermatia are to be formed, the protoplasm accumulates around the nucleus in the middle of the cell and becomes surrounded by a thin membrane, while the rest of the contents develop into two appendices, first described by ROSANOFF and named "oreillettes".

The orifice of the cystocarpic conceptacles is clothed with similar elongated, hair-shaped cells like those of the antheridial conceptacles, but more numerous; they are directed inwards or downwards in the under part, upwards in the upper part of the orifice. The carpospores are only produced at the periphery of the conceptacle; in the central part of the floor carpogonia are still visible, when the carpospores are well developed (fig. 155 B). As to the structure of the procarps I



Epilithon membranaceum, vertical section of antheridial conceptacle. 500:1.

cannot give any certain statement; they seem to resemble those of *Lithothamnion polymorphum*.

The species, referred by earlier authors to the genus *Melobesia*, had been transferred by HEYDRICH in 1897 to a new genus *Epilithon*, which was re-

duced in the following year by FOSLIE to a subgenus of *Lithothamnion*, with which it agrees by the fructification. The want of differentiation in hypothallium and

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perithallium seems to justify the distinction of the genus *Epilithon*. Another important generic distinction seems to exist in the position and development of the antheridia, which in the genus *Lithothamnion*, as far as known, are not seriate, and always placed on a system of branched filaments filling the cavity of the conceptacle



Fig. 155. Epilithon membranaceum, vertical sections of cystocarpic conceptacles. A, showing the orifice, B, showing carpogonia at the centre and carpospores at the periphery. 350:1.

The species usually grows on Furcellaria fastigiata, but occurs in the Kattegat also on Chondrus crispus, and has likewise been met with on Phyllophora rubens and Ph. membranifolia. It is rather common in the Danish waters within Skagen to the western Baltic Sea, but does not occur in the Limfjord (and in other fjords), and in the Sound it has only been met with north of Helsingør. It has been

(see above pp. 213, 218).

found in depths between 1 and 20 meters, and there is in this respect no difference between the different waters. Its absence in the Skagerak depends probably on the want of protection in this agitated water.

Localities. Kn: Marens Rev, Deget a. o. locality near Frederikshavn; FF and FE, Trindelen, 9-15 m; UB and TG, north of Læsø. — Ke: IM, Fladen, 16 m. — Km: XB, south of Kobbergrund; NV, off Randers Fjord. — Ks: FO, Havknude Flak; GG, Sjællands Rev, 4 m; D; EJ, entrance to Isefjord; RL, near Ostindiefarer Grund, 15 m; OO, Søborg Hoved Grund, 8,5 m. — Sa: FT, north of Samsø, 5,5 m; DK, Bolsaxen; AH and AH<sup>1</sup>, Lillegrund north of Fyens Hoved; MQ, south of Paludans Flak; AY, Ashoved. — Lb: AX, Bjørnsknude, 9,5 m; north of Fænø Kalv; Fænø Sund; UX, at the north end of Ærø, 9,5 m. — Sb: DN, Vengeance Grund; Spodsbjerg; DT, off Magleby, Langeland. — Sm: Venegrund. — Su: BQ, off Ellekilde; off Aalsgaarde. — Bw: DU, off Dimesodde, 11,5 m; UL, Øjet, 20 m; KZ, off Kramnisse, 4,5 m.

### Melobesia Lamour. emend.

The extent of the genus *Melobesia* has in course of time been repeatedly altered, certain species or groups of such having at various periods been detached therefrom and referred to new or other previously known genera. Thus in 1889, SCHMITZ removed *Melobesia Thuretii*, and gave it the name of *Choreonema Thuretii*; in 1897, *M. membranacea* was established by HEYDRICH as representative of a new genus, *Epilithon*, related to *Lithothamnion*. FOSLIE again, in 1898 (List of sp. p. 11) and 1900 (Rev. Surv. p. 21) placed *M. pustulata* and some related species under a new

genus, Dermatolithon, characterised by having a single apical pore in the hemispherical-conical conceptacles, sporangia "with short foot rising from the almost plain disc" and developing, according to Rosanoff, between club-shaped (?) paraphyses. In 1904 (Algol. Not. I. p. 3) however, he comes to the conclusion that these characters had not proved sufficiently constant, and did not form any distinct limit as against the genus Lithophyllum. He therefore no longer maintains Dermatolithon as a genus, but regards it as a sub-genus under the last-named genus, to which Heydrich had already previously (Corallinaceæ etc., Ber. deut. bot. Ges. 15, 1897, p. 47) reckoned Melobesia Corallinæ Crouan, and points out that it is further distinguished by its anatomical structure, the hypothallium being formed by a single layer of inclined cells. In 1909, (Algol. Not. VI, p. 57) however, it is again reinstated as a genus, Foslie now attaching greater importance to the mentioned anatomical character, and it was adopted by Svedelius in 1911. M. B. NICHOLS, who has subjected some species of this relationship to closer investigation, (Univ. of California Publ. in Botany vol. 3, No. 6, 1909) discusses some of the other characters cited by Foslie, viz: the presence of a "plug" in the orifice of the sporangial conceptacles united at the basis by a parenchymatic tap; the position of the sporangia at the bottom of the conceptacle, which in Melobesia is said to be almost flat, in Lithophyllum overarched; and the presence of a stalk cell under each sporangium in Melobesia. He adopts the standpoint which Foslie then adhered to; i. e. not maintaining Dermatolithon as a genus, but referring the species concerned to Lithophyllum, (L. macrocarpum, pustulatum, tumidulum). He points out, however, that in so doing, "the characters which separate Lithophyllum and Melobesia are not sufficiently well marked to warrant two separate genera" (p. 361). With regard to the structure of the conceptacles and the organs of reproduction, there is doubtless great similarity between the two genera; at any rate, no thoroughgoing differences appear to have been demonstrated up to now. The vegetative structure seems to me to present an excellent distinctive character, as in Melobesia, we never find transverse pits between the upright cell-series proceeding from the basal layer, whereas such are present in all Lithophyllum species, including the subgenus Dermatolithon. On the other hand, transverse fusions are of common occurrence in the Melobesia species, but are wanting in Lithophyllum. This seems, as a matter of fact, to be the best distinctive character between the two mentioned genera.

As to how far there may be reason to make further exclusions from the genus *Melobesia*, this must be left to further investigations to decide. Foslie, in 1900, (Rev. Surv. p. 21) established a subgenus *Heteroderma*, which he characterises as having the "thallus composed of more layers of cells" in contrast to *Eumelobesia*, which should have but one layer, except as regards the frond near the conceptacles. In 1905 however, (Remarks p. 102) a different limitation is made, and in 1909, (Alg. notes VI, p. 56) *Heteroderma* is raised to the rank of a genus, distinguished from *Melobesia* solely by the lack of hair-cells. I do not consider that we are justified in distinguishing between two genera merely by the presence or absence of hair-

cells, as the occurrence and frequency of these cells seems to depend to a great extent upon external conditions. I therefore attach but little importance to the fact that such have not hitherto been found in two of the species mentioned below (M. minutula and microspora) as it must be considered highly probably that they will be found on further investigation of a greater number of specimens. Moreover, hair-cells are found in M. Lejolisii, noted by FOSLIE under the genus Heteroderma (see fig. 156). On the other hand, I could well imagine that it may later on be found justifiable to distinguish between those species in which the trichocytes are terminal in the horizontal cell filaments, as in M. farinosa, for instance, and the other, doubtless far more numerous species in which they are intercalary. Another vegetative character which might be thought to furnish grounds for generic distinction, is the lack of cortical cells shown below in the case of M. microspora. This point, however, still needs further investigation. As regards the cortical cells, it may also here be noted that in M. trichostoma, several of these were found above one another, cut off successively by the same frond cell.

Where the frond consists of more than one cell-layer, there is often but slight difference between the basal layer (hypothallium) and the upright cell filaments proceeding therefrom (perithallium). Thus the walls forming the boundary between these two tissues often lie at different heights, as for instance in M. microspora (figs. 176—179) and M. trichostoma (174—175).

The number of spores in the sporangia is in most of the present species constant. In four species, 4 spores were found, in *M. subplana* a constant 2. In *M. minutula* only specimens with 4 spores were found, whereas Foslie gives 2, and in *M. Fosliei* some conceptacles were found with 4, others with 2 spores in the sporangia. — A small stalk-cell under the sporangium was found in *M. subplana*.

With regard to the antheridia, *M. Lejolisii* was found to differ from the other species in having the spermatangia formed at the end of long sterigmata, as first shown by Mrs. WEBER-VAN BOSSE. In the other species, the spermatangia are elongated cells, situate on the flat bottom of the antheridia-conceptacles. The orifice of the antheridia-conceptacles was in four of the present species often found drawn out into a spout, as first shown by Mrs. Weber-van Bosse in the case of *M. Lejolisii*. This is, however, not a constant character, as it may frequently be lacking in all the species concerned.

The carpospores are in all the cases investigated formed only in the periphery of the conceptacle, at the margin of the flat disc-cell.

#### 1. Melobesia Lejolisii Rosanoff.

Rosanoff, Rech. anat., 1866, p. 62, pl. I fig. 1-13, pl. VII fig. 9-11; Areschoug, Observ. phycolog. Part. III, 1875, p. 3; Hauck, Meeresalg., p. 264; A. Weber-van Bosse, Bijdrage tot de Algenflora van Nederland, Nederl. kruidk. archief. 2. Ser. 4. deel 4e stuk, Nijmegen 1886, p. 365; ead. in Hauck et Richter, Phykotheka univers. No. 163; Foslie, Remarks, 1905 (1906) p. 102 (f. typica); Mme P. Lemoine, Struct., p. 180, fig. 103; ead., Calcareous Algæ in Report on the Danish Oceanogr. Exped. 1908-10 to the Mediterranean etc. Vol. II, 1915, p. 19.

Among the distinctive characters of this species, used by ROSANOFF, in his important paper on the Melobesiaceæ, the want of "heterocysts" has been of special importance in distinguishing it from M. farinosa, as it permitted determination even in cases where the characters taken from the organs of reproduction could not be used. As shown by FOSLIE however, l. c. p. 103, the cells situated under the dichotomies are often larger than the others and resemble the heterocysts of M. farinosa. I can confirm Foslies' statement, having frequently found these cells in Danish

specimens of M. Lejolisii. They agree indeed completely with the heterocysts of M. farinosa, in bearing a hair or a scar left by a shed hair, in being poorer in contents and in bearing no cortical cells as do the other cells of the monostromatic frond. But they differ from the heterocysts of the lastnamed species in being derived, not from end-cells of filaments, which do not develop further, but from cells situated under



*Melobesia Lejolisii*, from Birkholm, **Sf**. *A*, vertical section of marginal part of frond, \* trichocyte. *B*, monostromatic frond seen from above; below a trichocyte, numerous fusions. *C*, marginal part of frond seen from above; two trichocytes are visible, one with hair. *D*, vertical section, not median, through a sporangial conceptacle; only undivided sporangia present. *E*, vertical section through emptied sporangial conceptacle. 350:1.

a ramification. I have convinced myself that this difference really exists by examining authentic specimens of M. farinosa. Where the included heterocysts of this species are present it is easily seen that the two cell-rows, the separating line of which goes in continuation of the heterocyst, are not given off from this, but from the adjacent cell-rows. As shown by SOLMS (Cor. p. 24), these cells produce a hair without formation of a transverse wall. The hairs are, according to the mentioned author, very short-lived, and fall off after a separation has taken place at their base by local incrassation of the longitudinal wall. This is also the case with those of M. Lejolisii; sometimes, however, they are more persistent, and appear as long hyaline hairs (fig. 156 C). Their wall is stained very intensely by hæmatoxyline, by which they become very obvious, and the same is the case with the basal part of the cell, after the throwing off of the hair. As these cells are very different from the heterocysts of the *Cyanophyceæ*, I think it better to give them another denomination; they must be named hair-cells or trichocytes (comp. p. 213). They are somewhat larger than the other cells. Sometimes also, other intercalary cells than the branch-producing ones may develop into a trichocyte, and it may also happen that a trichocyte produces a cortical cell. These cells appear to be of normal occurrence, though varying in number<sup>1</sup>.

In the monostromatic part of the crust the cells are  $7-10(11) \mu$  broad, and usually  $1-1^{1/2}$  times as long. The dimensions are somewhat variable (comp. figs. 156 and 158). In specimens from the inner Danish waters (Sf and Sm) the breadth



Melobesia Lejolisii. Vertical sections of conceptacles. A, from Stensnæs, Km, sporangial conceptacles. B and C from Kragenæs, Sm; B, with carpogonia, C, with undivided sporangia, in the middle a columella. 350:1.

in specimens from Lf and **Kn** it was up to 11 *µ*; this is possibly caused by the difference in salinity of the water. These cells often contain numerous starch grains, but the trichocytes contain no starch. The cortical cells are always longer in transversal than in radial direction. Transversal fusions between the cells may occur, sometimes in great number (fig. 156 B). In a vertical radial section the cells are seen to be of about the same height as breadth.

of the cells was only  $7-9\mu$ ,

The marginal part of the frond remains monostromatic, the small cortical cells not taken into account. Only in the immediate vicinity of the conceptacles the frond consists of 2—3(4) layers of cells. As the conceptacles are densely placed in the greater inner part of the crust, the frond is monostromatic only in the marginal part. The statement of Mme LEMOINE (Structure, p. 180, fig. 103) that the crust of

<sup>1</sup> The trichocytes appear to be variable in their occurrence also in *M. farinosa*. In specimens from LE JOLIS, Alg. mar. de Cherbourg no. 194, which, as shown by FOSLIE, is a typical *M. farinosa*, I found the characteristical trichocytes quite in accordance with the descriptions of ROSANOFF and SOLMS. On the other hand, in the *Melobesia* communicated in Crouan's Exsicc. no. 244, which indeed is referred to *M. Lejolisii* by FOSLIE, I did not find any heterocysts at all. This alga agrees, however, otherwise with *M. farinosa*, by the dimensions of the cells  $(11-14 \mu$  broad, about  $1^{1/2}-2$  times as long) and by the round, not transversely elongated cortical cells. I suppose therefore that it is a form of *M. farinosa*, in which no trichocytes have been developed. this species consists of three cell-layers, the middlemost of which is composed of high cells, must refer to the fertile part of the crust (comp. fig. 159 D); but the author says that she has observed three layers also at a great distance from the conceptacles. Possibly, the specimens referred to this species by Mme LEMOINE do not all belong to it. In Calc. Alg. Med., 1915, p. 19, the same author mentions specimens of this species from the Mediterranean consisting only of two layers of cells, the upper being the cortical cells; these specimens thus agree with the Danish ones.

The conceptacles of sporangia are usually densely crowded. They are low conical or, when very densely placed, depressed, with almost level surface (figs. 156 -158). The orifice is rather narrow, almost cylindrical, not enlarged upwards, clothed with unicellular hairs of varying length. In rare cases I found the hairs long and protruding outwards in a vertical direction (fig. 158 D), as drawn by Rosanoff in fig. 11, pl. I, l. c., but usually they are shorter, directed inwards horizontally and not protruding (figs. 156 E, 157 A, comp. Rosanoff's



Melobesia Lejolisii, from TG, north of Læsø. A, frond seen from above, at left a trichocyte. B, vertical section of antheridial conceptacle, not yet ripe. C, vertical section of antheridial conceptacle, not yet ripe. C, vertical section of sporangial conceptacle with well developed peristomial hairs. E, the same sporangium as seen in D, from a following section. B and C 650:1, the rest 350:1.

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fig. 8). The last quoted figure of ROSANOFF certainly represents a normal, fully developed state. FOSLIE, who did not find any protruding crown at all in examining numerous specimens, thought that this might perhaps be owing to the fact that he had only had dried material for examination, "or it may be that the cells of the corona have a short phase of development and are soon falling to decay". My investigations do not favour these suppositions; it must be supposed, that the development of the hairs is variable according to the various conditions. — The roof of the conceptacle is rather thin, consisting of about 2 (1—3) cell-layers, only a little thicker, if at all, near the orifice. The floor of the conceptacle consists of a single cell-layer; more rarely this cell-layer is absorbed (fig. 157 A). In some cases a sterile columella was observed in the centre of the conceptacle (fig. 157 C), but

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usually no such formation was to be seen. The sporangia are, when fully developed, four-parted,  $45-77 \mu \log$ ,  $32-49 \mu$  broad. While at first vertically placed, they may sometimes finally become horizontal, at all events when the conceptacle contains only one or two developed sporangia (fig. 158 D-E).

The antheridial conceptacles are small, often very small, and but little prominent if at all. As shown by Mrs. WEBER-VAN BOSSE (l. c.), the spermatia are produced at the end of long sterigmata developed from a layer of very small cells covering the basal layer (fig. 159 A, C). In some cases, however, the cells producing



the sterigmata are not placed directly on the basal laver (fig. 158 B, C). In some cases the conceptacle was found provided with a long slightly curved spout agreeing exactly with that described by Mrs. WEBER (fig. 158 C); but in most cases no such spout was to be seen. The ostiole was then

Melobesia Lejolisii. A and B from Holbæk Fjord, A, antheridial conceptacle. B, female conceptacle, showing carpogonia. C, antheridial conceptacle. D, cystocarpic conceptacle, C 650:1, the rest 350:1.

a simple small hole without any peristome. The spermatia appeared sometimes as slightly elongated cells with pointed ends (fig. 159 C).

Well developed female conceptacles were only rarely found. The conceptacles shown in figs. 157 *B* and 159 *B* are certainly female ones, containing unfertilized carpogonia, and fig. 159 *D* represents a cystocarpic conceptacle with the carpospores placed at the periphery only. A disc-cell could not be distinguished. Peristomial hairs seem not to be developed. The diameter of female conceptacles was found to be  $123-175 \mu$ .

Ripe tetrasporangia have been found in summer (June to September), antheridia in May and September, and cystocarps (with few spores) in May.

I have referred to this species all the specimens growing on old Zostera-leaves and referred by FOSLIE to *M. Lejolisii* f. *typica*, with the exception of one sample mentioned below under *M. subplana*. The species has also been found growing on *Ruppia*. The specimens growing on Algæ, on the other hand, seem to belong to other species, which are mentioned below. The species has been found in depths of 1-11 meters. Localities. Lf: Thyborøn; Nykøbing; LQ, Lendrup Røn; MK, Holmtunge Hage; F, Lunde Hage; ML, Gjøls Bredning; stone reef west of Draget; Hals. — Kn: TP, Tønneberg Banke; TG, near Syrodde Pynt. — Km: BO, Stensnæs; EZ and XC, south of Læsø. — Ks: NL, lsefjord; Lammefjord; Holbæk Fjord. — Sa: Besser Rev, Samsø, partly on Ruppia; MT, Horsens Fjord; Odense Fjord (C. Rosenberg). — Sf: Nakkebølle Fjord; Svendborg; U, Birkholm; EA, north of Rudkøbing. — Sb: Munkebo, Kertinge Nor; Avernakhage by Nyborg. — Sm: CM, Kragenæs; CO; CR, off Dyrefoden; Guldborgsund.

## 2. Melobesia subplana sp. nov.

Crusta orbicularis, 1—2 mm diametro, in statu adulto non nisi margine angusto monostromatico, ceterum 2—6 cellulis crassa, cellulis in parte marginali c. 7—8  $\mu$ latis, cellulis corticalibus rotundatis, in sensu radiali paulo elongatis, trichocytis intercalaribus. Fila verticalia partis frondis crassioris cellulis longitudine vario,  $6-9\mu$  crassis constituta. Conceptacula sporangifera dense posita, paulo prominula, diametro externo c. 150—200  $\mu$ , interno 70—105  $\mu$ ; sub conceptaculis 1—2 strata cellularum vegetativarum; tectum subplanum, c. 2—3 cellulis crassum, ostiolo cellulis paulo horizontaliter elongatis, non erumpentibus, vestito. Columella centralis conica. Sporangia 42—60  $\mu$  longa, 26—32  $\mu$  lata, semper disporica. Conceptacula mascula parva, immersa, nonnunquam tubo longo prorumpente munita, fundo cellulis spermatogenis numerosis elongatis, leniter curvatis, e strato cellularum rotundatarum egredientibus, vestito, spermatiis longis, clavatis, leniter curvatis, c. 11  $\mu$  longis, c.  $2\mu$  crassis. Sub conceptaculis masculis 1—3 strata cellularum vegetativarum. Conceptacula feminea parva, immersa, initio non prominula, stratis cellularum vegetativarum 1—3 suffulta. Cystocarpia non certe cognita.

The specimens which have served as base for this new species were collected near Horsens at the east coast of Jutland, growing on Zostera-leaves. They have been determined as M. Lejolisii typica by FOSLIE, and certainly resemble this species very much; they differ however so much from it in some respects that I have thought better to regard it as a distinct species.

The frond is polystromatic with the exception of a narrow marginal zone. It consists otherwise of vertical cell-rows composed of 2 to 5 cells, not including the small cortical cells, which are cut off by oblique walls. Near the border, the cortical cells are seen to be rounded, narrow, usually a little lengthened in a radial sense, sometimes placed not over the anterior border but over the middle of the cell (fig. 160 A). Hyaline hairs are sometimes numerous, given off from cells without cortical cells, also from the polystromatical part of the frond. The cells of the vertical cell-rows are of varying length. There is less contrast between the basal layer and the perithallium than in M. Lejolisii, the upper wall of the cells of the former falling not always at the same level, the cells thus being of somewhat varying height. While in M. Lejolisii the intermedial layer in thicker crusts consists only of one layer of long cells, it is in M. subplana usually 2—4 cells thick, its cells varying from 1 to 3 diameters in height, shorter and longer cells alternating irregularly, and the transversal walls falling at different levels in the different filaments.

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Transversal pores do not occur, but transverse fusions frequently take place, most frequently in the basal layer, but also between cells at a higher level. Abundant



Melobesia subplana. A, marginal part of frond seen from the face. B, vertical section of border of frond. C, vertical section of sporangial conceptacle. A and B 350:1. C 200:1.

starch-grains occur in the ordinary vegetative cells.

The sporangial conceptacles are numerous and densely crowded. They are only slightly prominent, but where they are very densely placed, the single conceptacles are often not prominent at all, the surface being even (fig. 160 C). It is therefore not always possible to indicate the outer diameter of the single conceptacles. The ostiole is lined by elongated cells radiating towards the centre of the canal. At last they assume the character of rudimentary hairs directed inwards. The middle of the conceptacle is

occupied by a conical columella of sterile cells, while the sporangia are placed in the outer part of the conceptacle. A little stalk-cell was frequently seen under each

sporangium. The sporangia are always two-celled. I have seen numbers of them, some preserved in alcohol, and can assert that they were really two-celled, also at maturity.

I have seen only one or two male plants containing some antheridial conceptacles. These are small, completely immersed. The bottom of the conceptacle is covered by a layer of small, somewhat rounded cells, from which are given off numerous elongated slightly curved spermatiaproducing cells a little incrassated upwards. I have not been able to follow the development of the spermatia, but I do not doubt that the elongated cells in question are the spermatangia, which produce long clavate, slightly cur-



Fig. 161. Melobesia subplana. Vertical section of antheridial conceptacle, at right presumed spermatia. 560:1.

ved spermatia (fig. 161). The spermatia are not formed at the end of long thin



Melobesia subplana. Vertical sections of carpogonial conceptacles, A with young, B with fully developed carpogonia. B, 485:1. B 420:1.

sterigmata. The ostiole of the conceptacle was in some cases provided with a long spout resembling that of *M. Leiolisii* (fig.

spout resembling that of *M. Lejolisii* (fig. 161), in other cases no such spout was present.

Very few conceptacles with carpogonia were seen. They were small, not prominent; the ostiole seems to be provided with a peristome similar to that of the sporangial conceptacles. Fig. 162 *B* shows fully developed carpogonia with long trichogynes penetrating through the ostiole. As to the structure of the procarps, my observations are so incomplete that I must content myself with referring to the figures without any interpretation. The bottom under the female conceptacles was composed of one to three layers of cells. Ripe cystocarps in good condition were not met with; they seem to be rather similar the tetrasporangial conceptacles.

As will be seen from the above description, this species differs from *M. Lejolisii* principally by the structure of the polystromatic frond, by the shape of the sporangial conceptacles, by the normal presence of a columella, by the two-spored sporangia, and seemingly by the formation and shape of the spermatia.

Locality. Sa: On Zostera-leaves at Horsens, September 1893.

## 3. Melobesia limitata (Foslie) K. Rosenv. sp. nov.

Melobesia Lejolisii Rosanoff f. limitata Fosl., Remarks 1905 (1906) p. 102.

In his valuable paper on the northern Lithothamnia (Remarks, 1905 (1906) p. 102) FOSLIE described a forma *limitata* of *Melobesia Lejolisii*, characterized principally by smoother and apparently more solid crusts, and by less crowded conceptacles, frequently a little higher and somewhat pointed or subhemisphericalconical, and more sharply defined. He referred to it almost all the Danish speci-

mens noted under the species mentioned but growing on Algæ instead of on Zostera. In examining these specimens, I have found that they not only differ in the characters named by FOSLIE, but that they must be regarded as representing another species distinct also in several other characters.

The crusts have a diameter of 3-4 mm, sometimes they reach 5 mm or more. They are more or less irregularly orbicular with lobed margin. Frequently several crusts are confluent. The frond may be monostromatic from the border to the conceptacles, or the inner part may be distromatic (figs. 166, 167) or even thicker (fig. 163 D). When seen from the face, the frond presents a similar aspect to *M. Lejolisii*, but the cells are usually somewhat longer, viz.  $(7-)8-10,5(-12) \mu$  broad,  $1^{1/2}$  to 2 times longer than broad. Transversal fusions





sometimes occur. The cortical cells are longer in transversal than in radial direction. Trichocytes usually occur; they may be cells situated under a ramification or ordinary intercalary cells in the radiating filaments. They usually lack cortical cells, but such may occasionally be produced (fig. 163 A at left). The conceptacles are scattered, usually not contiguous.

The sporangial conceptacles are conical or subhemispherical-conical, (170-)230-325  $\mu$  in diameter. The outer wall (the roof) is thicker than in *M. Lejolisii*, it is



Melobesia limitata from MH. A, vertical section of nearly emptied sporangial conceptacle. B, sporangium divided into more than four cells. 350:1.

beyond the border of the ostiole. The filaments forming the crown are given off not only from the inner face of the canal, as in *M. Lejolisii*, but also from the outer surface (fig. 165). In other cases, however, the filaments do not extent beyond the border of the ostiole and a crown is thus not developed. The ostiole has usually a constriction almost in or under the middle, and over this the ostiole is funnelshaped or barrel-shaped, according to the development of the upper peristomial

filaments (figs. 164, 165). This space is filled with a hyaline jelly. The converging filaments are easily observed when viewing the conceptacle from above. The bottom under the conceptacle consists of one or two layers of cells. The sporangia seem to be produced only in the peripheral part of the conceptacle, but there is no columella. The sporangia are fourparted, 46-77 µ long,  $21-46(-61)\mu$  broad. Un-



Melobesia limitata A, vertical section of sporangial conceptacle with well developed crown, 350:1. B, sporangium. 200:1.

3-5 cells thick and has its greatest thickness near the ostiole. It consists here of very distinct cellfilaments radiating inwards and upwards. The longest of these filaments are those directed towards the upper border of the ostiole, and which sometimes project as a crown divided and two-parted sporangia were frequently met with. In a specimen from the Limfjord, sporangia were found which were irregularly divided into more than 4 cells (fig. 164 B).

The antheridial conceptacles (fig. 166) occur in the same plants as the female ones. They are very small, e. g. 56  $\mu$  in inner diameter, totally immersed or only little prominent. The bottom is composed of one to two cell-layers. The cells of the roof are often partly disorganized. The ostiole is conical or conical-cylindrical, sometimes, but not always provided with a long spout resembling that in *M. Lejolisii*.

The spermatangia are cylindrical and form a dense covering on the flat bottom of the conceptacle; they are produced from low cells forming a layer over the bottom. The spermatia seem to be oblong, 2-3 times as long as broad. There are no long sterigmata as in M. Lejolisii.

The female conceptacles resemble the spor-

A

angial ones.



Fig. 166.

Melobesia limitata. Vertical sections of antheridial conceptacles. A-C from I, D from Amtoft Rev. A and B, before discharge of the spermatia. D, the ostiole is prolonged in a spout. A and D 650:1. C 560:1.

young stage with unfertilized carpogonia is shown in fig. 167 A; a number of carpogonial branches are placed on the bottom. The short cell under the carpogonium is probably the auxiliary cell. After fertilization, the surrounding elongated cells shown in fig. 167 A are dissolved, the developing cystocarp increasing at the periphery. A ripe cystocarp is seen in fig. 167 D, showing a number of carpospores produced at the periphery of the cystocarp, while numerous unfertilized carpogonia are still visible on the middlemost part of the floor. The cystocarpic conceptacles are  $210-325 \mu$  in diameter; they are of the same shape as the sporangial ones, and the roof and the ostiole have a similar structure. The ostiole is surrounded by similar inward and upward converging filaments, which may sometimes project outwards as a crown. A well developed crown is shown in fig. 167 C, where the free ends of the filaments are distinctly articulated. In fig. 167 D, which shows another conceptacle of the same plant, the free ends of the filaments seem to have been thrown off, for the converging filaments are only one- or two-celled, and remains of the free ends of the filaments are still visible at the border of the ostiole. On the other hand it is certain that a crown is not always developed, for ripe and emptied cystocarpic conceptacles may be found in which the structure of the ostiole



Melobesia limitata. Vertical sections of female conceptacles. A, young stage with unfertilized carpogonia. B, fully developed cystocarpic conceptacle with well developed crown consisting of articulated filaments. C, fully developed cystocarpic conceptacle in the stage of emptying; the crown has perhaps been thrown off. From Amtoft Rev. A, C, D 350:1. B 650:1.

agrees exactly with that of the young conceptacles shown in fig. 167 *A*, and which show no trace of a shed crown.

As will be seen from the above, this species differs from M. Lejolisii, besides the characters named by Foslie, principally by the thicker roof of the sporangial and cystocarpic conceptacles, and by the central part of the roof consisting of long converging articulated filaments, sometimes projecting outwards as a crown, and further by the structure of the antheridial conceptacles, the spermatia being not produced at the end of long sterigmata.

I refer to this species the specimens from Nykøbing, Mors referred by FosLIE with doubt to *Melobesia farinosa* f. *borealis* (Foslie, Remarks, p. 98). Foslie did not find any heterocysts, but I found some intercalary trichocytes with or without cortical cells, as

described above, thus different from those of *M. farinosa*, in which they are terminal. All the specimens referred to this species were growing on Algæ, particularly on *Fucus vesiculosus*, thus all the specimens found in the Limfjord, otherwise on *Chondrus crispus, Rhodymenia palmata* and *Laminaria digitata*. In the Limfjord it was always found growing together with *Lithophyllum macrocarpum*. Sporangia, antheridia and cystocarps were met with in August and September. The species is certainly annual. Localities. Lf: Søndre Røn by Lemvig; Thisted; off Skrandrup and off Hanklit, Thisted Bredning; Venø Bugt off Nørreskov; Nykøbing; Amtoft Rev and LQ, Lendrup Røn in Løgstør Bredning. — Kn: Deget by Frederikshavn, on Chondrus crispus; Nordre Rønner; UB, north of Læsø; Trindelen, on Rhodymenia palmata, 19 meters. — Sa: AY, off Ashoved, on Laminaria digitata, 10 meters.

## 4. Melobesia Fosliei sp. n.

Frons minuta ambitu irregulari, monostromatica vel prope conceptacula polystromatica. Cellulæ partis monostromaticæ  $(6-)7-9(-11)\mu$  latæ, diametro æquilongæ

vel ad sesqui longiores; cellulæ corticales parvæ, ellipticæ. Trichocyti plerumque adsunt. Conceptacula sporangifera hemisphærica vel subhemisphærica, diametro 80-140-185 µ, dum dense posita confluentia. Tectum 1-2 cellulis crassum. Cellulæ ostiolum circumdantes a ceteris paulo diversæ, nonnunquam ostiolum versus paulo elongatæ, vel papillas horizontales formantes. Ostiolum interdum in rostrum breve protractum. Sporangia quadripartita et bipartita,  $42-60 \mu \text{ longa}, 18-30 \mu \text{ lata}.$ Conceptacula mascula parva immersa, paulo prominentia; spermatia lineari-clavata, le-



Melobesia Fosliei. A-C, from Deget. A, monostromatic frond seen from above. B, vertical section of a sporangial conceptacle showing one fourparted sporangium. C, vertical section of sporangial conceptacle showing one two-parted sporangium. The orifice has not been hit by the section. D-E from Hirsholmene. D, orifice of sporangial conceptacle seen from above. E, tetrasporangium. 350:1.

niter curvata in fundo conceptaculi gignuntur. Conceptacula feminea eadem forma et structura ac conceptacula sporangifera.

The specimens referred to this species were found growing on the fronds of *Polysiphonia nigrescens*, *Corallina rubens*, *C. officinalis* and on Bryozoans living in company with these Algæ. They are rather variable in several respects, but as the differences are met with not only between specimens growing on different substrata, but also in specimens growing on the same alga, I do not hesitate in referring them all to the same species.

Most of the specimens were found growing on *Corallina rubens*; these specimens may first be mentioned here. The structure of the monostromatic frond much resembles that of *M. Lejolisii*, except that the lateral walls seem to be thinner (less incrustated ?). Lateral fusions are frequent. Trichocytes were usually present, situated at the offspring of ramifications, but in some cases they were searched for in vain.

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The conceptacles of sporangia are proportionally higher than in M. Leiolisii.



Fig. 169. Melobesia Fosliei, from Tønneberg Banke. A, vertical section of sporangial conceptacle with orifice prolonged in a spout. B, vertical section of cystocarpic conceptacle. A 350:1. B 560:1.

hemispherical or subhemispherical, the height being frequently the half of the breadth. The cells surrounding the ostiole are usually little characteristic, forming no real peristome; they may be somewhat lengthened towards the opening, but take, as it seems, scarcely the form of papillæ, and do not as a rule protrude outside the ostiolum. In some cases, however, they are elongated, going out in a prolongation of the surroundings of the ostiole in a short spout, resembling that of the antheridial conceptacles of M. Lejolisii and M. limitata, but thicker (fig. 169 A). This character, however, is not constant, being met with only in some of the conceptacles but wanting in others, usually most. When seen from above, the ostiolum appears sometimes surrounded by a rosette consisting, as it seems, of very low papillæ (fig. 168 D), in other cases no such structure is to be seen. 4-parted sporangia were found in all the specimens examined, but 2-parted ones of the same size were found in the same specimens. As I have

examined only dry specimens in which, as is well known, most of the sporangia have been emptied by the desiccation, it could not be stated whether the 2-parted sporangia were fully developed or not. I am inclined to suppose that 4-parted and 2-parted sporangia normally occur simultaneously.

The antheridial conceptacles were usually not well preserved in the dried material, but it could be seen that the spermatia were not produced at the end of long sterigmata as in M. Lejolisii. In one case the ostiole was found prolonged in a spout.

The conceptacles of cystocarpia were smaller than those of sporangia, and a little lower in relation to their breadth; the ostiole was similar in structure to these.

The specimens growing on Polysiphonia nigrescens agree in all essential points with the others; the cells of the monostromatic frond were only a little broader,  $9-13 \mu$ . A number of the conceptacles were provided with a well developed spout, containing elongated cells, the rest were without any projection. It appeared



Fig. 170. Melobesia Fosliei, from Bragerne. Vertical section of frond with antheridial and cystocarpic conceptacle. Below another section of the latter showing the orifice. 560:1.

to me that some of the first were cystocarpic ones. As shown in fig. 170 the antheridial conceptacles occur in the same fronds as the cystocarpic ones. The latter were rather small in these specimens.

The specimens growing on *Corallina officinalis*, collected north of Læsø (ZC<sup>1</sup>, 7658a, fig. 171), are more vigorous than the specimens previously mentioned. The structure of the frond is the same, but the conceptacles reach greater dimensions. They may be hemispherical,  $160-185 \mu$  in diameter, or they may be lower, frequently fusing together, when the conceptacles are densely placed. The ostiole was provided with small papillæ directed inwards in the conical space of the orifice.

When seen from above, the ostiole appeared surrounded by a rosette exactly like that shown in fig. 168 *D*. The remains of a columella were found in the case represented in fig. 171 *A*. The sporangia were always



tetrasporic, 44-50  $\mu$  long, 11-16 $\mu$  broad. Fig. 171.

Melobesia Fosliei growing on Corallina officinalis from  $\mathbb{ZC}^1$ , north of Læsø A, vertical sectionof frond with two conceptacles, one hemispherical, the other depressed. B, vertical sectionof frond with antheridial conceptacle.C, vertical section of cystocarpic conceptacle.A and C 260:1.B 420:1.

— The antheridial conceptacles are slightly prominent; the spermatangia are produced on the flat bottom of the conceptacle from small cup-shaped cells; they (or the spermatia) are linear-clavate, slightly curved, measuring  $7 \mu$  in length, about  $2 \mu$  in their broader end. — The cystocarpic conceptacles have the same shape and size as the sporangial ones and are, as those, provided with short horizontal papillæ in the ostiole, principally in its under part.

I have been much in doubt in determining the specimens referred to this species. Some of them, those from Bragerne, Skagerak, have been referred to M. Lejolisii by FOSLIE (Remarks, p. 106) and I have also been much inclined to consider them as a more or less reduced form of this species. However, I have judged it better to describe it as a new species, considering, besides other characters, especially the higher conceptacles of sporangia, the formation of the spermatia taking place in our species at the bottom of the conceptacle from short cells, while in M. Lejolisii they are produced at the end of long sterigmata, and the long curved spermatia, while those of M. Lejolisii are much shorter. The antheridial conceptacles

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tacles more resemble those of M. limitata, but this species is more different principally by the stronger development of the filaments surrounding the ostiole. It much resembles M. minutula Fosl. (comp. FOSLIE Remarks p. 107) from which it differs by its more incrusted frond and by the usual presence of trichocytes. Whether it can be kept distinct from it must be decided by further investigations.

Localities. Sk: YN<sup>2</sup>, south-east of Bragerne, on *Polysiphonia nigrescens* and *violacea*, July; Lønstrup, on *Corallina rubens*, washed ashore, June (C. H. Ostenfeld). — Kn: Within Deget near Frederikshavn, on *Cor. rub*. (C. H. Ostenf.); north-east of Hirsholmene, 6-7,5 meters, August, (C. H. Ostenf.); TL, north of Læsø, on *Cor. rubens*, Sept.; ZL<sup>1</sup>, north of Læsø, 9,5 meters, on *Corallina officinalis*, July; TP, Tønneberg Banke, 16 met., on *Cor. rubens*, Sept.

### 5. Melobesia minutula Foslie.

Foslie, Algolog. Notiser, 1904, p. 8; Remarks, 1905, p. 107.

Lithocystis Allmanni Harvey, Phyc. Brit. Vol. II, plate 166, 1849 (?).

Melobesia inæquilatera Solms, Corall., 1881, p. 12, Taf. III fig. 13-18 (?).

Non Epilithon Van Heurckii F. Heydrich in J. Chalon, Liste des Algues mar. obs. jusqu'à ce jour entre l'embouchure de l'Escaut et la Corogne, 1905, p. 207, fig. 1-5.

Foslie has referred to this species some specimens growing on Bryozoans attached to *Polysiphonia elongata* collected by me in the northern Kattegat (comp. Remarks p. 109). They form small, scarcely incrusted fronds consisting of a single layer of low cells, irregular in outline but not lacunose, wherefore it has been referred to f. *typica*. The frond is monostromatic in its whole extent to the border of the conceptacles. When seen from above, the cells are usually  $7-10 \mu$  broad, of the same length or a little longer. Very small hyaline cortical cells are as a rule present, covering the pericline walls. According to Foslie, they "mostly seem to be wanting", which statement is probably founded on the fact that they are only



Fig. 172.

Melobesia minutula. A, part of a frond seen from above, at right the primary disc. The cortical cells have not been drawn in the upper and under part of the figure. B, a tetrasporangium. 350:1.

inded on the fact that they are only discernible by rather high magnifying powers, owing to their small size and transparence. They are narrower than in the other Melobesiæ examined by me. They were also found over the periclinal walls situated under the pseudodichotomies (fig. 172), a fact in accordance with the complete absence of trichocytes.

The sporangial conceptacles are conical-hemispherical with a small orifice surrounded by a whorl of cells radiating towards it. I found

them about 90  $\mu$  in diameter (fig. 173). The sporangia were found to be tetrasporic (fig. 172 B), 43-54  $\mu$  long, 24-31  $\mu$  broad. Foslie found them only disporic. -

Further statements as to this species cannot be given owing to the very scarce material at hand.

The synonyms given are all dubious, as also mentioned by Foslie. The species described by HEYDRICH resembles Foslie's species by

the structure of the frond, but if his description is correct, it cannot be identical with it, and must even belong to another genus, as the conceptacle is said to have as many openings as it contains sporangia. HEYDRICH'S description of the cortical cells also does not agree with those of *M. minutula*, as they are said to cover the half of the cells of the disc; in *M. minutula* they are very narrow, covering only a small part of the underlying cells. It must therefore be concluded that HEYDRICH's species cannot be identified with *M. minutula*.



Fig. 173. Melobesia minutula. Part of frond with conceptacle, 200:1.

The plant was found growing not only on the Bryozoan but also on *Ceramium* tenuissimum attached to the same *Polysiphonia*.

Locality. Kn: TP, Tønneberg Banke, 16 meters, September.

## 6. Melobesia trichostoma sp. n.

Frons primo monostromatica, dein, saltim maxima ex parte, polystromatica, usque ad 8 cellulis crassa, plerumque tamen e pluribus lobis vel frondibus secundariis minoribus, partim sese invicem obtegentibus composita, lobis plerumque usque ad marginem polystromaticis. Cellulæ frondis monostromaticæ vulgo 7—8  $\mu$  crassæ, latitudine plerumque paulo longiores, cellulis corticalibus transverse ellipticis munitæ. Frons adulta e filis verticalibus composita, cellulis longitudine vario, latitudine 1—3-plo longioribus. — Conceptacula sporangifera verruciformia, parum elevata, superne applanata, diametro 160–280  $\mu$ . Tectum planum, crassum, c. 5 cellulis crassum. Ostiolum pilis numerosis, sursum longioribus, superioribus ex ostiolo prominentibus ornatum. Sporangia tetraspora, 42—63  $\mu$  longa, 17—29  $\mu$  lata. Conceptacula mascula non prominula, ostiolo in tubo longo, sæpe curvato, protracto. Spermatangia lineari-clavata in fundo plano conceptaculi e cellulis depressis procreata, dense stipata. — Conceptacula cystocarpifera eadem forma magnitudineque ac sporangifera et peristomio simili ornata.

The specimens on which this species is founded formed dull rose-coloured crusts on the shells of living *Trochus cinerarius* collected in the Limfjord. They were referred to *Lithothamnion Lenormandi* by FOSLIE in 1905 and are also rather like old specimens of that species, especially the forma squamulosa. The frond is at first monostromatic, and the marginal part may remain so, much resembling that of M. *Lejolisii*, with well developed cortical cells, which seen from above are elliptical. A parietal body, situated closely at the outer wall in these cells is very intensely

stained by hæmatoxyline (fig. 174 A). Trichocytes may occur. The greater part of the crust is polystromatic, being composed of vertical cell-rows, up to 8 cells high or more. The older parts of the crusts are very irregular, being composed of several smaller crusts or lobes growing partly over each other. These partial fronds or



Melobesia trichostoma. A, vertical section of the monostromatic part of a frond growing over the conceptacle of another frond of the same species.
B, monostromatic frond seen from above. C, vertical section of older, compound crust. D, vertical section of a thick lobe of frond. E, vertical section of sporangial conceptacle. C, 65:1, the rest 350:1.

parts of the frond, and growing over the neighbouring parts. — The length of the cells of the vertical cell-rows is highly variable, usually one to three times as long as the breadth, and irregularly varying in the same filament. The undermost cell-layer is not distinct from the others, its cells being of variable height. The cells contain often numerous starch-grains. Transversal pores between the cells of different cell-filaments never occur, but transversal fusions are frequently met with, between the cells of the basal layer and between cells of the upper parts of the vertical cell-rows as well (figs. 174, 175).

lobes are usually polystromatic to the very margin. The compound crusts may be composed of lobes of the same frond or of different fronds growing together; it is therefore impossible to state the diameter of the single frond. In the thicker fronds, the upper ordinary frond-cell may bear more than one cortical cell, frequently one over the other (fig. 174A, D). In the last-named figure the three undermost cells at right bear each a cortical cell, the explanation of which must be that they represent the monostromatic border of the frond, which has been overgrown by tissue produced by the neighbouring thicker part of the same frond. A similar process often takes place in various parts of the frond and gives rise to the complicated structure of the old crusts, new lobes developing from certain

The outer part of the sporangial conceptacles (fig. 174 E) is low, wart-like, with plane upper face. The outer diameter of the conceptacle is often difficult to state, as it is usually for a great part sunk in the frond, and the outer delimitation often indefinite. One to three layers of cells are present under the conceptacle. The roof is flat, thick, about 5 cells thick. The ostiole is clothed with numerous welldeveloped unicellular hairs, the uppermost of which are long, and protruding outside the ostiole; the undermost ones are shorter and more oblique or horizontal. They are all intensely stained by hæmatoxyline. The sporangia do not occupy the

central portion of the conceptacle, where a small columella of sterile cells is sometimes to be found. The ripe sporangia are always tetrasporic. A small stalkcell is present under the sporangia (not shown in the figure).

The antheridial conceptacles (fig. 175 A) much resemble those of *M. subplana* (comp. fig. 161), being provided with a similar tube, and the antheridia having the same shape and position as in that species.



Melobesia trichostoma. A, vertical section of antheridial conceptacle. B and C, vertical sections of cystocarpic conceptacles. A and C 350:1. B 65:1.

The cystocarpic conceptacles (fig. 175 B, C) have the same shape and size as the sporangial ones, and the ostiole is endowed with a similar peristome. The thick roof is plane, or a little depressed near the ostiole. The carpospores are, as usually, produced seriately at the periphery of the conceptacle.

The species appears fairly distinct from all hitherto described species of the genus *Melobesia*. The low conceptacles with the thick, flat or a little deepened roof distinguish it from other species of the genus having a well developed peristome (e. gr. *M. Lejolisii, coronata*). Its occurrence on mollusc shells, unusual for the genus *Melobesia*, might seem grounds for placing it in the genus *Lithophyllum*; the want of transversal pores between the frond cells and the fact that these cells are not arranged in transversal rows, however, preclude its adoption in that genus.

Locality. Lf: Søndre Røn by Lemvig, near the surface of the water, September.

## 7. Melobesia microspora sp. n.

Frondes suborbiculares, sæpe confluentes, 1-2 mm diametro, excepta parte marginali polystromaticæ, e filis verticalibus usque ad 7-cellularibus compositæ; cellulis filorum  $6-8 \mu$  latis, diametro vulgo 1-2-plo longioribus, cellulis strati basalis plerumque brevioribus. Cellulæ corticales desunt. — Conceptacula numerosa contigua vel subcontigua. — Conceptacula sporangifera depresso-hemisphærica vel conica, diametro  $120-140 \mu$ , ostiolo vix papilloso, medio nonnunquam columella munita. Sporangia parva,  $17-24 \mu$  longa,  $(9-)11-12(-16) \mu$  lata, semper 4-partita. Sub conceptaculis 1-4 strata cellularum vegetativarum. — Conceptacula mascula parva, paulo prominula vel omnino immersa. Spermatangia elongata vel clavata, fundum planum conceptaculi investientia. Spermatia lineari-clavata, nonnunquam leniter curvata, c.  $6 \mu$  longa,  $2 \mu$  lata. — Conceptacula feminea ut videtur forma structuraque conc. sporangiferis similia. — Hab. in fronde *Furcellariæ fastigiatæ*.

The species here described has only been met with once, viz. on a specimen dredged in the bay of Aarhus. The specimens were determined by FOSLIE as *Melobesia Lejolisii* Rosan. *forma*, but as will be seen from the description given here, it is very different from that species, particularly in the structure of the frond and the small dimensions of the sporangia.

The greater part of the frond is polystromatic; only the marginal part is monostromatic, but it is early divided by horizontal walls, and the frond is then composed of vertical filaments composed of from two to seven or eight cells. These filaments are usually  $6-8 \mu$  broad and consist of cells of varying length, usually 1 to 2 times as long as broad. The cells of the basal layer are rather varying in height, but they are usually lower than broad. There is thus no contrast between the basal layer and the perithallium. Seen from above, the cells of the basal layer show a breadth of  $5-8\mu$ , about the same length or a little more, and appear to be frequently connected by lateral fusions (fig. 176 C). Such fusions may also occur between cells above the basal layer, but transversal pores (secondary) nowhere occur. It is remarkable that cortical cells as those characteristic of the other Melobesia species do not occur. When seen from above, the superficial cells present themselves as nearly quadratic cells arranged in rows, but no small cells cut off from them appear, not even after staining with hæmatoxyline, by which treatment the walls of all the outer cells and the cuticle are very intensely stained. Hair-cells were not observed.

The conceptacles are numerous, occupying most part of the crust, frequently contiguous, giving the frond a vertucose aspect. The sporangial conceptacles are depressed hemispherical or more rarely low conical. A more or less developed central narrow columella is not infrequently present. The sporangia which do not occupy the centre of the conceptacle are remarkably small; they are always four-parted, the three septa approaching each other in the middle of the sporangium (fig. 177 A). When seen from above, the small ostiole is seen to be surrounded by

small-celled filaments radiating towards the centre. In a vertical section these filaments are only little conspicuous, and there are only feeble rudiments of papillæ

in a spout.

The spermat-

angia form a

covering on

the bottom of

the concep-

in the conical orificium (fig. 177). One to four layers of vegetative cells are to be found under the conceptacles.

The antheridial conceptacles are small, sometimes entirely immersed, usually, however, more or less prominent. The inner cavity has a flat bottom, and may be about  $40 \mu$  in diameter. The ostiole is not prolonged



Melobesia microspora. A, vertical section of sporangial conceptacle with a tetrasporangium. B, sporangial conceptacle seen from above. C, emptied sporangial conceptacle showing the rest of the columella. 350:1.





Melobesia microspora. A and B, vertical sections of frond with antheridial conceptacles. C, spermatangia and spermatia. A and C 560:1, B 350:1.

Fig. 176.

Melobesia microspora. A, vertical section of thin crust. B, surface view of crust near the border. C, basal layer seen from the face, showing numerous fusions. 350:1.

tacle; they are produced from small squarish or trapezoid cells, and are lengthened, upwards incrassated, sometimes a little curved cells. Sometimes the spermatangia are produced not directly from the small squarish cells but from cells of the same shape as themselves (fig. 178 C at left). The spermatia are clavate, broadest in the upper end, sometimes slightly curved, about 6  $\mu$  long, and 2  $\mu$  broad at their broadest end, (fig. 178 C). Under the bottom of the conceptacles up to 5 layers of vegetative cells may be found.

Of female conceptacles I have only met with very few, which gave no clear idea of their structure. They seem to be similar in shape and structure to the sporangial ones. Fig. 179 shows a conceptacle containing carpogonia and trichogynes; at left is shown a carpogonium from another section of the same conceptacle.

This species seems to be quite distinct from all well known species of the genus. The want of cortical cells is indeed so remarkable as possibly to suggest

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that it should be referred to another genus; but as other characters justifying its removal from the genus *Melobesia* are not known, I prefer to retain it under the



Fig. 179. Melobesia microspora. Vertical section of female conceptacle; at left a carpogonium from another section of the same conceptacle. 420:1. genus provisionally. The small size of the tetrasporangia seems to be a significant mark distinguishing it from other species. The want of transversal pores between the cells of the vertical filaments, and the fact that these cells are not disposed in transversal rows, exclude it from the genus *Lithophyllum*.

Only found once, growing on the frond of *Furcellaria fastigiata*, with ripe sporangia, ripe antheridia and carpogonia in April.

Locality: Sa: PP, Ryes Flak, 5 meters (no. 4670).

## Choreonema Schmitz.

## 1. Choreonema Thuretii (Bornet) Schmitz.

Fr. Schmitz, Uebersicht, Flora 1889, p. 21 (reprint); id. in Engler u. Prantl, Nat. Pflfam. I p. 541; Fr. Minder, Die Fruchtentwicklung von Choreonema Thur. Diss. Freiburg, s. a.

Melobesia Thuretii Bornet in Thuret, Etudes phycolog., 1878, p. 96, pl. 50, fig. 1-8; Solms-Laubach, Corallinenalgen d. G. v. Neapel, 1881, p. 12, 54, Taf. III fig. 1, 4-10.

Endosiphonia Thuretii Ardissone, Phycologia mediterranea. I. Varese, 1883, p. 451.

This interesting Alga, parasitic in *Corallina rubens*, has been met with in a few localities in the Northern Kattegat and perhaps also in the Skagerak. Unfortunately, the collected material was lost, except that from a single locality near Frederikshavn; I must therefore content myself with referring to the quoted publications.

MINDER has in his important paper given a thorough description of the development of the cystocarp, which in essential points modifies the statements of SOLMS-LAUBACH. After fertilization, the zygote gives off short sporogenous filaments, which gradually fuse with the auxiliary cells, but none of the numerous sporogenous nuclei enter into these cells. From the marginal lobes of the resulting great sporophytic cell (which is not produced by mutual fusion of the auxiliary cells, but has been nourished by them) the carpospores are produced, becoming cut off by watch-glass-formed walls.

As I have had very few specimens at my disposal, I cannot give any statement as to the fructification in the Danish waters,

Localities. Sk (?). — Kn: Within Deget near Frederikshavn (C. H. Ostenfeld), and perhaps a few other localities.

### Lithophyllum Phil.

### Subgenus Eulithophyllum.

# 1. Lithophyllum orbiculatum (Foslie) Foslie.

Foslie, Rev. survey (1900) p. 19 (without mention); Remarks (1906) p. 112. Lithothamnion orbiculatum Foslie, Norw. Lithoth. (1895), p. 143, pl. 22 fig. 10-11. The crust is generally orbicular, scarcely exceeding 2 cm in diameter. In one locality only I found larger crusts expanded over stones; as these crusts also in other respects differred from the others, they will be mentioned separately below. The crusts are 1 to 1,5 mm thick.

According to FosLie, the hypothallic layer mainly resembles that of *Lithoth*. *læve*, being rather feebly developed (Remarks p. 112). I found it, however, always consisting of one layer only, the upright filaments springing out from it in a vertical or nearly vertical direction. The thickness of the perithallic cells varies between 6 and 9  $\mu$ ; the height

is generally greater than the breadth, often about double (about  $13\mu$ ), but it may be of the same size or even smaller. FOSLIE describes these cells as squarish; I found them generally more or less roundish, frequently approaching the

ellipsoid or globe. They are connected with the cells of the neighbouring fil-



Lithophyllum orbiculatum. A, vertical section of crust; B, under part of the same crust. C, horizontal section of crust showing the tranverse pits. D, vertical section of margin of frond. E and F, vertical sections of aberrant specimen (no. 5341), F, showing the hypothallium. 350:1.

aments through transversal pits situated about in the middle of the cells; in transverse sections 3 to 5 such pits are seen in each cell (fig. 180 C). The crust is traversed by horizontal limiting lines which are stained intensely blue by hæmatoxyline; they are often seen crossing the middle of the cells (fig. 180 A). Mme LEMOINE did not find such limiting lines in any species of Lithophyllum (Struct. p. 28). The cells of the perithallium are frequently filled with starch grains, particularly in the under part of the crust. The surface of the frond is frequently much inclined towards the border, which in vertical section shows a great marginal cell (fig. 180 D).

The conceptacles of sporangia are completely immersed; they had in the specimens examined a transverse inner diameter of  $92-116 \mu$ ; they are generally almost globular in a vertical section. They have a single pore in the middle of the roof

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which is not surrounded by peculiarly shaped cell-rows. The sporangia are fourparted; I found them 70  $\mu$  long, 24—35  $\mu$  broad, thus somewhat smaller than indicated by FOSLIE. However, I have only met with a small number of well developed sporangia; I am therefore also unable to state whether they are placed over the whole conceptacle or only in its periphery. A group of sterile filaments in the middle of the floor was not observed. The emptied conceptacles are limited by a sharp inner contour.

Supposed antheridial conceptacles are shown in fig. 182. They had a transverse diameter of 60–77  $\mu$  and the slightly prominent pore surrounded by a number of



Fig. 181.

Lithophyllum orbiculatum. A, vertical section of tetrasporic conceptacle showing the pore. B, similar, but somewhat excentric section. C and D, feebly developed, not yet fully divided sporangia 350:1.

peculiarly formed narrow, obliquely upwardly directed filaments, forming the central part of the roof. The rather plain floor was in some cases covered by a very small-celled layer which had probably supported the spermatangia. In some of these conceptacles small bodies were seen which were supposed to be spermatia.

The conceptacles of cystocarps are entirely immersed (fig. 183); they have an inner diameter of  $112-142 \mu$ . (According to FOSLIE it is  $200-300 \mu$ , but it is not stated if it is the inner or the outer diameter). The pore is surrounded above by obliquely upward directed filaments resembling those of the antheridial conceptacles; but below them is situated an inner crown composed of obliquely downward directed cells. Fig. 183 A shows a number of carpogonia in the central part of the floor, those situated nearest the centre having the longest trichogynes. The carpospores are produced from the margin of the disc-cell at the base of the conceptacle (fig. 183 B). The inner crown of the peristome keeps for a long time in the overgrown conceptacles.

According to Foslie (Remarks p. 113) "the conceptacles do not become gra-
dually overgrown, as far as hitherto seen". It may happen that the emptied conceptacles are filled with filaments growing out from the bottom of the conceptacle, but it also not unfrequently occurs that they are overgrown without being filled, and empty conceptacles are thus found at various depths in the thicker crusts. This was observed with all kinds of conceptacles.

As mentioned above, I found in one locality (TL, north-west of N. Rønners Rev, 4-5,5 m, Sept. 1894, nº 5341) some specimens somewhat different from the





Fig. 182.

Lithophyllum orbiculatum Supposed antheridial conceptacles. In A small bodies are seen which are probably spermatia. 350:1.





Fig. 183.

Lithophyllum orbiculatum. Cystocarpic conceptacles, A, showing the pore and the carpogonia. 350:1. B, excentric section showing the inner crown and two carpospores at the periphery of the disc. 200:1.

ones just mentioned. They form much more expanded crusts, up to 10 cm or more in diameter, and the cells of the perithallium are thicker,  $9-12 \mu$  broad,  $7-16(25) \mu$ long. These measurements, however, are only little different from those given by FOSLIE, who has also determined these specimens as *Lith. orbiculatum forma*. The hypothallium consists, as in the other specimens, of a single cell layer, but the cells are frequently elongated obliquely upwards, in the same direction as the perithallic filaments, and they are similar to the cells of these filaments (fig. 180 *E*, *F*). The examined crust contained sporangial conceptacles  $77-122 \mu$  in diameter, with a single pore; in an old conceptacle a few not exhausted two-parted sporangia were still present. It must be left to further investigations to determine whether these specimens really belong to *L. orbiculatum*. FOSLIE discusses (Remarks p. 113) the question, whether this species might possibly be a northern form of *Lithophyllum incrustans*. This supposition would not agree with the fact that the last named species, according to Mme LEMOINE (Struct. anat. pl. IV fig. 1), has a much developed hypothallium. On the other hand, a specimen collected by me at Cherbourg and determined by Foslie as *Lithophyllum incrustans*, showed a one-layered basal layer and on the whole the same anatomical structure as *L. orbiculatum*. The question as to mutual relation of the two species must therefore be left undecided.

The species has in the Danish waters only been found in the northern, eastern and southern Kattegat and in the Sound. It has been met with in depths from 16,5 to 24,5 meters. The aberrant specimens were dredged in a depth of 4-5,5 m.

Localities. Kn: TL, N.W. of Læsø, 4-5,5 meters, large crusts, Sept., nº 5341 (see above). — Ke: IR, Groves Flak, 24,5 meters; IK and IH, Lille Middelgrund; IA, Store Middelgrund. — Ks: HO, east of Hesselø. — Su: bM, south of Hveen, 12,5 meters.

#### Subgenus **Dermatolithon** Foslie.

As mentioned above, p. 236, the genus *Dermatolithon* was established by FOSLIE in 1898 (List of Spec., p. 11), only however as a nomen nudum, and the following species of Melobesia were referred to it: M. pustulata, Lejolisii and hapalidioides. In 1900 (Rev. syst. Surv., p. 21) the genus was described and M. macrocarpa was further referred to it, besides two uncertain species, while M. Lejolisii was removed from it. It was founded on characters of the sporangial conceptacles (comp. p 237). Later on (Algol. Not. I, 1904, p. 3), Foslie judged that these characters were of small systematic value, he pointed out the relations of these species to the genus Lithophyllum, and transferred Dermatolithon as a subgenus under Lithophyllum, characterized by having the hypothallium formed by a single layer of inclined cells, in contradiction to Eulithophyllum and Lepidomorphum, the hypothallium of which always consists of several cell-layers. Three years later (Algol. Not. VI, 1909, p. 58) Foslie raised it again to a distinct genus characterized only by the last-named character. As mentioned above, the species of Dermatolithon agree with Lithophyllum in the presence of transversal pits between the vertical cell-rows. A difference is certainly said to exist in the hypothallium being in Dermatolithon monostromatical, while it is polystromatical in Lithophyllum; but Foslie admits himself that the hypothallium may sometimes be partly polystromatical in Dermatolithon, (1909, p. 57). And in Lithophyllum orbiculatum mentioned above there is evidently a monostromatical hypothallium (fig. 180). Further, in Dermatolithon, the cells of the hypothallium are usually long and oblique, but they may also be rather short and only little inclined (fig. 189), which may likewise be met with in Lithophyllum, e.g. in L. orbiculatum, fig. 180 F. It must therefore be concluded that Dermatolithon cannot be kept distinct from Lithophyllum as a separate genus, at all events on the basis of the anatomical structure, but must be regarded only as a subgenus.

Lithophyllum Corallinæ (Crouan), which was already in 1897 transferred from the genus Melobesia to Lithophyllum, seems particularly to be a connecting link between Dermatolithon and the typical Lithophyllum.

#### 2. Lithophyllum macrocarpum (Rosan.) Foslie.

Foslie, Remarks, 1905 (1906), p. 128; M. B. Nichols, Contribut. to the knowledge of the Californ. spec. of crustaceous Corallines. II. University of California Publ. in Botany. Vol. 3, No. 6, 1909, p. 352, figs.

12, 15, 16, 17; Foslie, Algol. Notiser VI, 1909, p. 47. Melobesia macrocarpa Rosanoff, Recherches, 1866, p. 74, pl. IV, figs. 4-8, 11-20. Dermatolithon macrocarpum Foslie, Rev. Surv., 1900, p. 21; Algol. Not. VI, 1909, p. 58.

#### f. typica Foslie.

L. pustulatum (Lamour.) Foslie f. macrocarpa (Rosan.) Fosl., Remarks, p. 117.

It seems that only the specimens from one locality growing on *Phyllophora membranifolia* are with certainty referable to the typical form which, according to FosLIE, differs from the following form by the frond attaining a greater thickness and by the sporangial conceptacles being up to  $600 \mu$  in diameter but a little lower proportionally to the diameter. The frond of the named specimens, however, attains only a thickness of  $200 \mu$ ; the sporangial conceptacles measured over  $500 \mu$ , and under them were 3-4 layers of cells. The other specimens referred by FosLIE to this variety are partly sterile and only determined with doubt, or they seem not to possess the characters named.

Localities. **Kn:** Trindelen, 15 meters, on *Phyllophora membranifolia*, July, with ripe sporangia. — Further recorded with doubt from the following localities. **Lf:** Nykøbing, on *Chorda Filum*, (Th. Mortensen). — **Kn:** Hirsholmene, on *Fucus vesiculosus*; Nordre Rønner, on *Fucus vesiculosus*; TG, north of Læsø, 9,5 m, on *Phyllophora membranifolia*, sterile.

#### f. intermedia Foslie.

Foslie, Remarks, 1905, p. 117; Nichols, Crustaceous Corallines, II, 1909, p. 352, plate 11 fig. 12, pl. 12 figs. 15-17.

L. pustulatum (Lamour.) Foslie f. intermedia Foslie, Remarks, p. 128.

Most of the specimens of this species have been referred by FOSLIE to the f. intermedia, which has later been carefully described by NICHOLS, I. c. I have nothing to object against the determinations of FOSLIE, and I shall not enter into the question as to whether the species can be kept distinct from *L. pastulatum*, but will merely remark that I have always found two-parted sporangia. In referring to the quoted descriptions and figures however, some remarks on the Danish species may be added.

These are almost all growing on *Fucus vesiculosus*, where they form crusts measuring 4-7,5 mm in diameter, frequently confluent. The border of the frond, which is not always adherent to the substratum, consists of a single layer of long oblique cells, each bearing a cortical cell cut off by an oblique wall. Later on, the long cells are divided by a transversal wall, the crust thus being composed of two

layers of cells, not including the cortical cells, and further transversal divisions frequently do not occur except in the immediate vicinity of the conceptacles; it may even happen that the frond is monostromatic in almost its whole extent. The long cells in the upper layers are always connected with transversal pits (fig. 184). The thickness of the frond is rather variable. Monostromatic fronds were  $25-42 \mu$ thick, fronds consisting of two layers of cells  $67-105 \mu$  and fronds containing three layers were  $91-123 \mu$  thick. The fronds are frequently growing over each other. It also frequently happens that new growing edges are produced from certain parts of the frond, growing over the neighbouring parts the growth of which has ceased. The long cells contain a small nucleus in the upper part of the cell, and a number



#### Fig. 184.

Lithophyllum macrocarpum f. intermedia. Vertical sections of fronds. A, margin of frond. B, part of monostromatic frond showing a hair-cell and two cortical cells cut off from one cell. C, part of thicker crust; transversal pits between the cells of the two upper layers. 350:1

of small chromatophores spread in the cell. The cortical cells are produced early, immediately after the formation of the long cells by the division of the marginal cell. But at some distance from the margin a new cortical cell may be cut off under the primary one by a horizontal or inclined wall (fig. 184 B), and this process may be repeated several times. Hyaline hairs may be produced from long cells seemingly not different from the others, and provided, like these, with a cortical cell (fig. 184 B). The length of the long cells of the frond varies greatly; when the crust is polystromatic, the cells of the under-

most layer are often rather short. When these cells or those of the monostromatic frond are long, their undermost part is usually more inclined than their upper part (fig. 184 *B*, comp. NICHOLS, l. c. fig. 12, 15).

The sporangial conceptacles are very prominent, conical with rounded or applanated top,  $300-500 \mu$  in diameter. Under the conceptacle 1-3 layers of sterile cells are present. Papillæ projecting inward and upward, lining the pore, as described and figured by NICHOLS, may be found in the under part of the pore, but they are usually slightly developed. Seen from above, the superficial cells surrounding the pore appear scarcely different from the others, the nearest being only a little smaller (fig. 185 B). The sporangia are only placed in the peripheral part of the conceptacle, the central part being occupied by sterile cells forming a conical columella. NICHOLS found also sporangia in the central part, though less numerous there than at the periphery. As shown by this author, each sporangium is born by a stalk cell. A "plug" was found in some rare cases in the ostiole, forming a continuation of the central sterile cells (fig. 185 A), but it seems to be usually wanting,

and was not found by NICHOLS. The sporangia are disporic; they were found to be  $105-140 \mu \log, 35-60 \mu$  broad; the smallest ones, however, were perhaps not ripe.

Antheridial conceptacles were not observed.

Cystocarpic conceptacles were only found in specimens from one locality (Kalö). They are of the same shape and size (about 400  $\mu$  in diameter) as the sporangial ones, and the ostiole is of the same structure, being without or only with poorly developed papillæ in the under part. The carpospores are only produced at the periphery.

This variety has only been found growing on *Fucus vesiculosus* and *Fucus serratus* a little below low-water mark. It is particularly abundant in the Limfjord, probably owing to the high salinity and the high summer temperature of this



Fig. 185.

Lithophyllum macrocarpum f. intermedia. A, vertical section of not quite ripe sporangial conceptacle. B, orifice of sporangial conceptacle seen from above. C, vertical section of orifice of cystocarpic conceptacle. A and C 200:1. B 350:1.

water. Ripe sporangia have been met with in summer, June to September. In April two-parted sporangia were found, but not fully ripe, and in the same month cystocarpia were found.

Localities. Lf: Søndre Røn by Lemvig; Oddesund; MH, bank of Skrandrup, MG, off Hanklit, and Thisted in Thisted Bredning; I, Venø Bugt; Nykøbing; Sallingsund, pier; Amtoft Rev; LQ, Lendrup Røn; Løgstør. — Kn: Hirsholm and Kølpen near Frederikshavn. — Ks: Isefjord: on the beach near Frederiksværk (Th. Mortensen); Lammefjord; Holbæk Fjord. — Sa: Reef near Kalø; Æbelø. — Sf: near Birkholm.

#### 3. Lithophyllum Corallinæ (Crouan) Heydr.

F. Heydrich, Corallineae, insbes. Melobesieae. Ber. deut. bot. Ges. Bd. 15, 1897, p. 47. Melobesia Corallinæ Crouan, Florule du Finist., 1867, p. 150, pl. 20, genre 133 bis, fig. 6—11. Lithophyllum pustulatum (Lamour.) Fosl., f. Corallinæ (Crn.) Foslie, Remarks, 1905, p. 118.

In two localities in the Skagerak a few specimens of a calcareous alga were found growing on *Corallina officinalis* and agreeing with the short description and

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the figures of *Melobesia Corallinæ* CROUAN (1. c.). These specimens have not been examined by FOSLIE, but as this author regarded CROUAN's species as being only

a form of Lithophyllum pustulatum, he would probably have referred our plant "as a denominated form" to L. macrocarpum, whereas it has disporic sporangia. A closer examination of my specimens, some of which were preserved in alcohol, showed me, however, such differences from the named species that they cannot, in my opinion, be referred to it, but must be regarded as representing a different species bearing CROUAN's name.

The crust is in some cases surrounding the *Corallina*-frond, being attached to it in its whole extent and fusing together where the borders meet. In other cases it is only attached by its central thicker portion, while the thinner edges of the orbicular, peltate frond are free (fig. 187, comp.



Lithophyllum Corallinæ, from Hanstholm, vertical sections of scutate fronds with free edges. Sporangial conceptacles in A and C, cystocarpic conceptacles in B. Overgrown conceptacles in B and C. 65:1.



Lithophyllum Corallinæ, from Hirshals. A, vertical section of edge of frond. 560:1. B, vertical section of frond near a conceptacle. 350:1. C, section of frond with sporangial conceptacle. 65:1.

CROUAN, l. c. fig. 6, 7). In the first case the frond was up to  $105 \mu$  (over 12 cells) thick, in the latter the central part was about 250  $\mu$  thick, the inner edge 70–105  $\mu$  thick. The diameter of the peltate fronds is 2-2,5mm. The edge of the frond is thick, polystromatic to the very margin or nearly so, the cells cut off from the marginal cell dividing early by transversal walls. The marginal cell is much smaller than in L. macrocarpum (fig. 186 A). The undermost cell in the vertical or ascending cellrows constituting the frond is not longer than the others, frequently even shorter, being only 1-3 times as long as broad; these cells are usually inclined. The cells of the upper cell-layers are frequently much longer; the transversal pits of these cells are always distinct; they are shown in fig. 186.

The sporangial conceptacles are only little prominent, forming low warts with a more or less plane upper face, the cavity being entirely or for the most part sunk in the frond. Their outer diameter is therefore often difficult to state, but it reaches at least  $350 \mu$ . The cavity is nearly globular or usually more or less flattened. The ostiole is without or provided with poorly developed papillæ in its under part. In some cases the ostiole was found to be excentric. The sporangia are only placed at the periphery of the conceptacle, the central part being occupied by a conical



columella. The sporangia are always disporic, 50-88  $\mu$  long, 18-32  $\mu$ broad. The number of sterile celllayers under the conceptacle varies greatly according to the thickness





*B* Fig. 188.

Lithophyllum Corallinæ. A, vertical section of sporangial conceptacle. 205:1. B, vertical section of upper part of a similar one. 350:1.

Fig. 189. Lithophyllum Corallinae. A, Vertical sections of antheridial conceptacles. In A some spermatia show two nuclei. A 350:1. B 370:1

and age of the frond. In thicker, older fronds the first produced conceptacula after evacuation become overgrown by the continued growth of the surrounding tissue and are later found as empty cavities in the under part of the crust, while new conceptacula are formed at a higher level (fig. 187).

The antheridial conceptacles are entirely sunk in the frond, not prominent, rather low, with a flat bottom and a shorter or longer orifice. The spermatia are produced at the end of long sterigmata given off from small cells covering the bottom of the conceptacle. The ripe spermatia are globular-ovoid, at one end (the basal one) drawn out in a short point. Two nuclei were distinctly visible in isolated spermatia (fig. 189 A).

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The cystocarpic conceptacles have the same shape and size as the sporangial ones. The papillæ lining the ostiole were found more developed than in the sporangial conceptacles. The structure of the cystocarp rather resembles that of *Corallina*,



Lithophyllum Corallinæ. Vertical section of cystocarpic conceptacle. 350:1.

a large disc-shaped cell occupying the bottom of the conceptacle giving off at the periphery seriate carpospores and covered with numerous closely placed oblong cells filled with protoplasmatic contents, the morphological character of which could not be determined, as trichogynes were in no cases observed (fig. 190). The cystocarpic conceptacles become overgrown and sunk in the crust as also the sporangial conceptacles.

The structure of the frond, being polystromatic to the margin, and the slightly prominent conceptacles being sometimes overgrown and deeply sunk in the frond, are the principal characters distinguishing this species from the foregoing, with which it agrees in its disport, though smaller sporangia. It is apparently not identical with *Melobesia Corallinæ* SOLMS (Corall. p. 9, Taf. II, fig. 25, III fig. 21-24) which differs, to judge from the figures, by tetrasport sporangia, occupying the central part of the conceptacle, by the want of columella, and apparently by the structure of the frond, the basal cell-layer being very low.

Found with sporangia and cystocarps in July and August.

Localities. Sk: YT, YU, Hanstholm, 2--6 meters; Hirshals, on the mole.

# 4. Lithophyllum pustulatum (Lamour.) Foslie forma?

Mention may be made here of an alga recorded once growing on *Corallina officinalis* but which could not be identified with certainty on account of the incomplete state of the present material. It forms thin red crusts, the peripheral part of which is monostromatic with cortical cells, only  $14-20 \mu$  thick, while the central portion, consisting of 2-3 cell-layers, besides the cortical cells, has a thickness of up to 80  $\mu$ .





The cells of the vertical cell-rows are proportionally short, and connected with transversal pits. Only empty conceptacles were found. They are about  $420-500 \mu$  in diameter, conical-subhemispherical, somewhat lower in proportion to the breadth than in *L. macrocarpum*. The roof is of solid structure and is very thick near the ostiole. The cells surrounding the upper part of the ostiole are elongated but not projecting as free papillæ. Our alga reminds one of *L. pustulatum* f. *australis* Foslie (Remarks, p. 117, NICHOLS, Contrib. II, 1909, p. 356, fig. 21-24) from which it differs, however, to judge from NICHOLS' description, by the want of papillæ surrounding the ostiole. As the conceptacles were empty, their nature could not be determined.

Locality: Ke: Store Middelgrund 19 meters, May.

#### Corallina L.

#### 1. Corallina officinalis L.

Linné, Fauna Suecica 1761, p. 539; Kützing, Phyc. gener., 1843 p. 388, Taf. 79, Fig. 1; Harvey, Phyc. Brit. II, 1849, pl. 222; J. E. Areschoug in J. Agardh, Spec. II, 2, 1851-52, p. 562; Kützing, Tab. phyc. Vol. 8, 1858, Tab. 66-68; Kny und Magnus, Ueber ächte und falsche Dichotomie im Pflanzenreich. Botan. Zeit. 1872 Sp. 708; Thuret, Études phycologiques, 1878, p. 93 pl. 49; Solms, Corallinenalg., 1881 (Corallina mediterranea); Hauck, Mceresalg., p. 281; Guignard, Dév. et const. des anthérozoïdes. Revue gén. T. I, 1889, extrait, p. 50, pl. VI fig. 24-26 (spermatia); B. M. Davis, Kerntheilung in der Tetrasporenmutterzelle bei Corallina offic. Ber. deut. bot. Ges. 1898, Bd. 16 Heft 8, p. 266; K. Yendo, Corallinæ veræ japonicæ. Journ. Coll. of Science. Imp. Univ. Tokyo. Vol. XVI. Art. 3, 1902, p. 28, pl. III fig. 11-13, pl. VII, fig. 10-13; id., Study of the genicula of Corallinæ. Ibid., Vol. XIX, Art. 14. 1904; id., A revised list of Corallinæ. Ibid., Vol. XX, 1905, p. 29; Oltmanns, Morph. u. Biol-d. Algen, I, 1904, p. 562.

The articulated fronds are given off from a basal crust much resembling some crustaceous *Lithothamnia* (comp. HARVEY, l. c.). In some cases it is rather small and gives off numerous closely placed fronds from almost its whole surface. In other cases it is widely extended, up to 2,4 cm. in diameter or more, and bears

only a small number of erect fronds (fig. 192). The border is lobed, the lobes being now broad, now narrow. In the latter case the lobes are more or less branched and often keep their independence, being separated by deep furrows when meeting, but it also happens that they grow partly over each other; in other cases, however, they are confluent. Concentric zones are sometimes very distinct. In the anatomical structure they resemble the crustaceous *Lithothamnia*, showing a hypothallium consisting of long cells running in a horizontal direction and a perithallium composed of ascending filaments of shorter cells. The last cell of the latter is very short, the penultimate proportionally long. There seems to be a continuous layer of non-



Fig. 192. Corallina officinalis. Basal crust with scattered articulated fronds or scars after them; at right it meets with a crust of a Lithothamnion. 4:1. dividing cover cells similar to that pointed out for the articulated fronds and for *Lithothamnion* by SOLMS (Corall., p. 27 and 29). The cells of the hypothallium and those of the inner perithallium were, in a specimen collected in July, filled



Fig. 193. Corallina officinalis. Border of basal crust in vertical section. 390:1.

with starch grains, while the cells of the outer perithallium showed numerous disc-shaped chromatophores and a single nucleus.

The articulated fronds are connected with the crust by a geniculum. The ramification is monopodial, in the typical form pinnate. The branches usually arise near the growing point. At an early stage three (or more) small protuberances are seen at the upper end of the last joint, the middlemost of which develops in continuation of the axis. This has been interpreted as trichotomy, or polychotomy (KNY 1872, Sp. 704, SOLMS 1881, p. 30); I think, however, with MAGNUS 1872, p. 721, that there is

no reason for this interpretation, and that the middlemost outgrowth must be regarded as the principal axis, the others as lateral branches. In f. *typica* each joint bears two opposite branches, all in the same plane, having for the most part a limited growth, being "pinnulæ", but there is no distinct difference between the pinnulæ and the longer branches with continual growth. It frequently happens, however, that some joints produce more than two branches; 6 branches are not rarely met with and I have found up to 10 lateral branches placed in the same plane on the upper border of a much flattened joint (fig. 194 A). More rarely the supernumerary branches are given off in different directions at the same level, being thus verticillate (fig. 194 B, Plate IV fig. 5); in a specimen from Frederikshavn, a whorl of 8 pinnulæ was

found on a joint. It may happen also otherwise, that normal branches are exceptionally given off in a direction diverging from the ordinary plane of ramification. The joints bearing a great number of branches occur principally in the upper part of the shoots produced in a period of growth. Besides the normal branches, adventitious ones occur, though rather rarely (Comp. Solms l, c. p. 29). Their position is less regular than that of the normal branches, and they are usually given off from the under part of the joints.

While in the f. *typica* every joint bears usually two opposite branches, other specimens, especially those growing in deeper water, are less branched



Fig. 194. Corallina officinalis. A, seriate branches placed on the border of a joint. B, upper part of frond with verticillate branchlets. 3:1.

those growing in deeper water, are less branched, a greater or lesser number of joints bearing no branches, or only one. In these specimens the joints are cylindrical or nearly so, while the joints of the much branched forms are usually more complanated, especially in the upper end of the shoots (Plate IV fig. 6). In specimens from deeper water it sometimes happens that some of the branches assume a special character, growing out as slender, unbranched, irregularly curved organs taking not the upward direction but growing in a transversal direction or more downwards. They resemble either rhizomes or tendrils but have usually not the function of either of these organs (Plate IV fig. 7). It may however happen that the end of such a branch fixes itself on any solid substratum, f. inst. molluscs, *Furcellaria, Zostera*, developing an adhesive disc similar to the primary crustaceous frond. It is connected with the ultimate joint by a genicle. Such adhesive discs may also develop at the end of ordinary fronds coming accidentally in contact

with any solid body (fig. 195). These discs have the power of producing new articulated fronds, in a similar manner to the primary ones (fig. 195 B).

The age of the articulated fronds is not known. They reach a length of up to 16 cm, usually however only 10 cm. Supposing that a long pinnated shoot is produced every year, it seems probable that the age of the erect fronds does not exceed 3 or 4 years.

The joints consist of a central tissue of elongated cells and a cortex not sharply limited from it, the cell-rows at the periphery of the central tissue bending outwards and consisting of cells becoming gradually shorter outwards. The cells of the central tissue are usually 5—8 times as long as broad; they are disposed in transversal zones, their end-walls being situated about at the same level, the limiting lines being, however, convex upwards (comp. Mrs. WEBER, Siboga pl. XVI fig. 15, 1904). The cells are as usual connected with primary

pits at the end walls, while secondary pits do not occur<sup>1</sup>), but lateral fusions between the cells of the central strand are very numerous and more than two cells frequently fuse together. As mentioned above, p. 211, I found these fusions followed by a fusion of the nuclei in a tetraspore-bearing plant.

In a female specimen with ripe cystocarps collected in winter at Frederikshavn similar cell-fusions were found, but the behaviour of the nuclei was different, those of the central tissue having divided in two to four, while such divisions were not observed in the tetraspore-bearing plants. It was therefore not easy to decide whether fusion of the nuclei took place in the female plant. It should be of much interest to decide whether there is such a constant difference between the tetrasporebearing and the sexual plants.

The cortex of the joints is covered with a continuous layer of low cover-cells (comp. Solms, Corall. p. 29).

<sup>1</sup>) PILGER states, however, that the longitudinal walls in the central tissue of *Corallina* are provided with pits (1908. p. 252).



oped from the ultimate joint

of a shoot coming in contact with a rhizome of Zostera;

scars after articulated fronds developed from the disc but

fallen off are visible. 3:1.

The nodes (genicula) consist of a single layer of very long cylindrical cells with attenuated ends continuing into the joints connected by the node. The statement of SOLMS (l. c. p. 28) that these cells are later on divided by a number of thin transversal walls has not been confirmed by YENDO (Genicula, 1904, p. 30), neither have I found these walls. The longitudinal walls of the genicular cells are not incrustated with calcium carbonate, while the attenuated ends (their extrageni-



Fig. 196. Corallina officinalis. Part of frond with fused male conceptacles. 18:1.

cular portions, YENDO) are incrustated as the cells of the joints between which they are inserted. For further information on the chemical qualities of the walls of the genicular cells comp. YENDO (l. c.). The node is more or less covered by a cortex which is interrupted in the middle (comp. KÜTZING, Phyc. gen. pl. 79, I).

Hyaline hairs were not observed in the Danish specimens of this species, but as they have been figured by THURET in *C. mediterranea* (Ét. phyc. pl. 49 fig. 2 and 4) they will probably also be found in the typical *C. officinalis*.

The three kinds of conceptacula occur, as far as known, always on different individuals (comp. THURET, l. c. p. 93). They are either terminal in the ends of shorter and longer branches, or lateral, sessile on the joints, and the three kinds of conceptacula may all be apical or lateral as well (comp. SOLMS, l. c. p. 5). The lateral conceptacula are frequently placed on the edges of the joints, but their position may also be more irregular on various sides of the branches. In a male specimen which was very densely beset with conceptacles, many of them were fused together. Two or three of them were frequently placed at the same level, forming an incomplete ring at the upper end of the joint, with the ostioles more or less drawn out in a horizontal slit (fig. 196).

As to the structure and development of the conceptacles, reference may be made to the repeatedly quoted papers of THURET and SOLMS

on Corallina mediterranea, which must be supposed to agree with the typical C. officinalis in this respect.

As shown by THURET (l. c. p. 93, pl. 49 fig. 6), the antheridial conceptacles differ from the others in having a conical prolongation containing the ostiole. 1 found the same in the Danish specimens. The development and structure of the spermatia have been studied by THURET (l. c. p. 95, pl. 49 fig. 7–9), SOLMS (l. c. p. 36, Taf. II fig. 21-23) and GUIGNARD (l. c.).

The development of the cystocarp has been thorough described by SOLMS and I must content myself with referring to his paper, remarking however, that the subject needs further examination after the important paper by MINDER on Choreo*nema Thuretii.* I have only examined a few fully developed cystocarps on slides made by microtome, and they showed that the formation of carpospores is not always limited to the periphery of the conceptacle, but may also take place from the inner part of the great disc-shaped cell at the bottom of the conceptacle, perhaps only because the border of this cell is lobed.

Referring for the structure and development of the conceptacles of sporangia to THURET (l. c. p. 94, pl. 49 fig. 4–5) and SOLMS (l. c. p. 31, Taf. I, fig. 6–7), I shall as to the sporangia only mention that, after the division of the primary sporangial nucleus into four, a fairly long time elapses before the cell-division begins. A great number of sporangia with four nuclei situated about (not exactly) in a vertical series are therefore to be found (fig. 197 *B*). This was already observed by THURET, who remarks (l. c. p. 95): "La formation des cloisons est précédée de l'apparition d'espaces clairs qui occupent le centre des futurs spores (fig. 5)".

As elsewhere (comp. THURET, l. c. p. 95, SOLMS, l. c. p. 5), the sporangia-bearing specimens seem to be more frequent than the sexual ones also in the Danish waters, but I have not sufficient observations to affirm this with certainty.

The species is, as elsewhere, rather variable, but cannot be divided into well defined varieties. When growing at low-water mark or in shallow water it is markedly pinnate, almost every joint bearing a pair of branches, and must be referred to f. *vulgaris* Kützing (Tab. phyc. VIII, p. 32, Tab. 66 fig. 2; C. officinalis a, Areschoug I. c. p. 562; C. offic. f. typica Kjellman, Alg. Arct. Sea p. 86 (114); C. offic.  $\gamma$ ,

Yendo 1902, p. 29, pl. VII, fig. 12, comp. Plate IV figs. 5—6). The specimens growing in deeper water are sometimes not much different from the ones just named, but are usually less branched and have longer joints. In f. *valgaris*, the length of these does not reach 2 mm, while in the specimens from deeper water it not rarely reaches 3,5 mm, and even a length of 4,5 mm has been met with. In the extreme forms, the ramification is scarce and irregular, not pinnate, and the branches are often given off at various sides, though a tendency to branching in one plane is to a certain degree pronounced. Such forms may be named f. *profunda* Farlow (Mar. Alg. New. Engl., 1881, p. 179). In the Kattegat and the Samsø waters they are frequently coarser than the typical form, the joints being cylindrical, about 1 mm thick, and agree then fully with the description of f. *robusta* Kjellm. (l. c. p. 86 (114)). This form has been collected in several places in the named waters in depths from 10 to 19 meters (Plate IV fig. 8).

The species is commonly spread in all the Danish waters with proportionally high salinity, including the Samsø waters, where it is very common. It grows usually on stones, but may also be fixed to shells of molluscs (*Purpura, Littorina, Buccinum*, bivalves), on wood, and more rarely on Algæ (*Furcellaria*). It often forms associations

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Corallina officinalis. A, with undivided nucleus; B, with four nuclei but yet undivided; C, with completed divisions. 230:1.

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from ordinary low-water mark to two or four meters depth on moles and boulders in Skagerak, the northern Kattegat and the Limfjord, and it does not avoid exposed places. In summer, a narrow belt of dead Corallina may be found at low-water mark when the upper part of the Corallina-association has been exposed to the air during a long period of low-water. It can also occur abundantly and form associations in deeper water, on gravelly or stony bottom, e.g. in the eastern Kattegat, but it is then frequently associated with *Lithothamnia*. In the sublittoral region it descends frequently to 19 meters depth, but it has been met with at a depth of 29 meters in the northern Kattegat. As to the vegetative development of the frond during the year I have no personal observations, but it must be supposed that the growth begins in the last part of the winter and ceases in summer, and that old fronds are thrown off in autumn. NELSON and DUNCAN (Histology of cert, spec. of Corallinaceæ, Trans. Linn, Soc. Bot. Ser. 2 Vol. I. 1876 p. 203) indicate that there is not much carbonate of lime in the frond in spring. Old fronds are often corroded by various organisms. Ripe tetrasporangia were repeatedly met with in the months of May to July, unripe in March. Ripe antheridia were found in May, ripe cystocarpia in May and December.

Localities. Ns: ZO, jvdske Rev. 24,5 m; groin at Thyborøn; Klitmøller, 2 m. - Sk: Hanstholm, various places, 4-15 m; YM, YN, Bragerne, 1-10 m; Bulbjerg and Svinkløv, washed ashore; SZ, Løkken, ZK<sup>1</sup>, ZK<sup>7</sup>, Lønstrup; Hirshals, mole and boulders near land, and 2 miles N.W. of Hirshals, 11 m; Højen, c. 5 m. - Lf: Lemvig; Ydre Røn by Lemvig; ZY; Oddesund; MD; MF, MG, MH, Thisted in Thisted Bredning; harbour of Struer; I; various places in Sallingsund; LS1; MI; Ejerslev Røn; Holmtunge Hage: Amtoft Rev; LO. - Kn: Harbour of Skagen; KC, TV, Krageskovs Rev; Hirsholmene; Kølpen: Deget: Frederikshavn; Marens Rev, Borrebjergs Rev; Nordre Rønner; TJ; TL; TH; UC; UB; ZL; Jegens Odde; Trindelen; FF, FE; IX; ZB, 29 m; TG. - Ke: IM, VY, IP, Fladen; XA, Lille Middelgrund: EU. ET. II. IK. f. robusta, dominant, at 14 meters depth. Store Middelgrund: ID, (f. robusta, 19 m), IB, HX, IA, 11-19 m; OO, Søborg Hoved Grund, 8,5 m. - Km: XF, Læsø Rende; ZC, Kobbergrund: XB: XD; XC; TS; bK; FM; FN (f. robusta); ND. - Ks: Pakhusbugt, Anholt (loose); EM and EJ, Lysegrund; HS. Briseis Grund: OS. Hastens Grund; OU, Schultz's Grund; D. Grønne Revle north of Isefjord; aU, off Lumbsaas; GF, Siællands Rev; FO, off Havknude; NB; FP, Jessens Grund. - Sa: MZ; KK and KJ, south of Hjelm; KM; BE and BF, off Sletterhage, f. robusta, 10 m; MY; PL; Begtrup Vig; Kalø Rev; harbour of Aarhus; PK; FS, Vejrø Sund N.E. of Samsø (f. robusta); MP; DK, Bolsaxen (f. robusta, 14 m); MO: AH1; Korshavn; Hofmansgave (Car. Rosenberg); NZ; PK, Norsminde Flak; BC; aX, south Side of Endelave; Al' and DJ, by Æbelø; FY, off Bjørnsknude, 5,5 m. - Lb: Only found at the harbour of Bogense and at FZ, Kasser Odde, the north side of the reef, 6,5 m. Never met with in the neighbourhood of Middelfart and Fænø, where numerous dredgings have been made. - Sb: Harbour of Kerteminde; NR, at the entrance to the harbour of Korsør, only 1,5 m high, on stones picked up in the belt (Nyborg). - In the German part of the western Baltic Sea REINKE records the species from the isle of Als and from Neukirchner Grund in Flensborg Fjord. At Kullen on the west coast of Sweden I have not met with it.

#### 2. Corallina rubens L.

Linné Syst. nat. Ed. 12. Vol. I. p. 1305. Kützing, Tab. phyc. 8. Band, 1858, p. 38, Taf. 80; Solms, Corall., p. 42; Hauck, Meeresalg. p. 278.

Jania rabens Lamour.; Kützing, Phyc. gener., 1843, p. 389, Taf. 79 II; Harvey, Phyc. Brit. pl. 252, 1851; Areschoug, in J. Agardh, Sp. g. o. Vol. II 1852, p. 557; Kny, Bot. Zeit. 1872, p. 350; Thuret, Études phyc. 1878, p. 99, pl. L, LI. This species is usually classed under the genus Jania, established by LAMOUROUX. This genus, however, is, as shown by ARESCHOUG (l. c. p. 554), scarcely different from Corallina by other characters than the normally forked frond. Mrs. WEBER has later (Siboga, p. 85) stated that there is also an anatomical difference, the cells of the central tissue in the joints being of almost the same length as those of the genicula, while they are much shorter in the true Corallina. I prefer, however, to regard Jania as a subgenus of Corallina.

The articulated fronds are given off from a small thick crust with lobed outline, resembling that of *C. officinalis* but of smaller size. From the crusts examined

by me only a small number of fronds. usually 1-3, were given off. The fronds are connected with the crust by a geniculum which may be rather broad (high) (fig. 198A). The fronds are normally forked, the point of vegetation producing by the ramification no shoot in continuation of the axis, but two diverging equally from its direction. The bifurcations occur in greatly varying frequency, the number of interjacent joints varying from 1 to 10 or more. The planes of ramification of the successive bifurcations do not coïncide, but cross each other under various angles (comp. KNy, 1872 p. 707). In most of the Danish specimens this is the only ramification existing; but pinnate ramification may also occur. A greater or smaller number of the joints may be complanated, obsagittate and bearing on the up-



Fig. 198. Corallina rubens. A, basal part of an articulated frond springing off from the basal disc. B, adhesive disc developed at the end of a branch. 65:1.

wardly directed points two opposed simple articulated pinnulæ consisting of a small number of joints. When these pinnulæ are produced in a greater number, on several successive joints, we have the f. corniculata, which has been regarded as a distinct species, but which cannot be kept distinct from the typical species. The joints at the base of the bifurcations may also bear pinnulæ, under the forking branches. The pinnulæ, no doubt, usually arise later than the branches of the bifurcations, and may then perhaps be regarded as adventitious organs; but it seems that opposite lateral pinnulæ or pinnæ may sometimes arise at the growing point, for according to KNY (l. c. sp. 707) "trichotomies" may also occur. This must take place when the ramification is pinnate. In such cases the middlemost shoot certainly represents the continuation of the axis, and the two lateral ones correspond to the branches of an ordinary bifurcation; I have not, however, examined such ramifications. In rare cases the lateral shoots showed a more vigorous development, and were bifurcate as the ordinary shoots. Supernumerary adventitious pinnulæ may

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sometimes occur under the normal ones. — Hyaline unicellular hairs covering the surface of the frond have been mentioned and figured by THURET (Ét. phyc. p. 96, pl. L, LI, fig. 1, 9, 15, 18). Their occurrence seems to be dependent upon the season, as 1 found them in specimens collected in July while they were wanting in specimens from August.

The cortical layer consists of two or three cell-layers. It is covered by a continuous layer of low cover cells. The cells of the central tissue are, as mentioned above, almost of the same length as those of the genicula (fig. 199). Lateral fusions



Fig. 199. Corallina rubens, longitudinal section of joint. 350:1.

take place between the cells of the cortical layer and of the central tissue as well.

Adhesive discs are not seldom produced at the end of branches which accidentally come in contact with any solid body, e. g. an Alga or a shell of a bivalve. They are, as in *Cor. officinalis*, connected with the frond by a geniculum (fig. 198 *B*).

As to the organs of reproduction and the germination, reference may be made to the splendid work of THURET (l. c. p. 99, plates L, LI); it should only be mentioned that there are but two kinds of individuals, the sexual plants being monoecious. In the Danish waters only tetrasporangiabearing plants were found.

The species has been met with in several places at the shore of the Skagerak and in the northern Kattegat. In the Skagerak it occurred partly as f. corniculata or a transitional form; in Kattegat it occurred only as f. typica. It was found growing on several Algæ, in particular Ahnfeltia plicata, further Chondrus crispus, Phyllophora rubens, Delesseria and Corallina rubens. It grows partly in small depth,

about 1 meter, near the coast, partly deeper, up to 23,5 m depth. It reaches a length of 2-3 cm or a little more. It has been met with both in summer and winter, with ripe tetrasporangia in June to August.

Localities. Sk: YM<sup>1</sup>, Bragerne, 1–2 m; Lønstrup, washed ashore, partly f. corniculata, (C. H. Ostenfeld); Hirshals, 2 m and washed ashore, partly f. corniculata. – Lf: ZY, Nissum Bredning, a small specimen between loose Algæ. – Kn: Hirsholm, about 2 m; N.E. of Hirsholm, c. 7 m (C. H. Ostenfeld); Deget; GM, Engelskmands Banke, 6 m; TP, Tønneberg Banke, 15,5 m; FF, Trindelen, 15 m; TR, near Trindelen, 23,5 m; UB, east af Nordre Rønner; TL and ZL<sup>1</sup> E. of Nordre Rønner.

# Fam. 10. Gloiosiphoniaceæ. Gloiosiphonia Carmichael.

#### 1. Gloiosiphonia capillaris Huds. (Carm.)

Carmichael in Berkeley, Gleanings of British Algæ, 1833, p. 45, Tab. 17 fig. 3; Harvey, Phyc. Brit. plate 57, 1846; J. Agardh, Spec., II, p. 161, 1851; Flora Danica, tab. 2574, 1852; Ekman, Bidrag till käuned.

af Skand. hafsalger. Stockh. 1857, p. 8; Nägeli, Morph. u. Syst. d. Ceram., Sitzber. Münch. Akad. 1861, II, p. 387; J. Areschoug, Observ. phycol. III, Upsal. 1875, p. 10, Tab. I, fig. 4; Bornet et Thuret, Notes algologiques, I, 1876, p. 41, pl. 13; Schmitz, Untersuch. Befr. Florid., Berlin 1883, p. 224, 230, etc., Taf. V fig. 8 – 15; Oltmanns, Z. Entwickl. d. Florid., Botan. Zeit. 1898, p. 109, Taf. V; Oltmanns, Morph. u. Biol. d. Algen I, 1904, p. 572, 698; Kolderup Rosenvinge, Hyaline unicell. hairs, Biol. Arb. til. E. Warming, 1911, p. 205, fig. 1–2.

Fucus capillaris Hudson, Fl. Angl. 1762, p. 591.

Gigartina lubrica Lyngbye, Hydroph., p. 45, Tab. 12 A (teste specim.).

The structure of the frond has been described by NÆGELI (1861), BORNET and THURET (1876) and OLTMANNS (1904); reference may be made to the quoted works. The outer cells of the frond contain narrow branched chromatophores; the number

of the latter could not be determined. The Danish specimens, collected in June to August, were always provided with numerous hyaline hairs, at least on the young parts of the frond, but sometimes also on the older parts (comp. KOLDERUP ROSENVINGE l. c.). Strange to say, they have not been mentioned and figured by BORNET (l. c.) who examined plants collected at St. Malo in June. On the other hand, KUCKUCK has found hairs terminal on the erect filaments given off from the germ-disc (fig. 356 in OLT-MANNS' Morph., p. 572).

As shown by KUCKUCK in the figure quoted, several fronds are given off from a monostromatic basal disc bearing on its upper face numerous short simple or slightly branched cell-filaments. The fronds arise by transforma-



Gloiosiphonia capillaris. Sporelings. A and B two days old, C three days, D 6 days, E 10 days and F 29 days old. 350:1.

tion of some of these filaments; one of the fronds shown in the figure mentioned arises from a branch of a cell-filament. The fronds are divided by transversal walls in low segments, early producing verticillate branches, and afterwards dividing by vertical walls. — The earlier stages of development have been studied in July 1914 at Hirshals, where the carpospores were brought to germinate (fig. 200). The globular spores after having been fixed to the substratum, e. g. a slide or a cover-glass, surround themselves with a membrane, and frequently show the first signs of germination within 24 hours, a germinating tube being produced at one side and separated from it by a wall. The circular spore-body is frequently divided by a wall, the orientation of which to the germinating tube is not constant. After 2 days the germinating filament was 3—4 times as long as the spore-body, usually two-celled, the ultimate cell being densely filled with protoplasm, while the undermost were almost empty, and the spore-cell as well. Sometimes two germinating tubes are given off from the same spore, either diametrically opposed or diverging under an obtuse angle. After four days the first germinating spores had produced long germinating filaments which commenced to branch, producing usually alternating branches at their distal end. The following day a great number of the sporelings had produced a multicellular monostromatic disc arising by further branching and fusing together of the branches, and being terminal on a shorter or longer filament. After ten days the germ discs were larger, some of the cells were divided by transversal walls, and several hairs were given off from the upper surface. Some sporelings continued growing as long unbranched filaments, but producing no disc; they were growing obliquely upwards against the light. It is probably the want of contact with any solid substratum which has caused the absence of a disc. The cultures were continued during up to a month. The sporelings showed at the end of that time no essential differences; they were only somewhat larger, having increased by marginal growth and cell-



Gloiosiphonia capillaris. Part of transversal section of frond with antheridia. 670:1.

divisions, and most of the cells were divided by a horizontal wall, which may signify that the upper cell formed may be the mother-cell of a vertical filament as described by KUCKUCK, but these filaments were not yet formed in their definite shape. Numerous hairs were frequently produced by the disc. Fronds emerging from the discs were not observed; they are probably only produced in the following year, the plant wintering probably in the disc-shaped stage. The outline of the discs is nearly orbicular. The number of the cells in the basal germ filament is rather variable; usually it is small, and the filament may be

wanting, the branches continuing to the spore-cell. — A similar formation of the germ disc, not from the spore-cell but from the germ-tube produced by it, is known also for other Florideæ, e. g. *Dudresnaya* (KILLIAN, Entw. ein. Florid. Zeitschr. f. Botanik. VI, 1914, p. 237).

The antheridia are, as shown by BORNET and THURET (l. c. p. 42) found in spots scattered on the plants which bear the carpogonia. They are oblong or obovate, and are produced by transversal divisions of narrow cells covering the surface of the plant. These cells branch, being divided by oblique walls (fig. 201).

Regarding the development and structure of the cystocarps, reference may be made to the important paper by OLTMANNS in 1898 (see also 1904) where it was proved that the double fertilization, presumed by SCHMITZ for this plant, do not take place.

The tetrasporangia were unknown to J. AGARDH, as late as in 1876 (Epicrisis p.115) although they were described by EKMAN in 1856 and by ARESCHOUG in 1875. They are, according to the named authors, cruciately divided, though often very irregularly; the sporangia-bearing specimens are much branched above, bearing dense bushes of branches. Such specimens were found at Christianssund on the west coast of Norway in August, later on the coast of Bohuslän in June by KYLIN. On the Danish shores, sporangia-bearing specimens have never been found. All the specimens examined (nearly 200) were sexual plants.

The species occurs on stones in exposed places in small depths (1-5 meters).

It can support a strong surf and is then living in much polluted water. It attains a length of 15 cm in the Skagerak, 8 cm in the Limfjord. It has only been collected in June to August. Nearly all the specimens bore cystocarpia. It has only been found in the saltest waters.

Localities. Sk: YN, within Bragerne, 5 m; washed ashore on Grønhøj Strand (Miss Ellen Møller); Hirshals, mole and reefs, 1-5 m. - Lf: Sallingsund, near Nykøbing, east side of Odden (Th. Mortensen, !) and off Grønnerup. In the herbarium of the Botan. Museum at Copenhagen a specimen is to be found, labelled Limfjorden Aug. 1869, probably collected by J. P. Jacobsen.

## Some general remarks on the Cryptonemiales.

1. Intercalary cell-divisions. The species belonging to this order appear as a rule to follow with great regularity the rule pointed out by SCHMITZ<sup>1</sup>) for celldivision in Florideæ: that only the terminal cells in the filaments, of which the frond is composed, divide by transverse walls. Some cases occur, however, where transverse divisions of the segment cells have been noted. Thus, according to BREBNER, intercalary transverse divisions take place in Dumontia incrassata in the short-celled filaments, which grow out from the basal disc and form the upright fronds (see above p. 156). Another instance I have noticed in *Hildenbrandia prototypus*. where intercalary divisions may occur in the radiating filaments forming the basal layer, which makes itself apparent in the fact that the cells are shorter at some distance from the margin than at the margin itself (p. 203 fig. 121). It should further be mentioned, that the filaments in several Melobesieæ (Lithothamnion, *Corallina*) terminate in a covering cell, which does not divide, and which forms. together with the covering cells of the adjacent filaments, an outer layer, incapable of development, the penultimate cell in the filament taking over the function of the terminal cell as an initial one. A deviation from the order of succession in cell division as noted by SCHMITZ may also be found in some species of Melobesia and Lithophyllum, where two or more cortical cells, likewise incapable of division, are cut off one below the other at the end of the same mother cell (p. 254 fig. 174 and p. 264 fig. 184 B)<sup>2</sup>).

2. Cell-fusions. Secondary pits, which are commonly found in the Rhodomelaceæ and several other families of the Florideæ<sup>3</sup>) appear to be altogether lacking in most Cryptonemiales. I have only found them in the genus *Lithophyllum*. As

<sup>1</sup>) FR. SCHMITZ, Untersuch. über die Befrucht. d. Florideen. Sitzungsber. d. Ak. d. Wiss. Berlin 1883, p. 216.

<sup>2</sup>) Intercalary divisions appear to occur throughout the whole of the frond, at any rate in the perithallium in the genus *Porolithon*, to judge from the drawings of Mme LEMOINE in BØRGESEN, The Marine Algæ of the Danish West Indies, III Rhodophyceæ. Dansk Botanisk Arkiv. II p. 177 and p. 179.

<sup>3</sup>) Comp. L. KOLDERUP ROSENVINGE, Sur la formation des pores secondaires chez les Polysiphonia. Botan. Tidsskr. 17. Bind. Kjøbenhavn, 1888, p. 10. mentioned on p. 210, this genus is characterised by the fact that the cells in the upright filaments, of which the frond (the perithallium) is composed, are connected by transverse pits, the origin of which must be of a secondary nature. I have not, however, been able to follow their development, and particularly did not succeed in ascertaining the co-operation of the nuclei in their formation. In the remaining members of the family of Corallinaceæ, on the other hand, there is a different method by which the cells in various filaments may enter into direct communication one with another, to wit, by dissolution of the separating wall, whereby an open connection is established between the cells. This feature has already been referred to above (p. 210) where it was also pointed out that more than two cells may fuse together, and that the cell-fusions may involve fusion of the nuclei (cf. figs. 136, 139, 156 and many others), Only in two of the Danish Corallinaceæ have the fusions hitherto not been shown (*Melobesia minutula* and *Choreonema Thuretii*).

Entirely similar cell-fusions were demonstrated in various Squamariaceæ, viz, Cruoriopsis danica (p. 185 fig. 107), Cruoriopsis gracilis (p. 188 fig. 111), Rhododermis elegans (p. 198 fig. 118) and Rhododermis Georgii (p. 199 fig. 119). In Hildenbrandia, on the other hand, they were not found.

That cell-fusions are important as facilitating connection between cells and cell-filaments not directly in communication by plasma-continuity can hardly be doubted. We find them also particularly numerous in the "roof" above the conceptacle in the Corallinaceæ, i. e. between cells whose indirect connection below has been interrupted by the formation of the conceptacle. Comparison with *Hildenbrandia*, which lacks cell fusions, supports this view, as the roof of a conceptacle, which grows in extent through the continued sporangia formation, consists of dead and more or less disorganised cells, save at the margin, undoubtedly owing to the fact that the connections below have been interrupted, and those to the sides are wanting (cf. p. 204 and figs. 125, 126.).

3. Alternation of generations and alternation of nuclear phases. As we know, there has in several Florideæ been shown to exist a regular alternation between a haplophase, consisting of the sexual generation, and a diplophase, consisting of two generations, viz; the cystocarp or gonimoblast, and the tetraspore-bearing plant<sup>1</sup>). A like course of development must be presumed to take place in all Florideæ with normal fertilisation, and having tetrasporangia. SVEDELIUS has called these Florideæ diplobiontic, in contrast to the haplobiontic, which lack tetraspores, and in which the chromosome reduction takes place by division of the zygote nucleus<sup>2</sup>). Here then, we have but two generations, the sexed plant and the cystocarpium, both

<sup>1</sup>) Comp. H. KYLIN, Die Entwick. u. syst. Stell. von Bonnemaisonia asparagoides etc. Zeitschr. f. Botanik, 8. Jahrg., 1916, p. 570. — J. BUDER, Zur Frage des Generationswechsels im Pflanzenreiche. Ber. deut. bot. Ges. Bd. 34. 1916, Heft 8. — O. RENNER, Zur Terminologie des pflanzlichen Generationswechsels. Biolog. Centralblatt. Bd. 36, 1916, p. 337.

<sup>2</sup>) N. Svedelius, Zytolog.-entwickelungsgesch. Stud. über Scinaia furcellata. N. Acta reg. soc. sc. Upsal. Ser. IV. vol. 4 no. 4. Upsala 1915, p. 42.

haploid, and the diploid phase is restricted to the undivided zygote cell. To these Florideæ belongs, among the species mentioned in the present paper, *Halarachnion ligulatum*. *Gloiosiphonia capillaris* must also be haplobiontic on the coasts of Denmark, where, as on those of France, tetrasporangia-bearing plants have never been found, though they have been met with on the coasts of Norway and Sweden (see p. 278).

On the other hand, there are species which only propagate by tetraspores, not sexually. This applies first of all to the *Hildenbrandia* species, which are extremely common with tetraspores, but have never been found with sexual organs. In *Cruoriopsis gracilis* also, and *Rhododermis Georgii*, sexual organs are quite unknown. *Rhododermis elegans* again, has always been found with tetrasporangia only, save for the case of some specimens from North-east Greenland, which bore antheridia. There are moreover some Corallinaceæ which have hitherto been found in Danish waters only with tetrasporangia (*Lithothamnion læve, glaciale, Sonderi, norvegicum,* and *lævigatum*). In all these, at any rate those first named, tetraspore formation must be supposed to take place without reduction of the chromosomes.

It should further be noted that in some species, albeit possessing both kinds of spores, the two kinds do not occur with like frequency. This is probably the case with several of the *Lithothamnion* species just referred to, the sexual plants being presumably not altogether lacking, but merely rarer than those bearing tetraspores, and have therefore not hitherto been found. On the other hand, sexed plants of *Polyides rotundus* seem to be far more common than the tetraspore plants in the Danish waters. All this might seem to suggest that these species have no regular alternation of generations, such as takes place in the typical diplobiontic Florideæ, in which sexual plants and those bearing tetraspores are nearly alike in point of frequency.

Parthenogenesis has been shown with certainty in *Platoma Bairdii* by KUCKUCK. In the Little Belt, it appeared in the same manner as at Helgoland, the antheridia lacking, whereas cystocarpia and tetrasporangia were found. Here also the tetrasporangia must be formed without reduction of the chromosomes. Possibly parthenogenesis may also occur in other Cryptonemiales. Some observations would seem to suggest that this may be the case in *Furcellaria fastigiata*. The fact that I did not find the spermatia attached to the trichogynes I do not consider as of great importance; more significant, however, is the finding of an unfertilised carpogonium with a short trichogyne, but which had nevertheless formed an outgrowth which could only be regarded as a sporogenous filament (cf. p. 169, fig. 85 D). — In Petrocelis Hennedyi I found, in some instances, sporogenous filaments growing out from carpogonia which showed no interruption of the plasmatic connection with the trichogyne (fig. 98 E, 99 E) and here also, no spermatia were found attached to the trichogynes.

Finally, some cases have been noted where tetraspores and sexual organs appeared in one and the same individual. This has occasionally been found in

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Petrocelis Hennedyi and Cruoria pellita. Here also it must be presumed that the tetrasporangia are formed without reduction of chromosomes.

There are thus a considerable number of Cryptonemiales which differ with regard to the course of development from the typical diplobiontic forms.

SVEDELIUS<sup>1</sup>), referring to the simultaneous occurrence of monospores and tetraspores in one and the same individual of Chantransia efflorescens, considers it not altogether impossible that future investigation of the cruciate tetrasporangia may show them to have been produced without reduction of chromosomes. Up to the present, however, no Floridea with such sporangia has been subjected to closer cytological investigation. The Swedish writer points out in this connection, that such sporangia are first divided by a transverse wall, and thereafter by two perpendicular partitions, which he considers would hardly fit in with a reduction division. It should nevertheless be borne in mind that we find, both in Archegoniates and in flowering plants, cruciate sporangia as well as zonate sporangia, - though the latter, it is true, are more rare - and it seems not to be apparent that the formation of a cell-wall on the first division would preclude the reduction of chromosomes. As regards the zonate division, it has in several of the Corallinaceæ been demonstrated with certainty that the three cell-divisions take place almost simultaneously, and that the nuclear divisions are completed before the celldivision sets in (see p. 273). It is hardly likely that there should be any difference in principle between the cruciate and the zonate division; among other reasons, because we find both occurring in the species of the genus Hildenbrandia, - which are doubtless very closely related — where the sporangia must also be presumed to divide without reduction of chromosomes (cf. also Lithothamnion Sonderi, fig. 137). If Svedelius' supposition were correct, it would involve either that the reduction division must take place by the division of the zygote nucleus, in spite of the presence of tetrasporangia, or that it never occurred among Cryptonemiales, since the tetrasporangia, as far as we know, here never divide tetrahedrically, but always by parallel or cruciate walls, often markedly inclined. The latter alternative would further imply that the cystocarpia were throughout developed by parthenogenesis, which is not in accordance with the actual facts, as, though fertilization has not, it is true, been cytologically demonstrated in any of these algæ, which are furnished with tetraspores<sup>2</sup>), yet spermatia have at any rate been found attached to the trichogynes in Dumontia incrassata (see above p. 158), Polyides rotundus (THURET, Et. phyc. Pl. 38 figs. 14–18) and in certain Corallinaceæ (Choreonema Thuretii, SOLMS, Corall. Taf. III, fig. 4, Corallina mediterranea, SOLMS, l. c. Taf. III, fig. 19).

On the other hand, it must be presumed that reduction division may also be lacking in tetrahedrically divided sporangia, as cases are also known where such

<sup>1</sup>) N. Svedelius, l. c. p. 50.

<sup>2</sup>) The fertilization has been cytologically demonstrated in *Gloiosiphonia capillaris* by Oltmanns; but this Alga has usually no tetrasporangia.

sporangia occur in the same plant as sexual organs, (e. g. Callithamnion corymbosum, cf. THURET in LE JOLIS' Liste d. Alg. mar. de Cherbourg, p. 112).

As will be seen from the above, there are many features in the Cryptonemiales which call for further cytological investigation, especially with regard to the presence of a fertilisation process and the manner in which nuclear division takes place in the tetrasporangia. The latter point will doubtless be the easier to decide, as the tetrasporangia are in many species easily found, and contain large nuclei.

# EXPLANATION OF PLATES.

# Plate III.

All the figures are microphotographs after microtome-sections taken by Mr. A. HESSELBO.

- 1. Lithothamnion læve Strömf. Tetraspore (dispore), showing the nucleus with nucleolus (fallen out) and the structure of the protoplasm. (Specimen from Aalsgaarde). About 225:1.
- 2. Lithothamnion Lenormandi (Aresch.) Foslie. Vertical section of antheridial conceptacle. (Specimen from TF<sup>1</sup>). About 200:1.
- 3. Lithothamnion Lenormandi (Aresch.) Foslie. Vertical section of conceptacle of cystocarp. (Specimen from XQ). About 200:1.
- 4. Lithothamnion glaciale Kjellm. f. Granii Fosl. Section of crustaceous frond with conceptacles of sporangia. (Specimen from Læsø Rende). About 180:1.
- 5. *Lithothamnion polymorphum* (L.) Aresch. Vertical section of female conceptacle showing procarps. (Specimen from Store Middelgrund, May).
- 6. Lithothamnion polymorphum (L.) Aresch. Vertical section of emptied conceptacles of sporangia with covering tissue. (Specimen from reef near Korsør).

### Plate IV.

#### All figures from photopraphs in natural size.

- 1-4. Lithothamnion glaciale Kjellm. f. Granii Fosl. 1 and 2 attached to stones, 3 free, 4 similar one being on the point of dividing. (Specimens from IH, 3375).
- 5-6. Corallina officinalis L., f. robusta Kjellm. (Specimen from YU, Hanstholm. 7286). In fig. 5 the branchlets are partly verticillate.
  - 7. Corallina officinalis L., slender, slightly branched form with some stoloniform branches growing out in a transversal direction. (Specimen from UC, north of Læsø, 5625).
  - Corallina officinalis L. f. robusta Kjellm. With lateral conceptacles. (Specimen from MZ, 4058).



Phot. by A. Hesselbo.

