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PHYLLOPHORA BRODIÆI AND ACTINOCOCCUS SUBCUTANEUS

BY

L. KOLDERUP ROSENVINGE

WITH ONE PLATE

KØBENHAVN
HOVEDKOMMISSIONÆR: ANDR. FRED. HØST & SØN, KGL. HOF-BOGHANDEL
BIANCO LUNOS BOGTRYKKERI
1929

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I. Historical Account.

The reproduction of *Phyllophora Brodiæi* (Turn.) J. Agardh has been much disputed for more than a century. Everywhere within the area of this Subarctic-North-Atlantic species globular bodies of various sizes, up to 3,5 mm. in diameter, have been found sessile on the upper border of the frond or on particular small shoots. TURNER who first described it in 1809 (Turner 1809, plate 72) as a species different from *Ph. membranifolia* stated that the small spherical tubercles were composed of "jointed parallel, fibres, closely matted together, and mixed with irregularly rounded seeds". LYNGBYE (1819, p. 11) was much in doubt as to whether these tubercles were really the fructification of the alga; he did not succeed in finding the seeds described by TURNER and stated that he had earlier described and pictured these fruits in ms. under the name of *Chætophora membranifolii,* thinking that it was some parasite growing on *Ph. membranifolia* and so giving it the character of *Ph. Brodiæi.* On the authority of TURNER, however, he maintains the latter species. In 1834 LYNGBYE took up again more positively the hypothesis of parasitism of the tubercles, giving in Flora Danica tab. $2135,_2$ a picture of the filaments composing the tubercles with the text here reproduced: *Chætophora subcutanea* Lyngb. Mnscr.: cespite roseo, filis, stellatim radiatis, simplicibus et ramosis moniliformibus. — *Chæto-*

1*

phora membranifolii Lyngb. l. c. p. 11 t. 3 B f. 3. — The alteration of the specific name is certainly due to the fact that Lyngbye now considered *Ph. Brodiæi* a well characterized species, and the specific name alluded to the fact that the radiating filaments are covered by a distinct cuticle. Greville (Alg. Brit. 1830, p. 133) pointed out that the joints ("granules") of the filaments are "made up of three or four smaller ones", from which it may be concluded that he saw the formation of tetrasporangia in the filaments. The hypothesis of the parasitism of these bodies was taken up by Suhr; he sent them, under the name of *Rivularia rosea,* to Kützing, who described and pictured them in 1843 (Phyc. gen. p. 177, Taf. 45. Fig. IV, 1, 2) under the name of *Actinococcus roseus* with the following diagnosis: A. marinus, parasiticus roseus; cellulis hinc inde quadripartitis. In der Ostsee an Coccotylus Brodiaei und anderen Algen: v. Suhr. Kützing seems, however, to have no idea of the identity of this supposed parasite with the "sirothelia exacte sphaerica, laevia petiolata" described in the same work p. 412 as the fructification of *Coccotylus Brodiæi.* Fig. 2 shows the cells divided into four, but the orientation of the cells in the tetrads is very variable and not in accordance with reality. J. Agardh (Sp. g. o. Alg. II, 1, p. 330, 1851) describes the nemathecia, as these bodies were named by C. Agardh (Spec. Alg. Vol. I, 1822, p. 228), and states that the joints of the radiating filaments develop into tetrasporangia (sphærosporæ) which are cruciately divided, but he maintains that the plant has also "kalidia" (cystocarps) which are said to resemble the nemathecia very much. The existence of such nemathecia-like cystocarps has, however, never been confirmed.

The question of the nature of the nemathecial bodies was first taken up for thorough examination by FR. SCHMITZ in a paper on the genus *Actinococcus* (1893). He had worked at the question for several years and had reached the conclusion that *Actinococcus roseus* must be considered as a parasite growing on *Phyllophora Brodiæi*, a view he expressed already in 1899 in the survey he published of the hitherto known genera of Florideæ (Flora 1889), and this view was adopted by REINKE in his Algenflora der westl. Ostsee published in the same year. SCHMITZ found that the medullary cells of *Phyllophora* in the interior of the nemathecial fruit are separated more or less from each other and the interstices filled up with a complex of smaller cells forming branched rows of cells. In the outer cortex, these filaments continue as the radiating filaments in the nemathecial wart where they later form the seriate tetrasporangia. But with these fertile filaments, groups of short cortical filaments originating from the sterile frond are frequently intermixed, in particular in young nemathecial warts. When two such warts of different ages are to be found on the opposite faces of the same segment of the frond, as will frequently happen, the filaments constituting the one wart can be followed into the interior of the fertile section of the frond and from thence to the opposite nemathecial wart. Moreover, several quite young warts may fuse together to form one nemathecial wart. In quite young warts the "fertile" cells do not become connected through pits with the cells of the sterile tissue. Such a connection seems only to be established with certain cells which then become larger and rich in protoplasm. The alleged facts could, in SCHMITZ's opinion, only be explained by the supposition that there are two different organisms, a host plant and a parasite. The origin of the latter was not, however, explained. The name *Actinococcus* is then given to the parasite that comprises not only the nemathecial bodies but also the intramatrical filaments. At the end of Schmitz's paper the parasite is given the name of *Actinococcus subcutaneus* (Lyngb.) Rosenv.[1]

Schmitz's discoveries were tested by the French algologist Gomont who convinced himself of the accuracy of Schmitz's observations by an anatomical investigation of material in the Muséum d'histoire naturelle in Paris. On the other hand, Reinke became doubtful as to the correctness of the independence of "*Actinococcus roseus*", which was no doubt connected with the fact that O. V. Darbishire, then assistant at the Botanical Institute at Kiel, was working at the question. In a preliminary note (1894) and a very valuable monograph of the *Phyllophora* species in the western Baltic (1895) Darbishire described the structure and development of the organs of reproduction and as to the nemathecia arrived at a view opposite to that of Schmitz. He gave a careful description of the antheridia which arise in crypts sunk in the cortical layer of particular small shoots, "spermophores" at the upper end of the flat fronds. He further described the female shoots that, when young, much resemble the spermophores and like these are placed at the upper end of the frond (comp. fig. 47 I), whereas the older carpophores are said to be placed like those of *Ph. membranifolia* at the borders of the flat frond and have much the same appearance as those of this species. He found procarps, not before observed, in the young female shoots, and imagined that these shoots

[1] Lyngbye's specific name of 1834 remained unnoticed till I called attention to it (1893, p. 822).

grow out into flat leaves on the borders of which the cystocarps arise, much as in *Ph. membranifolia*. If this were correct, the origin of the carpophores would be very different from that in *Ph. membranifolia* where the carpophores arise on the border of the older segments of the frond and the procarps arise in their interior some time after their formation.

As I have never seen specimens of *Ph. Brodiæi* with cystocarps in the Danish waters, and such specimens have not been mentioned by other authors, it was of interest to me to see the specimens on which DARBISHIRE has founded his statement of the presence of lateral carpophores and cystocarps in this species. Through the kind assistance of Dr. CURT HOFFMANN I have been able to examine the cystocarp-bearing specimens collected by KUCKUCK at Kiel in 1891, referred to *Ph. Brodiæi* and mentioned by DARBISHIRE (l. c. p. 32); they turned out to be female specimens of *Ph. membranifolia* erroneously referred to *Ph. Brodiæi*; they belong to the narrow form of the former species, common in the inner Danish waters. I have no doubt but that a similar mistake has taken place with the large "typical" plants with well developed lateral carpophores containing a cystocarp mentioned by DARBISHIRE as found at Helgoland. At any rate I cannot see why the plant pictured in fig. 46 (l. c. p. 32) should necessarily be referred to *Ph. Brodiæi* and not to *Ph. membranifolia*. Until better evidence is forthcoming it must be taken for granted that cystocarps have never been ascertained in *Phyllophora Brodiæi*.

The nemathecia, according to DARBISHIRE, arise in the first months of the year in the interior of the small fertile shoots, near their apex, single cells in the inner cortex producing from their surface cells that grow out into cell-filaments forming a particular tissue in the inner part of the leaflet, which causes a swelling of the latter; the peripherical filaments may force their way through the cortex and form a nemathecium. The author confirms the statement of Schmitz that the filaments may grow out onto the opposite face of the leaflet and form a new or several new nemathecial cushions. Further Darbishire made the important observation that the tetraspores from the nemathecia that ripen in winter are able to germinate in cultures independently of any host-plant, forming deep red cell-filaments and cell-discs or cushions that he thinks would under better conditions develop into basal discs of *Phyllophora Brodiæi.* Darbishire concludes from his observations that the nemathecia in *Ph. Brodiæi* are the true and only organs that produce tetrasporangia in this species.

Unfortunately Schmitz was prevented from further investigation of this problem, as he died after a short illness in January 1895.

Darbishire's conception of *Actinococcus* as an organ belonging to *Phyllophora Brodiæi* was accepted in my second paper on the marine Algæ of Greenland (1898, p. 33), while I had followed Schmitz in 1893 (p. 822). I now relied on my own observations too, having never in the Danish or the Greenland waters met with cystocarp-bearing individuals of *Phyllophora Brodiæi.* Schmitz's view would lead to the absurd conclusion that this species does not possess any kind of spores.

In the following years Darbishire pursued his investigations on this subject at Kiel and published a new paper in 1899, On *Actinococcus* and *Phyllophora,* in which, strange to say, he accepted the view of Schmitz. Darbishire had observed that the antheridial cavities of *Phyllophora Brodiæi* often accompanied the presence of *Actinococcus subcutaneus,* and after a close investigation of this coincidence he made out that it was possible to explain it by supposing that *Actinococcus* is a parasite that "only can enter the host when the male (or the female?) organs of the latter are present". He thought that he had observed the entrance of *Actinococcus* by the small ostioles of the antheridial cavities. "The immediate product of germination seems to be a small heap of perhaps 4—8 cells, one of which always comes to be near an ostiole leading to an antheridial cavity. . . . A filament is then formed, which passes into the host-plant through the antheridial ostiole (Plate XV, Fig. 1)". However, the figure quoted gives no evidence of the correctness of the given interpretation. An antheridial cavity seems to be faintly seen under a bunch of filaments, but it is situated at a lower level than the normal antheridial cavities, and it can by no means be taken for granted that the filament has entered the host at this place; it would be equally probable that the small heap of cells on the surface of the *Phyllophora* had been produced by a filament forcing its way outwards through the cortex, perhaps through an antheridial cavity, and that it was on the way to forming a nemathecium. Darbishire maintains that the presumed parasite "is unable to pierce the outer covering of the host, when entering the latter. It can only attack the latter through the antheridial ostioles". He thinks, however, that *Actinococcus* may also be able to enter the host by means of the opening caused by the projecting trichogyne, as he has "seen *Actinococcus*-bearing shoots of *Phyllophora,* in the cortical layers of which could be seen what were apparently remains of undeveloped carpogones"

(l. c. p. 258). This latter remark is of interest, as it refers to an important fact which will be mentioned later, but it has a quite different meaning to that suggested by the author. Darbishire adds that antheridia and procarps do not occur on the same plant, but this is not in accordance with my observations, as will be mentioned later. He supposes that the antheridia appear in the autumn and that the parasite then enters the host-plant through the ostioles. He imagines that "it is not unlikely that what we see germinating on *Phyll. Brodiæi* in the autumn is really a carpospore", (l. c. p. 263) produced by an unknown sexual generation. He finally relates that "In discussing the question a short time ago with Professor Reinke, the latter suggested as a possibility, which ought not to be dismissed prima facie, that *Actinococcus* might really be an asexual generation of *Phyll. Brodiaei*, growing parasitically on the sexual generation" (l. c. p. 264). But the author does not consider it very probable that this represents the true state of affairs, and he maintains the view that the nemathecia of *Phyll. Brodiæi* have not yet been found.

It will be seen that the problem is still very dubious after Darbishire's last paper. It has not been treated later on by researches or experiments, but R. W. Phillips has given a valuable critical survey of it in 1925. In citing Darbishire's reference to cystocarps in *Phyll. Brodiœi* he states that these organs have never yet, as far as he can ascertain, been collected in British waters. He further states, in accordance with Darbishire, that he has "seen what seemed to me to be derelict procarps . . . in the neighbourhood of the *Actinococcus* nemathecia" (1925, p. 252). Reinke's suggestion is mentioned; Phillips points out that the carposporophyte in diplobiontic Florideæ is always parasitic on the gametophyte generation and asks whether it is impossible that in this case the tetrasporophyte is so also[1].

II. The Reproduction of Phyllophora membranifolia.

Before describing the development and the fate of the procarps of *Ph. Brodiæi* I shall briefly mention the reproduction of the related *Ph. membranifolia*. This species is a typical diplobiontic Floridea, having sexual and asexual

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

individuals. The first are of two distinct kinds, male and female. The male individuals produce the antheridia in particular yellowish or nearly colourless, up to 2 mm long, folioles borne on the upper border of the flat fronds. The antheridia, as shown by DARBISHIRE (1895, p. 30), arise in small globular crypts sunk in the outer cortical layer of the spermophores and provided with an orifice in the roof (fig. 1). — The procarps arise in the cortical layer of particular oblong or nearly globular short-stalked carpophores borne on the upper part of the cylindrical and the

[1] H. PRINTZ (1926, p. 60) has mentioned some specimens of *Phyllophora Brodiæi* collected in August at Trondhjem with young nemathecia not identical with the nemathecia of *Actinococcus*. Upon enquiry Prof. PRINTZ has kindly answered me that he is not now able to give any information about this observation which was made many years ago, and that he has not access now to the specimens in question.

lower part of the flat thallus of the female plants. The carpogonial branch is three-celled, borne on a large bearing

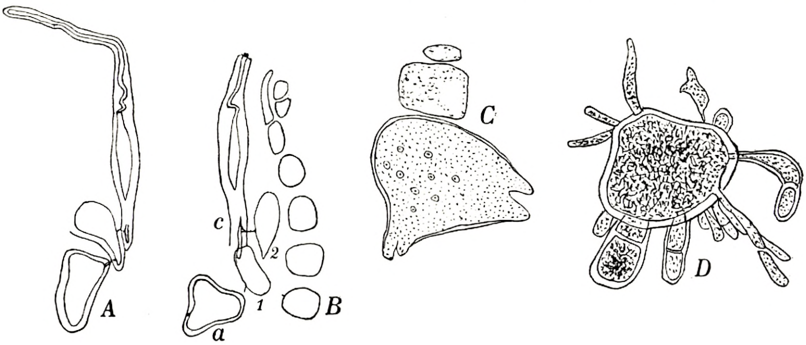

Fig. 2. *Phyllophora membranifolia.* *A*, carpogonial branch. *B*, procarp. *a*, auxiliary cell, *1*, *2*, *c* carpogonial branch. *C*, the auxiliary cell is plurinuclear. *D*, auxiliary cell pushing out numerous gonimoblast filaments. *A* 625 : 1. *B—D* 390 : 1.

cell that becomes an auxiliary cell. The carpogonium has a prolongation downwards which is laterally inserted by a pit on the second cell of the carpogonial branch (fig. 2 *A*, *B*). A spermatium seems to have been attached to the trichogyne in fig. 2 *A*. The fertilization and the transfer of the sporogenous nucleus to the auxiliary cell have not been observed, but the development of the latter is shown in fig. 2, *C*, *D*. While at first it contains one nucleus, it becomes plurinuclear and pushes out prolongations, first from the under side, later from all sides, which develop into

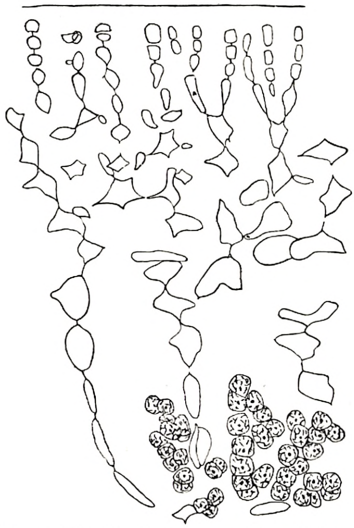

Fig. 3. *Phyllophora membranifolia.* Portion of transverse section of ripe cystocarp. November. 390 : 1.

gonimoblast filaments, becoming septate and branched. These gonimoblast filaments penetrate into the medullary tissue of cells rich in starch and produce numerous small carpospores. In the ripe cystocarp cell filaments originating from the medullary tissue are seen traversing the mass of carpospores (fig. 3). — The nemathecia arise in summer as deep-red wedge-shaped spots on both faces of the lower part of the flat frond. They are built up of parallel filaments of cells which develop into tetrasporangia with the exception of the outermost cells. The division of the sporangia takes place in winter (comp. DARBISHIRE 1895, p. 27); they are first divided by a transversal wall, later by two vertical ones.

III. The Sexual Organs of Phyllophora Brodiæi.

The principal points to be investigated when treating of the much disputed but still unsolved problem of the reproduction of this species were: 1) the first origin of the nemathecium-forming filaments, 2) the possible connection between the latter and the sexual organs of *Phyllophora Brodiæi* and 3) the fate of the germinating tetraspores. The sexual organs will first be mentioned.

DARBISHIRE maintains that *Phyll. Brodiæi* is dioecious (1899, p. 258), but that does not agree with my observations. Antheridia and procarps arise in particular sexual leaflets situated on the upper border of the flat fronds (fig. 5) or in the upper margin of the young segment of broad fronds (fig. 6). In both cases the two sexes usually occur in the same plant and often in the same organ, leaflet or margin. When the upper marginal zone of a frond becomes fertile, it increases considerably in a transverse direction and therefore becomes undulated (fig. 6), and it also increases in thickness. The small fertile shoots (fig. 5 *B*) are usually more or less flattened, but sometimes nearly terete or angulate; in the former case they may be canaliculate. Darbishire (1895, fig. 38 and 47) has figured them and mentioned them as spermophores and female shoots respectively, and it may happen that they contain only antheridia or procarps, but usually they contain both sexes though often in very different quantities,

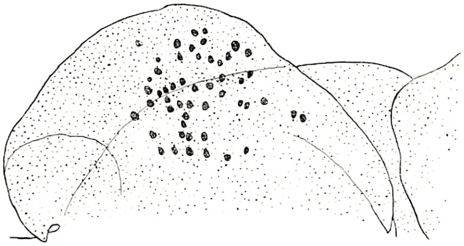

Fig. 4. *Phyllophora Brodiæi.* Fertile lobe of frond with a group of procarps made distinct by staining with hæmatoxyline. 47 : 1.

and sterile leaflets also occur. On cutting a number of leaflets by microtome one may convince oneself of the irregularity of the distribution of the sexual organs, and the same is the case with the fertile border of the broad fronds. In fig. 4 is shown a lobe of an undulated margin of a frond containing numerous procarps while most of the other lobes of the same frond were without procarps.

The antheridia are similar to those of *Phyll. membranifolia.* As shown by Darbishire (1895, p. 29, fig. 38—39, 1899, p. 257) they are developed in small flask-shaped or nearly globular cavities situated just within the surface of the sexual shoot and, when ripe, communicating with the exterior by a small ostiole (comp. fig. 7). Each cavity derives from one superficial cell. The crypts contain a number of converging filaments consisting of 3 or 4 cells

Fig. 5. *Phyllophora Brodiæi.* *A*, from a dredging south of Als in June, 8,5 m. depth, nemathecia in leaflets, terminal or marginal. *B*, from 12 metres' depth off Ballen, Samø in August; with nemathecia and new sexual leaflets. 1,8 : 1.

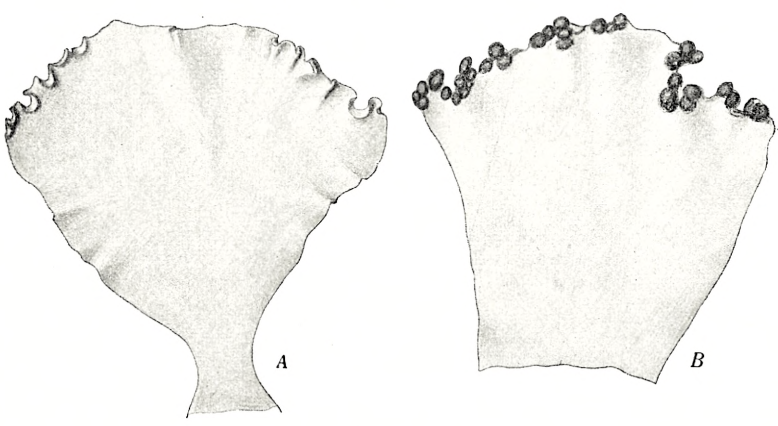

Fig. 6. *Phyllophora Brodiæi.* Lille Belt, 18—19 metres' depth, June. *A*, upper end of frond with undulated fertile margin. *B*, similar with young nemathecia. c. 5 : 1.

which produce the spermatia in descending sequence. DARBISHIRE calls each filament an antheridium (1895, p. 29). These cavities may form a continuous layer or they appear singly (fig. 7) and then project more or less over the surface. The antheridia were met with in the months of March and May to November. They are not restricted to the autumn, as supposed by DARBISHIRE.

For the examination of the procarps the material was in several cases treated with FLEMMING's weaker solution,

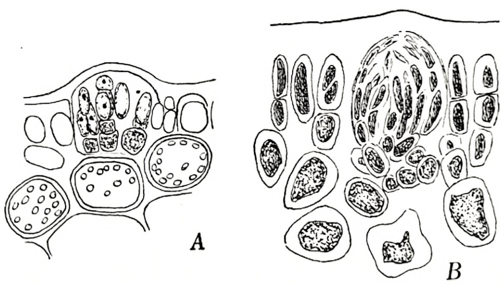

Fig. 7. *Phyllophora Brodiæi.* Two antheridial crypts. *A*, not fully developed. *B*, ripe, August. 625 : 1.

imbedded in paraffine and the microtomed sections stained a. m. HEIDENHAIN, but this method has the inconvenience that the sections are very liable to loosen from the slide owing to the great swelling power of the intercellular substance (SCHMITZ's 'collode') in water, so that most of the sections were lost in many cases. To avoid this, the sections were stained with hæmatoxyline (MAYER's hæmalum or HANSEN's hæmatoxyline), or the sexual shoots were cut with the freezing microtome and stained with the same reagents. Other fixing media used were: formaline-sublimate, Nawashin's treatment[1], and further formaline alone or 70—80 per cent alcohol. And finally, Dr. HENNING

[1] See J. CLAUSEN, Chromosome number and the relationship of species in the genus Viola. Annals of Botany, Vol. XLI. Oct. 1927, p. 678.

E. Petersen has kindly left at my disposal a valuable material from Ellekilde Hage in the Øresund, fixed by him with Juel's solution, June 30th 1910.

The procarps are situated in the inner cortex. When fully developed they are composed of a tricellular carpogonial branch and a large bearing cell which becomes an auxiliary cell, but it may happen that two carpogonial bran-

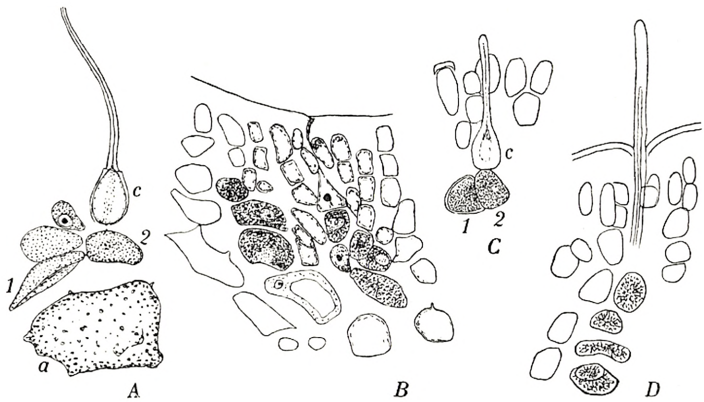

Fig. 8. *Phyllophora Brodiæi*, from Lille Belt, east of Hesteskoen, June 1922, frond with crenulated border. *A*, procarp; a two-celled branch issues from the first cell of the carpogonial branch; *a*, the auxiliary cell, *1*, *2*, *c*, the cells of the carpogonial branch. *B*, two procarps, that to the left without trichogyne. *C*, carpogonial branch isolated by pressure. *D*, protruding trichogyne, the base of which cannot be distinguished. 560 : 1.

ches are borne on the same bearing cell (fig. 10 *D*). Darbishire figures a young procarp with a short trichogyne projecting a little over the surface (1895, p. 33); he considers the bearing cell as the lowermost cell of the carpogonial branch which is therefore said to be four-celled. (Comp. above p. 6).

The procarps were examined in several specimens from various localities and at different seasons. They showed considerable differences so the particular specimens will be treated separately. It must first be mentioned that the great majority of the procarps observed were incompletely developed. These organs are easily recognizable by their staining power with hæmatoxyline (HEIDENHAIN, HANSEN's and MAYER's hæmalum) and their abundant protoplasmic contents, and the bearing cell, too, by its great size. The latter is always present, but the carpogonial branches are often more or less defective. Even when they are normally tricellular, the outmost cell is most frequently not developed as a normal carpogonium but roundish like the other cells of the branch (fig. 8 *B* to the left, 10 *B—D*, 11 *C*). A two-celled branch is shown in fig. 9. The best developed carpogonial branches were met with in May and June, when long, projecting trichogynes were often observed. That pictured in fig. 8 *A* shows the pit-connections between the bearing cell and the carpogonial branch and between the cells of the latter. The carpogonium has a well developed trichogyne but the ventral part is inflated, only poorly provided with protoplasm, and contains no nucleus; it is evidently avorted. The same is the case with that shown in fig. 8 *C* where the trichogyne is short, scarcely projecting over the surface, and the contents still more faint. The carpogonium fig. *B* shows a nucleus, but the protoplasm is feebly developed and the trichogyne only discernible as a canal through the outer wall. In fig. *D* a well developed trichogyne is seen protruding far above the surface, but its lower part was not present in the section. The carpogonium

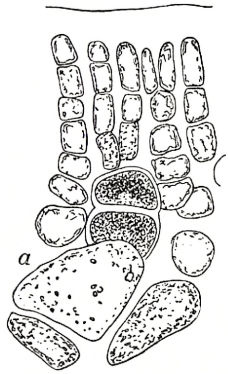

Fig. 9. *Phyllophora Brodiæi*, from the same specimen as fig. 8. Two-celled carpogonial branch. 560 : 1.

shown in fig. 10 *A* had a large nucleus situated near the lower end of the cell and was attenuated above into a

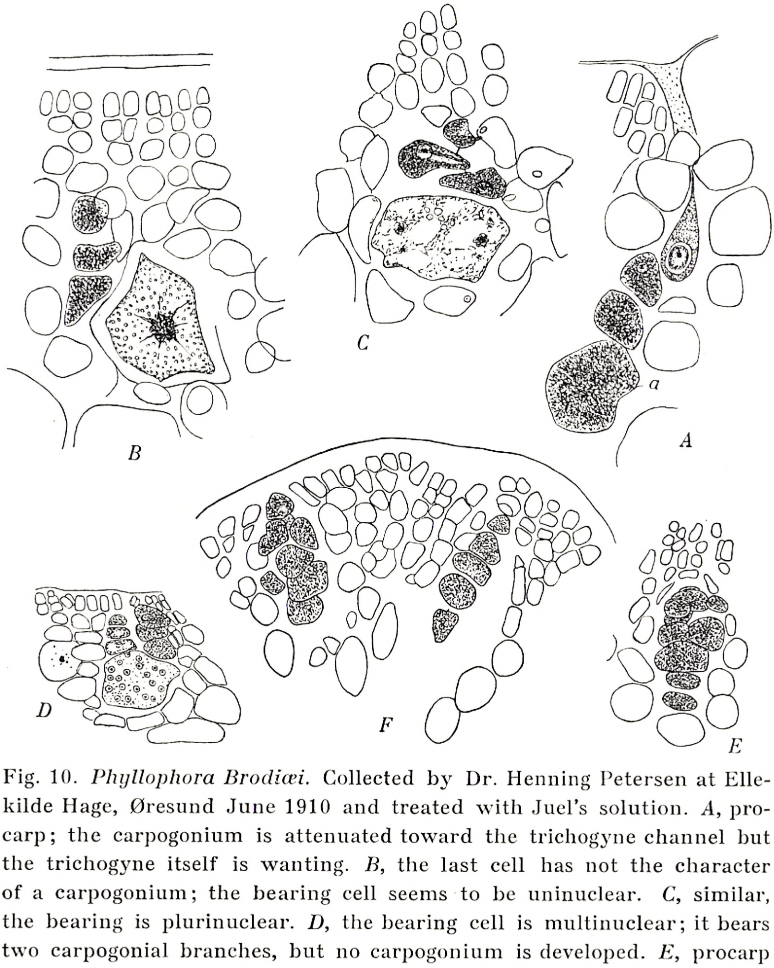

Fig. 10. *Phyllophora Brodiæi.* Collected by Dr. Henning Petersen at Ellekilde Hage, Øresund June 1910 and treated with Juel's solution. *A*, procarp; the carpogonium is attenuated toward the trichogyne channel but the trichogyne itself is wanting. *B*, the last cell has not the character of a carpogonium; the bearing cell seems to be uninuclear. *C*, similar, the bearing is plurinuclear. *D*, the bearing cell is multinuclear; it bears two carpogonial branches, but no carpogonium is developed. *E*, procarp showing more than the ordinary number of cells, without carpogonium. *F*, similar group to the left. *A*, *B*, 870 : 1. *C*—*F*, 480 : 1.

short thin thread, but the trichogyne itself was wanting, though the trichogyne channel was very distinct. In all these procarps, the carpogonium had a rounded or plane base.

In a specimen from Frederikshavn gathered in October I found carpogonial filaments of a different shape, having a carpogonium with oblique base (fig. 11 *A*). Still more aberrant is the carpogonial branch pictured in fig. 12 *A*. A small ovate cell is seen under the carpogonium, connected with it by a pit at its upper, pointed end and connected by a lateral pit with a larger cell which must be

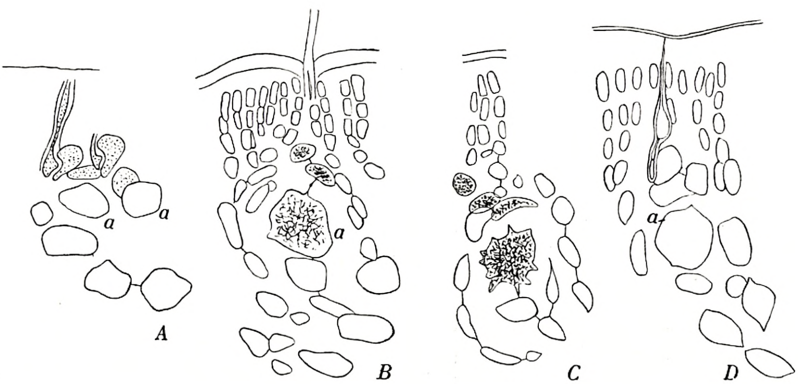

Fig. 11. *Phyllophora Brodiæi.* Specimen collected at Deget near Frederikshavn in October. *A*, two procarps with laterally inserted carpogonia. *B*, procarp; the carpogonium is not visible but a portion of the trichogyne is seen piercing the cuticle. *C*, the last cell of the carpogonium filament has not the character of a carpogonium, the bearing cell is stellate. *D*. The supposed carpogonium has produced a short septate, thin, downward growing filament. *A*, 560 : 1. *B—D*, 350 : 1.

supposed to be the first cell of the carpogonial branch, while the bearing cell is not to be seen. This branch shows some resemblance to the carpogonial branch of *Phyllophora membranifolia* if we compare the small cell with the prolongation downwards from the carpogonium in the latter species, but this prolongation is not separated by a transverse wall from the carpogonium. In other procarps from the same specimen I found a similar oblong smaller cell under the carpogonium. The procarp figured in fig.

12 *B*, met with in the same specimen, is better in accordance with *Phyll. membranifolia*; the lowermost flat cell must be the bearing cell. The fact that two different types of procarps, both different from that first described, are met

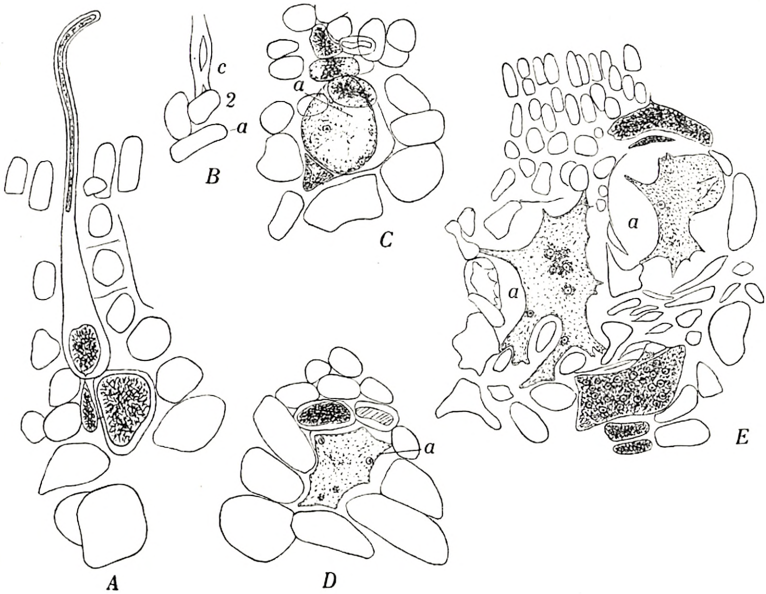

Fig. 12. *Phyllophora Brodiæi.* From a specimen collected in Store Belt in May, fixed with formol-sublimate. *A*. Three cells only are to be seen in the procarp; the bearing cell seemed to be wanting in the section. *B*, procarp the interpretation of which was doubtful; no transverse wall was visible at the narrowing of the carpogonium. *C*. At least two nuclei were present in the bearing cell that is still round. *D*. The bearing cell is angular, plurinuclear. *E*. Three bearing cells, the two showing numerous nuclei, two producing prolongations forcing their way between the surrounding cells. *A*, 1000 : 1. *B*—*E*, 560 : 1.

with, suggests that the procarps in this species are in a stage of degeneration. The first described type is perhaps the most reduced one, as it is most remote from that of *Phyll. membranifolia*.

In no case were spermatia found adhering to the trichogynes and no other signs of a fertilization were observed. The case represented in fig. 11 *D* might suggest a transferring of a nucleus from the carpogonium to the auxiliary cell, but the narrow downward growing septate filament which has not the appearance of containing a fertile nucleus, and the long distance between the supposed carpogonium and the bearing cell do not favour this interpretation. Moreover, I do not feel convinced that the carpogonium-like body is really a carpogonium; it might perhaps be some endophytic Rhodophycea.

IV. The Origin of the Nemathecia-producing Filaments.

It happens that procarps consist of more than four cells. As shown in fig. 8 *A*, carpogonial branches may bear a two-celled branch on their lower-most cell, and procarps without distinct carpogonium may sometimes consist of a greater number of irregularly arranged cells (fig. 10 *E*, *F*). I was for some time inclined to believe that such groups of cells might be able to give rise to the nemathecia-producing filaments; but I found no facts to support this supposition. After searching for a long time I finally succeeded in finding the origin of the filaments referred to by following the fate of the bearing cell that should normally become an auxiliary cell. This cell is originally uninucleate as shown in fig. 8 *B* to the left, but the nucleus is not visible in most of the figures, in some cases it is hidden by the granular matter (fig. 10 *B*). Later a greater number of small nuclei appear, much as in the analogous cell in *Phyll. membranifolia* (fig. 2). In the case pictured in fig. 10 *D* the auxiliary cell shows some 20 nuclei and these must all have arisen by division of the original single nucleus, for a transfer of a fertile nucleus from the carpogonium cannot have taken place. The cell bore two carpogonial branches but neither of them had produced a normal carpogonium; the end-cells were filled with protoplasm in both branches, and one of them showed a distinct nucleus. A similar stage is shown in fig. 10 *C*, where the auxiliary cell also seems to contain several nuclei and no carpogonium is developed. In fig. 12 *D*, the bearing cell has taken an angular shape, but fig. 12 *E* shows more advanced stages; three bearing or auxiliary cells are here seen, one, very similar to that in fig. 10 *D*, having an irregular rectangular shape and bearing a two-celled carpogonial branch toward the lower surface of the leaflet, and two others, much larger, pushing out several long protuberances in all directions, partly penetrating between the surrounding cells of the foliole. The cell to the left contains several nuclei partly entering the protuberances. The carpogonial branches of these two procarps seem to be more or less degenerated. The next stage is represented in fig. 13 *B* where the auxiliary cell has become still more enlarged and the protuberances have produced, at their end, cells connected with the large cell by long threads of protoplasma. These cells form branched rows forcing their way between the surrounding cells of the gametophyte. A good deal of the parallel filaments above in the figure, forming a low excrescence on the mother organ probably derive from the auxiliary cell, but in the present case it was not possible to distinguish such cells from those of the gametophyte. The cells of the carpogonial branch could no longer be recognized. A similar or a slightly more advanced stage is shown in the Plate fig. I, where the large cell is seen near the centre of a young nemathecial wart.

This cell is shown more enlarged in figs. II and III, where the connection between the protuberances and the cells produced by them is very distinct. It seems that pit-connections may also be established between the large cell and cells of the gametophyte. As shown by DARBISHIRE, the nemathecia-producing filaments can be made more easily

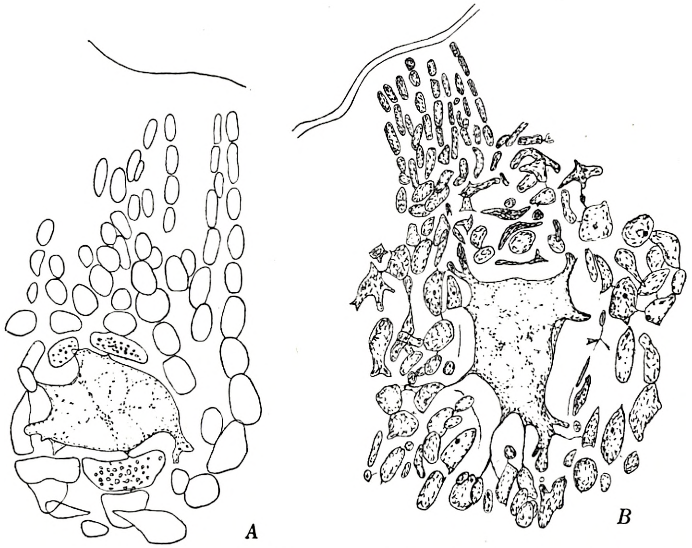

Fig. 13. *Phyllophora Brodiæi.* From Ellekilde Hage, Juel's solution. (Compare fig. 10). Auxiliary cells with protuberances. *A.* The protuberances penetrate between the surrounding cells. 625 : 1. *B*, more advanced stage. The protuberances have produced cells and cell-rows at their ends; some of these have begun to form a low tubercle, a young nemathecium. 390 : 1.

visible by the addition of iodine, when the latter will turn red-brown (not dark blue) owing to their contents of finely granulated floridean starch, while the cells of the mother plant remain unstained. In fig. V reproduced after such a preparation the nemathecia-producing filaments appear very distinctly owing to their dark contents. There seems in this case to be more than one fertile auxiliary cell, or, as they may be named here, central cells, from which the starch-containing filaments radiate toward the periphery, having not yet pierced the cuticle. This has taken place in the case shown in fig. VII where a number of filaments issuing from a strongly developed intramatrical tissue are on the point of producing small cushions on the free surface of the frond. More advanced stages are shown in figs. IV, VI and VIII, where a large cell is seen at the centre of the nemathecial body. In most cases this cell has not longer a stellate shape but is roundish and surrounded by more or less densely jointed small round cells forming a medullary tissue while the outer part of the nemathecial body is built up by radiating filaments. The central cell in fig. VIII contains at least one small cell encompassed by the pseudopodes of the large cell which here and there form fusions.

The large cells just mentioned were observed by Schmitz (1893, p. 378) who, however, interpreted them as sterile cells of the host-plant attacked by fertile filaments, belonging, according to Schmitz, to the parasitic *Actinococcus subcutaneus*, which surround them and become connected with them by pits, where-upon the named cells increase to larger cells with abundant plasmatic contents, and he refers to fig. 2 on plate VII in his paper where a cell of stellate appearance is situated at the centre of the supposed parasitic cushion. A similar large stellate cell is figured by Schmitz under the young nemathecia of *Gymnogongrus Wulfeni*, they are interpreted by this author as a parasite named *Actinococcus aggregatus* (l. c. figs. 4—7). Here too we would remind the reader that Darbishire and Phillips observed in the neighbourhood of the nemathecia

(*Actinococcus*) what they supposed to be undeveloped procarps.

As shown by SCHMITZ and DARBISHIRE, the nemathecia-producing filaments force their way through the surface of the plant, in several places forming small cushions fusing together to one nemathecial body which at last becomes globular. In some cases one cushion only arises, on the upper face of the fertile frond, corresponding to the face where the procarp was situated; the intercellular filaments of the tetrasporophyte do not reach the opposite face of the frond (fig. IV). But usually a new cushion arises later, the filaments of the tetrasporophyte forcing their way to the opposite face of the frond where they pierce the surface at several points (fig. VII), forming a number of small cushions fusing into one. The lower cushion in fig. VIII has evidently originated from the same central cell as the upper one, but later than this, and its origin from a number of distinct points is still easily to be distinguished at the lower boundary of the cushion though the outline of the cushion does not show any traces of the early fusion. The original surface of the frond is very distinct as a dark line interrupted by bright spots where the filaments have pierced it. Two such opposite cushions may finally fuse into one globular nemathecium encompassing the foliole. In fig. VI is given a transverse section of a young globular nemathecium showing a large central cell in the middle and radiating filaments directed to all sides, but exhibiting nothing of the gametophyte except the central cell and some of the surrounding cells.

V. The Nemathecia.

As mentioned above, p. 13, the procarps arise either in particular small sexual leaflets springing from the upper border of the flat fronds or in the upper marginal zone of young flat fronds, and accordingly the nemathecia are either placed on the folioles (fig. 5) or are sessile in great number in the undulated upper margin of flat frond segments (fig. 6). In the first case they are either stipitate, the short stipe representing the lower, sterile portion of the leaflet, while the nemathecium occupies its upper end (fig. 5 *A* above, *B*), or the nemathecium is inserted at the base or at the margin of a leaf which was small at the moment when the procarps arose but which may sometimes attain a considerable size (fig. 5 *A*), in particular when the leaf is inserted at some distance under the upper margin (fig. 5, comp. Flora Danica tab. 1476, Kützing, Tab. phyc. XIX Taf. 74). Some of the nemathecia shown in fig. 5 *B* were probably inserted on the base of the leaves, issuing close to them.

The nemathecia arise, usually in the spring as it seems, and seem early to attain a considerable size. The maximal size is 2 to 3,5 mm. The full development is reached at the close of November when the sporangia begin to ripen, and ripe nemathecia were met with in December to February, but nemathecia with the maximal diameter are generally met with already in June and July, and in March to May they were found 1—1,5 mm. in diameter. As nemathecia of considerable size are to be found in early spring, and as the nemathecia occurring in winter are of different sizes it is probable that some nemathecia which are small in December may be kept without producing tetrasporangia and continue their life in the following season, whereas most nemathecia perish after the production of tetraspores.

When the nemathecial bodies have attained a certain degree of development they show a differentiation in an inner medullary tissue composed of roundish cells and an outer portion built up of radiating filaments consisting of

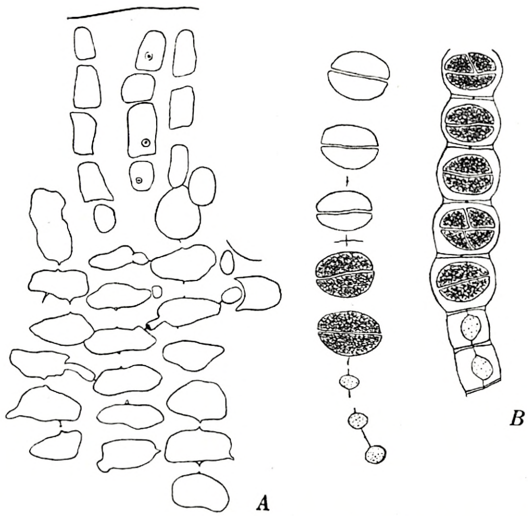

Fig. 14. *Phyllophora Brodiæi.* *A*, specimen from Middelfart, April; radial section of young nemathecium, showing the outer sterile cells and the fertile ones, the latter connected by primary pits and partly by secondary pits with cells of the contiguous filaments. *B*, fertile filaments from specimen gathered in Store Belt, November 24th, with sporangia in division. 625 : 1.

rather low cells connected by pits in the transversal walls (fig. 14). The 3 or 4 outermost cells in the cell-rows are longer and narrower and remain sterile, while the other cells develop into tetrasporangia (comp. Darbishire 1895, p. 24). As the sterile outermost cells are early differentiated and seem not to remain meristematic, and as the number of the fertile cells increases considerably during the development of the nemathecium, an intercalary division of the inner cells seems to take place; but this question deserves further investigation. Moreover, it is remarkable that the fertile cells in the cell-rows are sometimes connected with cells in the contiguous cell-rows by secondary pits, formed in the usual way by the cutting off of a small cell by a longitudinal wall of one of the cells and fusing of it with a cell in the contiguous row (fig. 14 *A*). It should be of interest to study the fate of the migrating nuclei in this process.

The sporangia are first divided by a transverse wall and some time thereafter by two vertical or slightly inclined walls. They begin to ripen at the end of November, and nemathecia with ripe sporangia were met with in December to February.

VI. The Germination of the Tetraspores.

As mentioned above, Darbishire obtained germination of the tetraspores of *Ph. Brodiæi* and stated that they produce filaments and small more or less irregular cushions which he thought, in 1895, would develop to basal discs of *Phyllophora Brodiæi* under better conditions.

For studying the germination of the tetraspores fresh material was dredged in the Great Belt at the close of November 1925. The nemathecia-bearing plants were brought home to Copenhagen, cleaned and put in glass-vessels filled with filtered sea-water from the Great Belt, covered with glass-plates and placed in an unwarmed room facing north (Nov. 26th 1925). In some cases a little potassic nitrate was added to the water. The plants were placed so that the spores dropped on slides deposited on the bottom of the vessels, in some cases on shells of *Mytilus modiola*. After one to two weeks numerous spores were set free, and the plants were then removed. The water in the vessels was now and then renewed and the slides cleaned with caution, diatoms, Cyanophyceæ and other Algæ being removed so far as possible.

The spores newly set free are globular naked cells (fig. 16 *A*) 7—9 μ in diameter, mostly 7—8 μ, containing a large

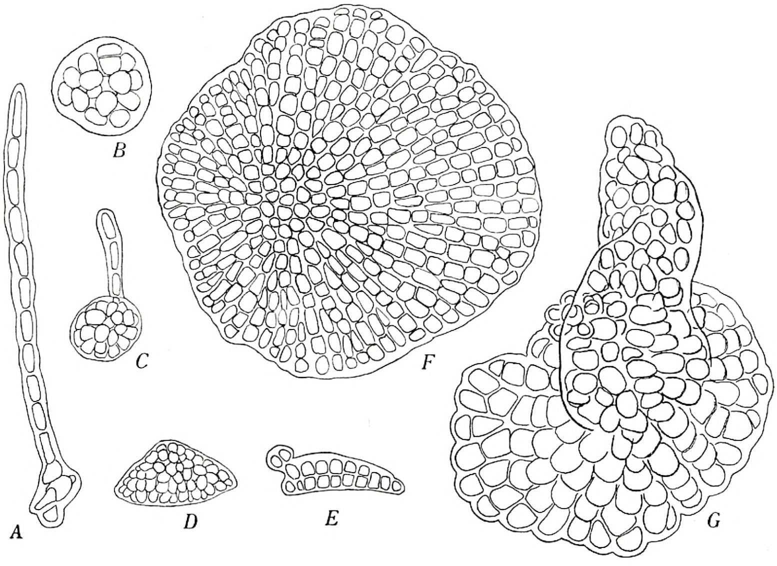

Fig. 15. Germlings from tetraspores of *Phyllophora Brodiæi* sown in the beginning of December 1925. *A—B*, $3^1/_2$ months old, $^{22}/_3$ 1926. *C—F*, $6^1/_2$ months old, $^{29}/_6$ 1926. *G*, 7 months old, $^8/_7$ 1926. *E*, optical vertical section. *A*, *C—F*, 350 : 1. *B*, 410 : 1. *G*, 560 : 1.

chromatophore, a hyaline, feebly refractive body, probably the nucleus, and a great number of small refractive grains. A month later (January 11th) numerous spores had surrounded themselves with a membrane and were divided by a vertical wall into two cells, more rarely into three. In most cases the bodies had not changed shape but were a little enlarged in circumference; only a few of them were about to produce a thinner prolongation before or after the formation of a new partition wall. In March the plants had developed into small multicellular, often irregular cushions, partly with long filamentous outgrowths (fig. 15 *A*, *C*); sometimes the filamentous portion was most developed (fig. 15 *A*). At the close of June the best developed germ-

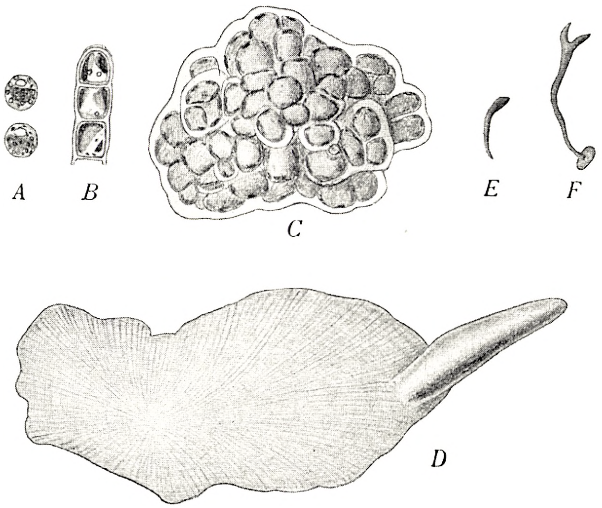

Fig. 16. *Phyllophora Brodiæi.* Germlings from tetraspores sown in the beginning of December 1925. *A*, spores newly liberated. *B*, portion of filament from germling. *C*, eight months old germling, 14/8 1926. *D*, 14 months old germling with upright shoot springing near the border 10/2 1927. *E* and *F*, 20 months old germlings, 18/8 1927. *A*—*C*, 625 : 1. *D*, 70 : 1. *E*—*F*, 6 : 1.

lings were regular orbicular discs without filamentous outgrowths, built up of regularly radiating, closely united filaments, but polystromatic and thicker in the middlemost part (fig. 15 *F*). The discs were rich in starch. In other cases they were smaller and thicker, often conical (fig. 15 *D*). At that time some of the cushions produced an upright shoot from the upper face, usually from the centre (fig. 15 *G*). The cultures were kept going during the following year, but owing to the bad conditions in the old cultures the germlings now grew very slowly if at all. The best developed germlings were obtained from the bottom and the side walls of a glass-vessel in which a nemathecia-bearing plant had been laid down. Fig. 16 *D* shows a well developed, about 14 months old, oblong basal disc much resembling that found in the Baltic Sea by DARBISHIRE and figured by him in 1895 fig. 24. It bears a young terete upright shoot near the margin. The germlings drawn in fig. 17 are about 18 months old; they have a large roundish basal disc and a simple, terete or somewhat complanated upright shoot springing from the centre. Those pictured in fig. 18 are about 14 months older; they have a flat upright frond terete at the base, flattened and branched upwards, on the sides or at the top, in fig. 18 *B* by dichotomy. The disc shown in fig. 18 *D* bears two erect shoots near the border. A better developed 3 mm. high, dichotomously branched 20 months old frond is shown in fig. 16 *F*. The two and a half year old plants shown in fig. 18 were up to 2 mm. high.

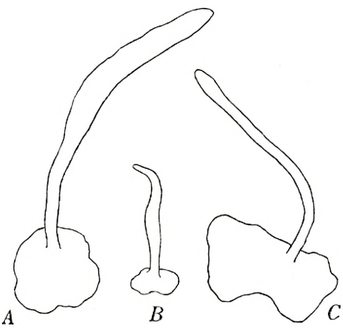

Fig. 17. *Phyllophora Brodiæi.* Germlings from the bottom of a glass vessel in which a fructiferous plant was deposited at the close of November 1925, picked up 18/6 1927 (18 months old). 33 : 1.

The dimensions of the last-named fronds are evidently very small for plants of that age, but that is certainly only due to the bad conditions, in particular in the old cultures which were not sufficiently taken care of. At any rate, they agreed as well with young fronds of *Phyllophora*

Brodiæi found in nature as could be expected under these conditions, and there can be no doubt of their identity. The germination of the spores of the nemathecia then shows conclusively that the latter do not belong to a parasite but that they represent a link in the development of *Phyllophora Brodiæi.*

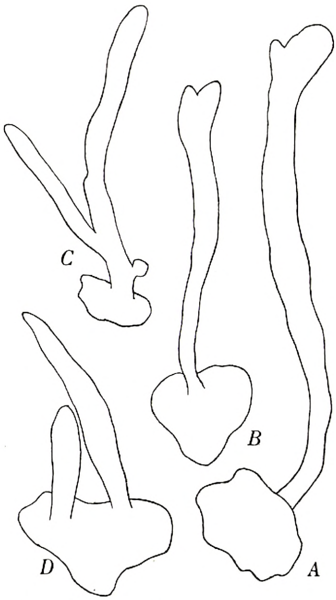

Fig. 18. *Phyllophora Brodiæi.* 32 months old germlings from the walls and the bottom of the vessel mentioned in fig. 17. 33 : 1.

Chemin has recently (1927) observed the germination of the tetraspores of another nemathecium interpreted as a parasite, namely that of *Gymnogongrus norvegicus* described by Schmitz as *Actinococcus peltæformis* (Schmitz 1893, p. 387). The spores sowed in glass-vessels developed basal discs which after two to three months produced upright shoots of the same structure as in *G. norvegicus.* As ascertained by Chemin, this species has distinct sexual and asexual individuals; the author has found no facts supporting the hypothesis of the parasitical nature of the nemathecia, and he therefore considers *Gymn. norvegicus* as a normal diplobiontic Floridea.

Conclusions.

From what has been shown above il must be concluded that all individuals of *Phyllophora Brodiæi* are (actually or virtually) sexual plants and that free-living tetraspore-bearing plants do not exist. The antheridia and the procarps usually occur on the same individual; they arise either in particular sexual folioles or in the upper margin of the flat fronds. The antheridia quite agree with those in *Phyll. membranifolia*. As in this species the procarps consist of a three-celled carpogonial branch and a bearing cell or auxiliary cell, but the carpogonial branch is rather variable, perhaps a consequence of degeneration, and it is probable that fertilization does not take place; at all events it has not been ascertained. The auxiliary cell much resembles that in *Ph. membranifolia*; in both species it has first one nucleus but later becomes plurinuclear. But while the latter is a typical diplobiontic species in which the auxiliary cell pushes out a number of outgrowths developing into the gonimoblast filaments, the auxiliary cell in *Ph. Brodiæi* likewise pushes out a number of protuberances, but these give rise to cell-filaments forcing their way between the cells of the gametophyte in various directions but at first especially outwards where they give rise to a wartlike excrescence which develops into a nemathecium in the inner part of which the enlarged auxiliary cell or central cell is to be seen. The radiating filaments of the nemathecium give rise to seriate tetrasporangia, which ripen in winter. The system of cell-filaments issuing from the auxiliary cell in *Ph. Brodiæi* and their products thus represent the tetrasporophyte which is not here as in other Florideæ an independent free-living organism, but grows out in continuity with and "parasitically" upon the gametophyte generation. Cystocarps are never produced, the carposporophytic phase has been abandoned, and in its place a tetrasporophyte is developed. The vegetative part of the latter is only represented by the intramatrical cell-filaments.

The above mentioned suggestion of Reinke that *Actinococcus subcutaneus* might possibly be an asexual generation of *Phyll. Brodiæi* growing parasitically on the sexual generation is thus fully confirmed.

The reproduction of *Phyllophora Brodiæi* now elucidated is very peculiar; no other instance agreeing with it has hitherto been described. Only the remarkable reproduction in *Liagora tetrasporifera* Børgs. discovered by Dr. F. Børgesen (1927, p. 39) can be compared with it. Most of the species of this genus, belonging to the *Helminthocladiaceæ*, have normal cystocarps, arising probably after a fertilization directly from the carpogonium, and the end-cells of which give rise to a carpospore, while tetrasporangia are not known with certainty. The species referred to has apparent cystocarps arising in the same way as those of the other species, but the end-cells of the cystocarpial filaments undergo a quadripartition and yield each a cruciately divided tetrasporangium. Thus the "cystocarp" does not, properly speaking, deserve this designation; it is not a carposporophyte but a tetrasporophyte and can be compared with the tetrasporophyte generation of *Phyllophora Brodiæi*. There is, however, a significant difference in that the tetrasporophyte of *Liagora tetrasporifera* has the appearance and the structure of a cystocarp with the only difference that the carpospores are replaced by tetrasporangia, while the tetrasporophyte in *Ph. Brodiæi* is differentiated in an intramatrical, vegetative part and a number of extramatrical cushions fusing together into a large globular nemathecium showing no resemblance to a cystocarp but having a structure similar to that of the nemathecia in the diplobiontic species of the same genus.

The tetrasporangia appear in *Liagora tetrasporifera* within a systematic group which is typically haplobiontic, where these organs as a rule do not take part in the normal life-cycle. The extraordinary appearance in question within a genus which has otherwise normal cystocarps suggests that it is due to a mutation, tetrasporangia having appeared here instead of carpospores. In the case of *Phyllophora Brodiæi* it seems more probable that the origin of the parasitic tetrasporophyte has been occasioned by the degeneration of the procarps and the consequent absence of fertilization and of carpospores. The tetrasporophytes — like the gonimoblasts in *Ph. membranifolia* — arise as outgrowths from the bearing or auxiliary cell, but these outgrowths have not the character of gonimoblast filaments; they appear first as vegetative intramatrical filaments, and only later do the nemathecia arise. The whole tetrasporophyte has the character of a much reduced form of the normal tetrasporophyte as it is known in *Ph. membranifolia*; the reduction of the vegetative body is due to the parasitical life, and the globular form of the nemathecium is due to the small size of the latter.

For a full elucidation of the question here treated of, a closer cytological research has yet to be made. It ought in particular to be ascertained whether or not a fertilization takes place, and whether the formation of the tetraspores is initiated by a reduction division.

The other nemathecia occurring within the *Gigartinaceæ* and regarded by Schmitz as belonging to parasites analogous to *Actinococcus* and referred to the genera *Colacolepis* and *Sterrocolax,* will not be treated here. As mentioned above, Chemin has examined the nemathecia occurring on *Gymnogongrus norvegicus,* named by Schmitz *Actinococcus peltæformis*[1], and observed the germination of the tetraspores produced by them, and he found that these nemathecia are the true organs of the *Gymnogongrus,* occurring only on the asexual plants. I have found the same for the nemathecia of *Phyllophora epiphylla* (*Ph. rubens*), according to Schmitz belonging to a parasite *Colacolepis incrustans.* This will be mentioned in another paper where also the nemathecium of *Ahnfeltia plicata,* considered by Schmitz as a parasite, *Sterrocolax decipiens,* will be treated of.

I am much indebted to Dr. Henning Petersen for kindly giving me fixed material of *Phyllophora Brodiæi,* to the same and to Mr. Erik J. Petersen m. sc. and Mr. G. Nygaard m. sc. for their valuable aid in executing the photographs reproduced on the plate.

[1] Phillips erroneously names it *Colacolepis peltaeformis* (l. c. p. 251).

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Explanation of Plate.

Microphotographs of nemathecia of *Phyllophora Brodiæi*. Figs. I—III, VI, VII from a specimen from Ellekilde Hage, Juni 30th 1910, Henn. Petersen. Figs. IV, V, VIII from a specimen from Øresund east of Taarbæk Flak, October 7th, Søren Lund.

Fig. I. Section of young nemathecial body. 110 : 1.

Figs. II and III. The central cell of the former. 375 : 1.

Fig. IV. Vertical section of nemathecium only developed on one side of the frond. 57 : 1.

Fig. V. Section of frond with nemathecia-producing filaments, stained with iodine, radiating toward the periphery. 88 : 1.

Fig. VI. Transverse section of nemathecium. 77 : 1.

Fig. VII. Nemathecia-producing filaments forcing their way through the cortex. The medullary tissue, interwoven with numerous nemathecia-producing filaments is indistinct owing to the fact that this tissue was situated at a higher level. 96 : 1.

Fig. VIII. Vertical section of nemathecium showing the central cell and a smaller nemathecium on the under face of the frond, evidently arisen by fusion of several small cushions. 64 : 1.

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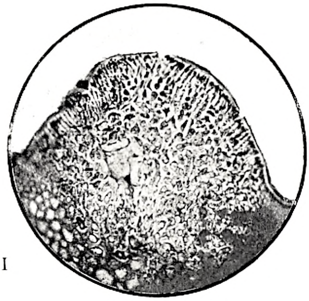

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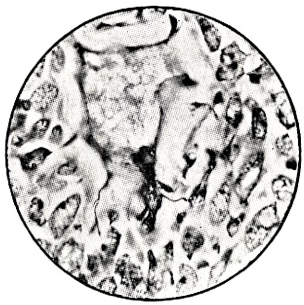

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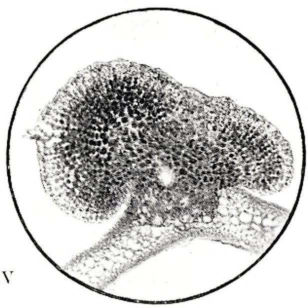

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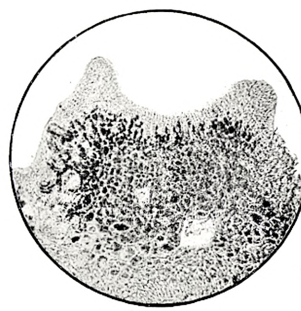

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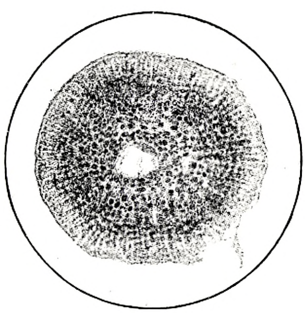

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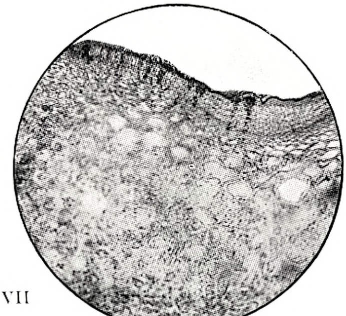

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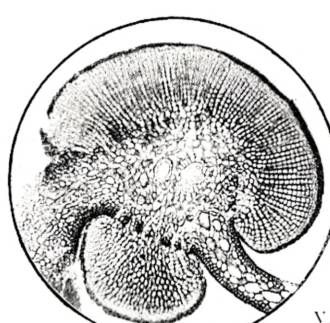

VIII

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8. BIND (under Pressen):

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