Det Kgl. Danske Videnskabernes Selskab.
Biologiske Meddelelser. **X,** 2.

THE REPRODUCTION OF AHNFELTIA PLICATA

BY

L. KOLDERUP ROSENVINGE

KØBENHAVN
HOVEDKOMMISSIONÆR: ANDR. FRED. HØST & SØN, KGL. HOF-BOGHANDEL
BIANCO LUNOS BOGTRYKKERI A/S
1931

Pris: Kr. 1,75.

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1. Introduction.

The relationship and delimitation of the genus *Ahnfeltia* have always been and are still very uncertain. The genus was first given a tolerably natural delimitation by J. G. AGARDH who distinguished it from the genus *Gymnogongrus* near which it was placed (comp. Spec. g. o. II, 1851, p. 310). In his Epicrisis (Sp. g. o. III, 1876, p. 205) this author gives the genus the same position and refers to it 6 species which he divides into three sections: *Ahnfeltia*, *Dictyogenia* and *Dianæma*, distinguished by differences in the anatomical structure of the frond. Nemathecia and cystocarps are mentioned or shortly and incompletely described in some of these species, but two kinds of reproduction are never recorded in the same species, and it is therefore doubtful whether all these species really belong to the same genus, even when taking into consideration the anatomical differences mentioned above. SCHMITZ in his paper on *Actinococcus* (1894, p. 396, see also SCHMITZ and HAUPTFLEISCH in ENGLER u. PRANTL 1896, p. 366) took the genus in a narrower sense, comprising only J. AGARDH's section *Ahnfeltia*, while he maintained that the other two sections must be united with *Gymnogongrus*. According to SCHMITZ, not con-

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

sidering the nemathecia, no organs of reproduction are known in the genus as founded by Schmitz; sex organs and cystocarps are entirely unknown. I can confirm this for the common European species *A. plicata* (Huds.) Fries of which I have examined numerous specimens from the Danish waters gathered in all seasons without detecting any trace of reproductive organs besides the nemathecia. As the nemathecia have no parallel within the Florideæ and as they have been variously interpreted, a closer examination of their structure and development is needed.

2. Earlier Investigations on the nemathecia.

The nemathecia of *Ahnfeltia plicata* seem to have been early observed, but it cannot always be seen from the short descriptions of the earlier authors whether the tubercles mentioned by them refer to the nemathecia or to the frequently occurring warts of vegetative character. The lowermost tubercle depicted in English Botany tab. 1089 (1803) agrees well with the nemathecia and undoubtedly represents such an organ. Lyngbye mentions (1819, p. 42) that the tubercles are in particular met with in spring, which is in good accordance with the behaviour of the true nemathecia; he did not observe any spores. C. Agardh (1822, p. 313) names them nemathecia and states that they are composed of articulate filaments. The following authors (Greville, Harvey, J. Agardh) confirm that and declare that they have not observed any spores, especially no tetraspores. Kützing (Tab. phyc. **19**, tab. 66) pictures a section through a nemathecium and, more enlarged, the radiating filaments, which are said to be composed of "Kettensporen". They are represented as long rows of very small oblong cells of equal size, but these cells are not the spores. These were first described in 1893 by BUFFHAM and SCHMITZ, who found that the nemathecial filaments produce at the end each a sporangium which gives rise to one monospore.

BUFFHAM observed the escaping monospores which were ellipsoid, about 15 μ long, and 7 μ thick, thus much larger than the cells of the nemathecial filaments. He gives good figures of these organs (1893, figs. 43, 44). As cited by BUFFHAM from a letter from BORNET, this prominent French algologist had observed such spores as early as 1857. SCHMITZ's observations on the spores agreed with those of BUFFHAM, but he also studied the structure of the nemathecia of this and the related species *A. setacea*, and arrived at the conclusion that the nemathecia were not organs of the *Ahnfeltia* but that they belonged to a parasite, which he called *Sterrocolax decipiens*, growing on the surface of *Ahnfeltia* and penetrating into the cortex of the latter with numerous "Senker". The author admits, however, that the phenomena here described, which he had observed most distinctly in *A. setacea*, were not easy to observe in *A. plicata*. SCHMITZ's inference as to the parasitical character of the nemathecia was only founded on the presence of the said processes penetrating into the cortex, and not on the study of the development of the nemathecia. His inference is, therefore, not conclusive, for the processes might also be explained as secondary formations developed from the base of the nemathecium produced by the *Ahnfeltia*. If the nemathecia were not organs of *Ahnfeltia*, it must be concluded that no kind of reproductive organs had ever been observed in these Algæ. SCHMITZ indeed draws this conclusion for the whole genus *Ahnfeltia* (1894, p. 397, 1896, p. 366), but this is *a priori* highly improbable, in particular for *Ahnfeltia plicata* which has been so often examined and is of such common occurrence and so easily propagated though it has no vegetative means of propagation. For the elucidation of this question I have examined 1) the development of the nemathecia and 2) the germination of the spores.

3. Development of the nemathecia.

At the coasts of Denmark the nemathecia arise in September. They are not of parasitical origin but appear as

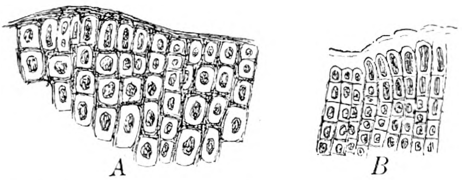

Fig. 2. First origin of nemathecia. September. 670 : 1.

small low cushions arising from a group of superficial cells growing out simultaneously and dividing by cross walls (fig. 2). In September I found the cushions very low, only 1—2 cells high. In the middle of October they reach a considerably larger size (fig. 3). The extension may be up to $^1/_3$ of the circumference of the frond, and this extension is accomplished by the continued production of new nemathecial filaments at the margin. The cells of the nemathecial filaments are longer than those of the cortical layer, usually 2 to 3 times as long as broad and thinner, often only 2 to 3 μ thick; the limit between the cortex and the nemathecium is, however, not always distinct. At the border of the nemathecium the filaments are shorter and bent somewhat outwards. The cells all contain one nucleus; the end-cells are scarcely different from the others except that they are richer in protoplasm.

At this period two kinds of cells different from the others appear in the nemathecial filaments. Some cells terminal on radiating cell-rows, usually directly on cortical cell-rows, become flask-shaped, being attenuated upwards,

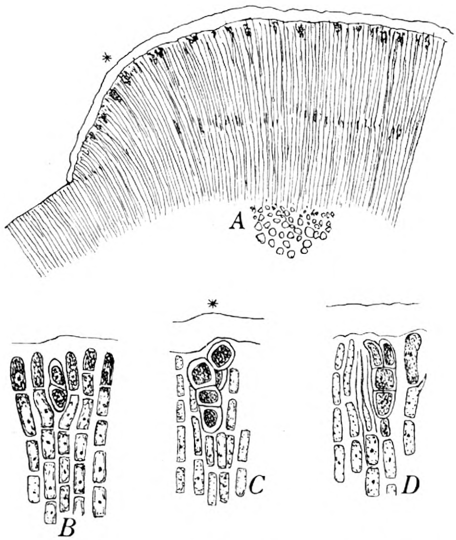

Fig. 3. Nemathecium, October. *A*, vertical section. 244 : 1. *B—D*, upper ends of nemathecial filaments with generative cells. 670 : 1.

thus reminding one of carpogonia and like these staining deeply with hæmatoxylin, but their content is homogeneous and the nucleus is usually not or scarcely visible. They often appear in great number at the bottom of the nemathecium, arresting the growth of the filaments on which they are terminal (figs. 3 and 4); but they are also to be found at higher levels, even near the surface, I have, however, never seen them protruding above the surface. Only in one case, in a wart from a plant having grown in an aquarium from

May to October, I found numerous similar carpogonium-like cells terminal on most of the filaments of the wart,

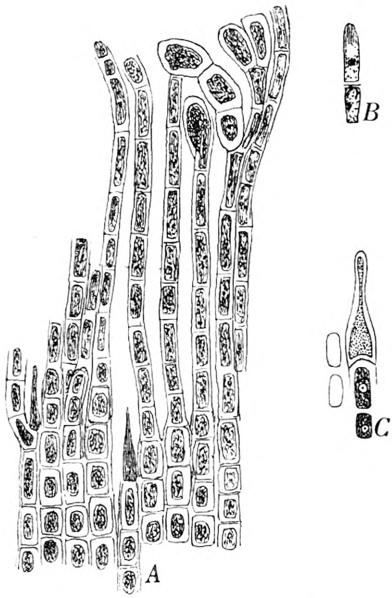

Fig. 4. Nemathecium, October. *A*, vertical section of nemathecial filaments showing flask-shaped cells below and generative cells above. *B*, upper end of primary nemathecial filament. *C*, flask-shaped cell. 1080 : 1.

in several cases protruding above the surface (fig. 5). In some of them a small nucleus was found in the lower or

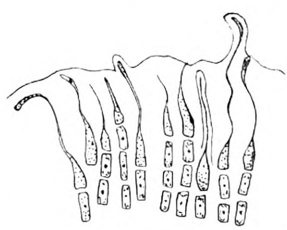

Fig. 5. Vertical section of cushion (anomalous nemathecium?) arisen in a plant kept in an aquarium from May to October. 860 : 1.

in the upper part of the cell. These cells might better be considered as sterile hair-cells though such hairs have not been met with on the fronds. Hyaline hairs have certainly been observed in the young disc-shaped germlings (see below p. 20, fig. 17), but they were long and had the typical cylindrical shape, not being attenuated upwards. It

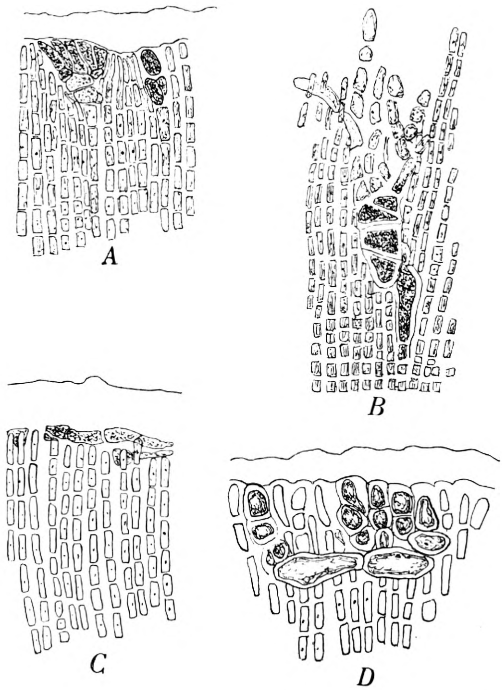

Fig. 6. Vertical sections of nemathecia, October, showing groups of generative cells and horizontal or obliquely upward growing cell-rows springing from them. 625 : 1. The group of generative cells in fig. *B* is situated at the boundary between the nemathecium and the cortex.

is doubtful whether this wart was a nemathecium or only a sterile wart; at all events it was not normal, but degenerated in the middle. The first described included carpogonium-like cells may perhaps also be considered sterile, undeveloped hair-cells. The fact that they are never borne on particular cells comparable to carpogonial filaments but always situated at the end of ordinary nemathecial fila ments or cortical cell-rows, and the absence of a well developed nucleus make it highly improbable that they should be comparable with carpogones.

The other kind of cells differ by their greater thickness and by richer contents. They arise at the upper end of the nemathecial filaments, terminal or lateral, singly or usually in small groups which seem to arise by division

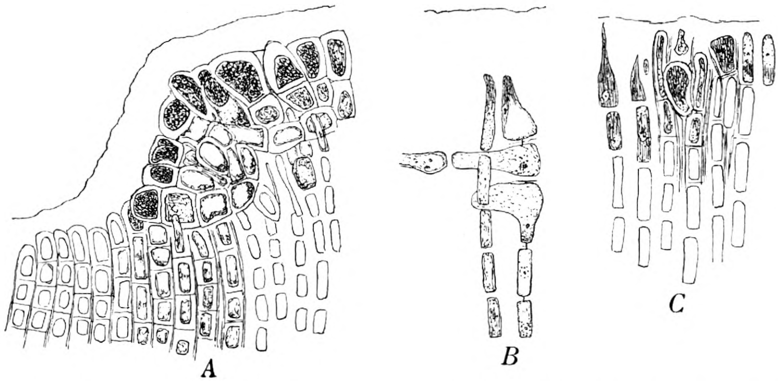

Fig. 7. From a nemathecium, October. *A*, vertical section of the border; the outer portion of the nemathecium is built up entirely of generative cells and their derivates. *B*, generative cells giving rise to horizontal cell-rows. *C*, generative and flask-shaped cells. *A* 960 : 1. *B* and *C* 1080 : 1.

of a single cell. They have the character of generative cells. Some of them, at least, grow out, in particular in a horizontal direction, between the nemathecial filaments, where their course may be rather irregular. The cells of these filaments are much larger than those of the nemathecial filaments and they become poorer in contents and therefore often rather hyaline. Fig. 6 shows a horizontal filament running just within the cuticle, and fig. 7 the border of a nemathecium the outer portion of which is exclusively composed of large cells of the same origin. In fig. 6 *B* is shown a group of generative cells, situated at a low level in the nemathecium, at the limit towards the cortex, from the upper cells of which group new branched cell-rows growing obliquely upwards are produced; these cell-rows are thicker than the nemathecial filaments between which they penetrate.

In specimens collected in the middle of November the nemathecia had grown thicker and had also increased in circumference, the marginal part growing along the surface

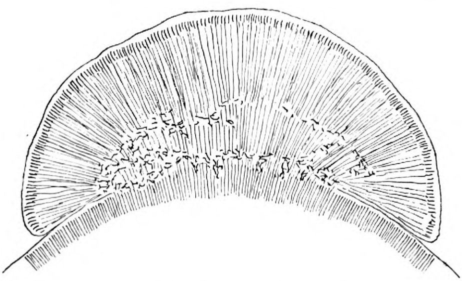

Fig. 8. Vertical section of nemathecium, November. 160 : 1.

of the frond from the insertion of the nemathecium, and the nemathecial filaments being here directed outwards. The outermost (lowermost) filaments are close to the surface of the cortex but not coalescent with it, and the cuticle of the frond remains easily discernible (fig. 8). No connections between the nemathecial and the cortical cells take place here. The large generative cells found in October are found again in the lower portion of the cushion, partly immediately over the limit towards the cortex, partly at a somewhat higher level. They are easily recognisable by their greater size, their irregular shape, their dense cell-contents and their high staining power with hæmatoxylin. A lively development of cell-filaments like that shown in fig. 6 *B* has taken place, a great number of upward growing cell-rows issuing from them. It seems probable to me that all or nearly all the cell-rows situated over the large cells in figs. 9 and 10 have been produced by these cells. These cell-rows resemble the primary nemathecial filaments but are at any rate at first thicker than the latter; they form new nemathecial filaments, continuing their way towards the sur-

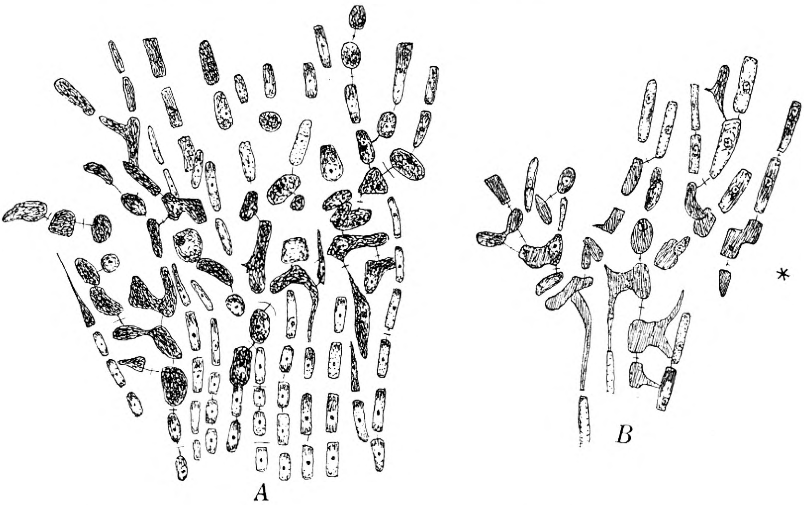

Fig. 9. Vertical section of lowermost part of nemathecium, November. The irregular cells rich in plasmatic contents are situated at the level of the surface of the frond *. 1080 : 1.

face of the nemathecium. The content of the generative cells is homogeneous and stains intensely by hæmatoxylin, but the nucleus is usually not very distinct or scarcely visible. The irregular shape of the cells depends partly on the fact that fusions often take place between cells of different cell-rows. The "Senker" mentioned and figured by Schmitz (l. c. p. 393 fig. 11 and 12) and interpreted by this author as haustoria penetrating from the supposed parasite into the host plant, are undoubtedly groups of the here described generative cells. The obconical shape of these groups of cells, in particular of those situated at the lowermost level of the nemathecia (figs. 6, 8, 9), is the same as that of the "Senker".

The marginal portion of the nemathecium is composed of horizontal cell-rows not connected with the cortex; these cell-rows have probably all taken their origin from the generative cells or their derivates, like those shown in fig.

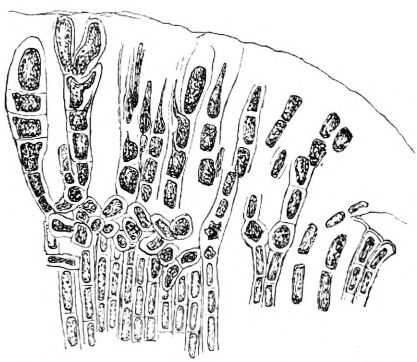

Fig. 10. Vertical section of nemathecium, near the border, December. 670 : 1.

7 *A*, and they must therefore be considered as secondary nemathecial filaments.

The development of the primary nemathecial filaments is, at all events to a great extent, stopped by the formations of the flask-shaped cells and the appearance and further development of the just described generative cells, and they are then replaced by the secondary nemathecial filaments produced by the latter. This arresting seems not only to be caused by the fact that the uppermost cells of the filament have developed into flask-shaped cells or generative cells, for the growth of other filaments also seems to be checked without producing generative cells. On the other hand, primary filaments seem in some cases to continue their way to the surface of the nemathecium without any connection with the generative cells, e. g. fig. 16 *E*. That, however, is a point that deserves further investigation. Fig. 10 drawn from a specimen gathered at the end of December favours the view that the nemathecial filaments situated over the generative cells are only or principally produced from them.

The narrow cells of the secondary nemathecial filaments

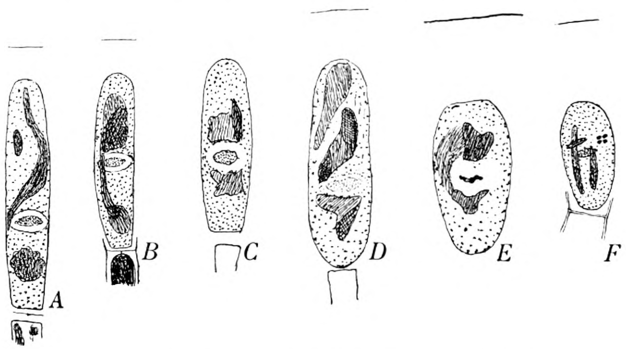

Fig. 11. From a nemathecium from Kerteminde, November (Flemming, Heidenhain). End-cells of (secondary) nemathecial filaments showing nucleus and chromatophores. The nucleus in *A—D* has a feebly stained homogeneous central body surrounded by a well limited halo. In *E* the substance of the nucleus is more condensed but shows no distinct chromosomes. In *F* the limitation of the nucleus is indistinct, a group of 4 chromosomes is situated to the right of the central body. 1800 : 1.

contain a small nucleus and one or more chromatophores. The apical cell has more plasmatic contents and a larger nucleus situated in the middle of the cell; it is at first not or scarcely thicker than the others, especially when the cell is still dividing (fig. 14 *A*, *F*, 15 *B*). Later on, when the apical cell gradually develops into a monosporangium, it takes an oblong, ovate or obovate shape. Ripe or nearly ripe spores may occur already in November, but the production of spores continues till May. The resting nucleus of the end-cell has a large nucleolus or central body, globular or usually somewhat depressed. It is homogeneous in structure and stains intensely or, with a high degree of differentiation, more feebly by hæmatoxylin after HEIDENHAIN. The material was fixed in FLEMMING's weaker solution or after NAWASHIN's method, but equally good results were obtained with material preserved many years ago in strong alcohol by Dr. HENNING E. PETERSEN. In some cases, in specimens preserved in FLEMMING's solution or in alcohol,

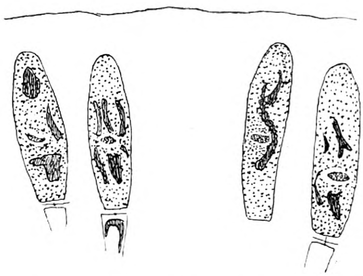

Fig. 12. Same material as fig. 11. Four end-cells from the same section showing nucleus and chromatophores, the latter apparently partly fusing together. 1800 : 1.

the chromatophores could not be observed, but usually they were very distinct in a number of 2 or 4 or rarely more. The shape of the chromatophores is very variable, ribbon-shaped, rod-shaped, linear with attenuated ends, sometimes very long and curved or spirally twisted. Their staining power after HEIDENHAIN's method is considerable, often greater than that of the nucleolus. The most remarkable feature in the young monosporangia is the fact that the chromatophores are not unfrequently found lying in pairs close together along their long axis as shown in several of the figures. When two chromatophores are exactly of the same length and are placed very close together, they would seem to be the product of a longitudinal division (figs. 12, 13, 15), but as such a division of chromatophores has not hitherto, to my knowledge, been ascertained,

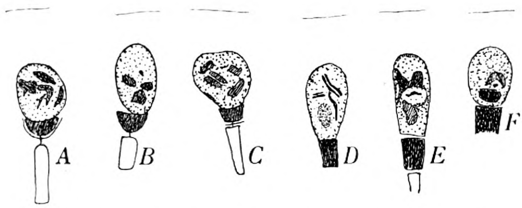

Fig. 13. From a nemathecium from Kerteminde, November (Nawaschin). The end-cells are swollen and show very distinct chromatophores, partly paired. The nucleus is indistinct in the three first figures. The cell beneath the monosporangium is short, deeply stained. 1015 : 1.

further proof must be demanded. On the other hand, the paired chromatophores might be supposed to be on the point of fusing together along the longitudinal axes, and this supposition is more in accordance with the cases

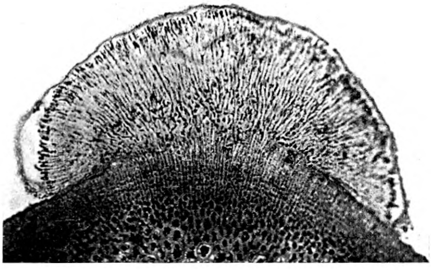

Fig. 14. Vertical section of nemathecium. Photograph. About 120 : 1.

where the paired chromatophores are of different lengths. This interpretation is corroborated by the fact that the ripe spores seem to contain one single chromatophore. Paired chromatophores were observed in end-cells which were still cylindrical and in more or less obovate, nearly ripe monosporangia.

As mentioned above, the resting nucleus in the terminal cell has a distinct outer limitation and a large homogeneous nucleolus or central body staining more or less intensely with hæmatoxylin (Heidenhain). In other cases the central body is differentiated into small grains which stain intensely with hæmatoxylin. The number of these grains, which must be supposed to be chromosomes, was often seen

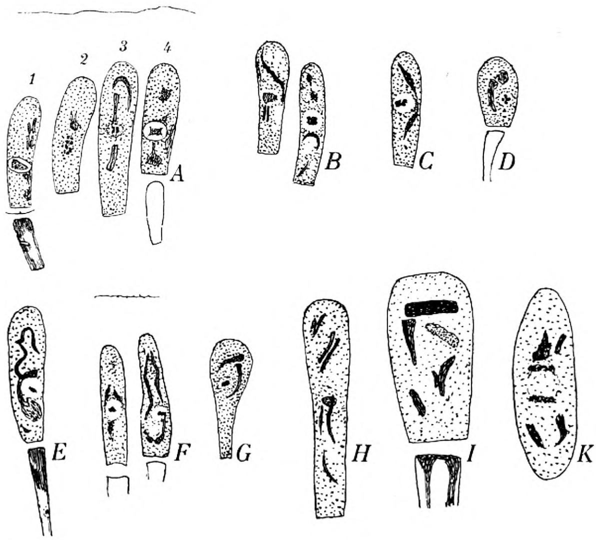

Fig. 15. From a nemathecium from Frederikshavn, Henn. Petersen, May (Alcohol, Heidenhain). End cells of nemathecial filaments showing very distinct chromatophores, partly paired, and nucleus. *A*, group of four end-cells; in *1* the nucleus is in the resting stage, in *4* apparently in the first dividing stage, in *2* the nucleus has lately divided and the two daughter nuclei show each four chromosomes but are still without nuclear membrane. Dividing stages further represented in figs. *B*, *C* (?), *K*. In fig. *I* the nuclear body is rod-shaped, homogeneous without nuclear membrane. *A*—*G*, 1015 : 1. *H*—*K*, 1800 : 1.

to be 4 (fig. 15). Dividing nuclei were rarely observed, most distinctly in the second cell from the left in fig. 15 *A*; two groups of 4 chromosomes each are here situated near one another in the axis of the cell, evidently arisen by division of a nucleus like that in the cell to the right of it. The two daughter nuclei are still without nuclear membranes. Another division stage is shown in fig. 15 *K*, but here the chromosomes are not distinct. The nuclear divisions observed were evidently all mitotic. No indication of a synapsis

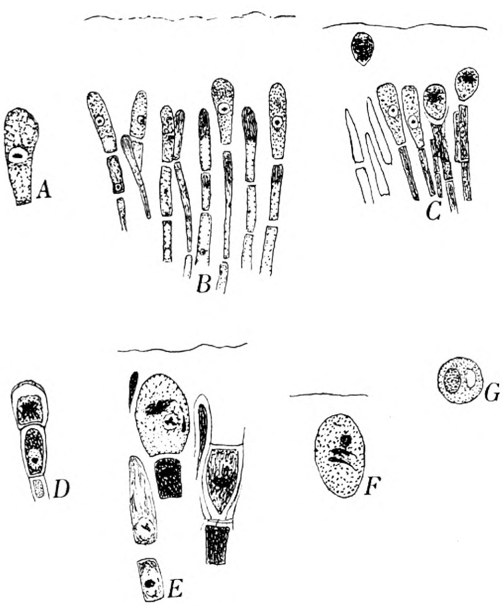

Fig. 16. *A—F*, from the same material as fig. 14. The chromatophores not distinct in figs. *A—C*. One end-cell in *B* contains two nuclei. Ripe monospores are present in *C*. *D*, the last cell contains a nearly ripe spore, a younger spore is developing in the cell beneath it. *E*, a spore has been exhausted to the right and a new monosporangium is developing beneath it. The narrow, clavate intensely stained cells are perhaps end-cells of primary nemathecial filaments. *F*, ripe monospore not yet set free showing nucleus and two chromatophores. *G*, living, ripe spore set free in May. *A—D*, 670 : 1. *E—F*, 1080 : 1. *G*, 670 : 1.

stage or a heterotypic division was ever met with. The formation of the monosporangia is thus not preceded by a reduction of the number of chromosomes, and this is in accordance with the fact that no fertilisation process has been ascertained. The number of chromosomes in the young still dividing end-cells of the nemathecium being four, it must be supposed that the vegetative cells of the nemathecium and probably also of the frond have the same number of chromosomes, but owing to the small size of the vegetative nuclei, the chromosomes are very difficult to distinguish. Some observations seem, however, to show that there are really four chromosomes in the nuclei of the cortical and the medullary cells of the frond[1].

The nemathecia ripen in winter and are still to be found with ripe spores in May, but then they die and in summer *Ahnfeltia* is always sterile. The ripe nemathecia are hemispherical or usually elliptical or oblong, their long axis being parallel to the axis of the frond (fig. 1). The colour is yellowish[2].

The ripe monosporangia are ellipsoidic or obovate, but the spores set free are globular, about 8.5 μ in diameter. They contain numerous small refractive bodies (starch) and one single yellow-brown chromatophore, situated a little excentrically, and beside it a hyaline round spot the nature of which was not ascertained (nucleus or vacuole?) (fig. 16).

3. Germination of the spores.

Spores were sown in May 1927, fronds of *Ahnfeltia* with ripe nemathecia being put down on slides, partly sandblown, at the bottom of glass-vessels filled with sea-water from the Great Belt, where the fronds had been collected, and placed in a room facing north. The presence of the

[1] I am indebted to Dr. C. A. Jørgensen, to whom I have shown some of my slides, for having called my attention to such nuclei, but the observations still need confirmation.

[2] Greville (1830 p. 150) described them as dark coloured.

evacuated spores was ascertained, but the first stages of the germination were not observed. About three months after the sowing, small violet orbicular discs composed of a single layer of cells appeared, the smallest ones consisting of about 30 cells, the largest of much more. In several cases the discs bore single hyaline hairs (fig. 17). The young plants were kept alive for two years, but in the latter part

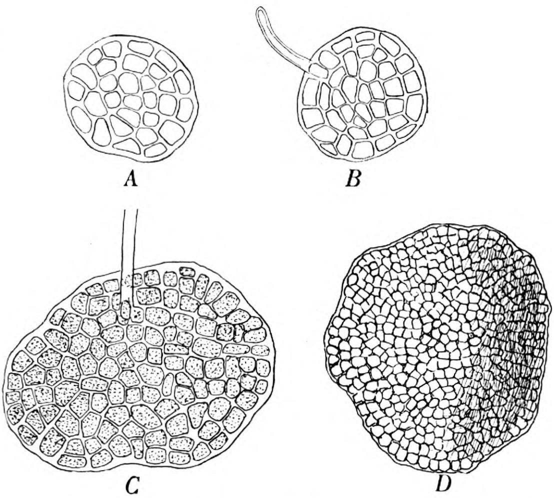

Fig. 17. Germlings obtained by sowing monospores in May 1927 on slides. *A—C* about three months old, in *B* a young hyaline hair springs from a marginal cell, in *C* a long hair springs from the disc. *D*, a two years old germling. *A—C*, 625 : 1. *D*, 350 : 1.

of this period they did not thrive well and finally perished. They had then increased considerably in circumference and were growing thicker in the middle owing to horizontal cell-divisions, but they showed no trace of an upright shoot. These small crusts agreed exactly in colour and structure with the expanded discs from which the upright shoots of *Ahnfeltia* spring (fig. 18), and there can be no doubt as to their identity. It must be emphasised that the basal discs of *Ahnfeltia plicata* in Nature often reach a considerable size before the formation of upright shoots takes place. — The development of the disc-shaped young plants from the germinating monospores thus tells directly against SCHMITZ's hypothesis.

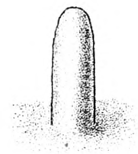

Fig. 18. Young frond springing from an expanded disc. 10 : 1 (?).

4. Conclusions.

The reproduction of *Ahnfeltia plicata* (and related species) is very peculiar and different from that of all other Florideæ. Antheridia, carpogonia, cystocarps and tetrasporangia are wanting. No organs of reproduction are known apart from the nemathecia. These bodies are different from other nemathecia known by their development and their function. While other nemathecia produce seriate tetrasporangia in the nemathecial filaments, those of *Ahnfeltia* produce monosporangia only in the last cell of the nemathecial cell-rows. But the cell-rows producing the monosporangia are not identical with the primary nemathecial filaments. These arise in autumn as outgrowths from a group of superficial cells of the frond dividing by transverse cell-walls. In these cell-rows two kinds of particular cells are early produced (in October):

1) flask-shaped cells arising from the end-cells of the cell-rows, most frequently at the bottom of the nemathecium and consequently often terminal on the cortical cell-rows. These cells remind one of carpogonial cells by their shape and like these stain deeply with hæmatoxylin, but this coloration touches only or in particular the cell-wall, whereas the content is feebly developed, homogeneous and apparently slightly stained and the nucleus not or scarcely visible. These cells are further terminal on

vegetative cell-rows, not at the end of particular carpogonial filaments lateral on the latter, as in other Florideæ, and they are always included, not with protruding end. It must therefore be concluded that they cannot be considered as more or less modified carpogonial cells. They might better be compared with the sterile hairs occurring near the carpogonial branches in *Ptilota* (comp. Davis, Bot. Gazette, **22**, 1896). They are doubtless reduced organs without function, not giving rise to any new formation.

2) The other kind of particular cells, the generative cells, as they have been named above, are, in contradistinction to the flask-shaped cells, productive. They arise at the top of the primary nemathecial filaments, by transformation of the end-cell or as a lateral outgrowth, they are rich in protoplasm and divide early with the consequence that they form small groups of active cells at the surface of the young nemathecium. From these cell-groups new cell-rows spring in a horizontal direction or directed upwards, with the result that numerous upward growing cell-rows are produced, forming a system of secondary nemathecial filaments issuing from an irregular layer situated near the bottom of the nemathecium. The cells of this layer are irregular of shape. The nemathecium is thus built up in two distinct phases. The primary nemathecium is a rather low cushion composed of closely placed primary nemathecial filaments of moderate length, being immediate continuations of the cortical cell-rows; at the border the cell-rows are shorter and diverging outwards. By the further development of the nemathecium the upper portion arises, exclusively or mainly, from the generative cells, or their derivates, and the secondary nemathecial filaments are, therefore, not continuations of the primary ones. The whole

complex of cells arising from the generative cells must be considered as representing a new generation, comparable to the sporophytic generation (*Actinococcus*) of *Phyllophora Brodiæi* (comp. K. Rosenvinge 1929) though there are essential differences. The *Actinococcus* generation arises in a fertile segment of the frond from an auxiliary cell, in a similar manner to a gonimoblast, which process, according to H. Clauszen (1929) and Kylin (1930 p. 27) must be supposed to have been preceded by a fertilisation, so that the nuclei of the sporophyte are diploid (8 chromosomes) whereas those of the gametophyte are haploid (4 chromosomes). The secondary (fertile) nemathecial cell-rows in *Ahnfeltia* arise from several, perhaps numerous, generative cells produced in particular organs: the primary nemathecia. The question then arises, what morphological significance must be attributed to the generative cells. Some would perhaps prefer to consider them as organa sui generis without any relation to other reproductive cells in the Florideæ, but this view, I think, is not satisfactory. The young groups of generative cells offer some resemblance with the incompletely developed procarps which occur so frequently in *Phyllophora Brodiæi* (K. Rosenvinge 1929 fig. 10) and it appears not unlikely that they are, like these, reduced procarps, though differentiated carpogonia and auxiliary cells have never been ascertained. If this interpretation is right, it must be assumed that there are a great number of starting points for the secondary nemathecial filaments in the same nemathecium, though perhaps not so many as might be supposed because several of the cell-groups may be produced by the horizontally running cell-rows (comp. fig. 6) and a number of the cell-groups do not perhaps produce nemathecial filaments. By this multiple origin of the sporogenous cell-rows the nemathecium of *Ahnfeltia* differs essentially from that of *Phyllophora Brodiæi*, where the whole complex of nemathecial filaments normally derives from one auxiliary cell.[1]

Further, as mentioned above, the nemathecial filaments of *Ahnfeltia* differ by not producing tetrasporangia but monosporangia which are not seriate but develop only in the end-cells. The question of the morphological significance of the monosporangia is no easy matter to solve. The fact that they occur in nemathecia suggests that they might be interpreted as originating from tetrasporangia which have failed to be divided owing to the wanting reduction division of the nuclei. Such a division at any rate does not take place in the monosporangia and it seems too to be precluded at any earlier moment; its occurrence seems further to be improbable as a fertilisation or an apomictic process has not been ascertained.

The secondary nemathecial filaments may also be interpreted as gonimoblast cell-rows arising by apogamy from the generative cells, and the whole complex of secondary nemathecial filaments would then be a compound cystocarpium, the gonimoblast filaments issuing from numerous generative cells. According to this view the monospores are to be regarded as carpospores: the nemathecia represent the carposporophytic phase and the tetrasporophytic phase is wanting. Such a compound cystocarp is not otherwise known among Florideæ.

The fact that the spores are terminal on sterile cell-

[1] It seems, however, that a large *Actinococcus* nemathecium may sometimes arise by fusion of primordia of nemathecia issuing from two or perhaps more contiguous auxiliary cells (comp. K. Rosenvinge 1929 p. 22 plate figs. V—VIII).

rows does not seem favourable to this view, as cystocarps of such a structure do not occur within *Gigartinales* to which the genus *Ahnfeltia* is usually referred. The interpretation of the secondary nemathecial filaments as gonimoblast filaments would be in better accordance with the facts known supposing that *Ahnfeltia* were related to the *Cryptonemiales* where both sexual and sporophytic nemathecia occur, and where cystocarps with a structure showing some resemblance to that of the nemathecia of *Anfeltia* are known (e. g. *Polyides*). The frond and the young, primary, nemathecia can be regarded as the gametophyte with modified procarps: the generative cells, which produce the secondary nemathecial filaments representing the sporophytic phase.

The number of chromosomes is four in the nuclei of the spores as well as in the nuclei of the secondary nemathecial filaments from which they arise, and probably the same number occurs in both phases of *Ahnfeltia*. This number must be the haploid number as no reduction of the chromosome number occurs and no fusion of nuclei has been ascertained, although not rarely fusions of cells occur in the first (gametophytic) phase as well as the sporophytic phase.

One or the other interpretation may be right, the nemathecium of *Ahnfeltia* will in any case remain a very peculiar formation otherwise hitherto unknown among Florideæ.

Postscript.

The researches of which the present paper gives an account were completed in the spring of 1930 and were intended to be embodied in the fourth part of my publication: The Marine Algæ of Denmark, which I hoped to complete at the end of 1930. As an illness prevented me from working for a long time, I preferred to publish my investigations on this subject in a separate paper which I succeeded in finishing and sending to the Academy for publication at the end of October 1930. It was only in November that I became acquainted with the note af B. D. Gregory: New light on the so-called parasitism of Actinococcus aggregatus, Kütz. and Sterrolax decipiens, Schmitz (Annals of Botany, vol. 44, no. 177, July 1930), which the author has kindly sent to me.

To judge from the short account of this note, the results of Gregory seem in the main to be in accordance with mine. The author maintains that *Sterrocolax* is not of parasitical nature but that the development of the cushions begins with a localized hypertrophy of the cortical tissue of *Ahnfeltia*. Within such a tissue he found filaments "terminated by darkly-staining somewhat pointed apices, and it is believed that these filaments give rise to the extra-matrical tissue of *Sterrocolax*". It seems not improbable that these filaments or their darkly-staining apices might be identical with the generative cells described above. The author observed fusions between the medullary cells in the neighbourhood of the nemathecia and he thinks it possible that they represent a very much reduced sexuality, a view with which I cannot agree. Monospores were grown in culture, but "after three to five months, only rudimentary disc-like structures have been obtained". GREGORY found in the medullary cells both a four and an eight chromosome complex, but he adds that it is not yet known whether the eight chromosome condition bears any relation to the cell-fusions. There is some evidence that there are eight chromosomes in the apical cells and in the monospores of *Sterrocolax decipiens*". As mentioned above, I found four chromosomes in the apical cells of the nemathecia; when eight chromosomes were observed in such a cell, it was shortly after the division of the nucleus. The author concludes that the mode of origin of *Sterrocolax decipiens* and its similarity in structure to *Ahnfeltia plicata* suggest the probability that it is the asexual biont of its so-called "host".

At the same time appeared another paper treating the same subject, namely E. CHEMIN: Ahnfeltia plicata Fries et son mode de reproduction. Bull. de la soc. bot. de France, t. 77 p. 342-354. The author examined the structure of the nemathecia but he did not observe the "Senker" of SCHMITZ. He points out that SCHMITZ did not say anything about the origin of the parasite and emphasizes the continuity of the cell-filaments at the boundary between the cortex and the nemathecium, but the photograph (plate IV) representing a vertical section of a nemathecium[1] also shows numerous cells intensely stained with hæmatoxylin in the bottom layer of the nemathecium. It seems probable that these cells are identical with those which I have described above as flask-shaped, though CHEMIN, who has observed them,

[1] Not a gall, as erroneously said at the foot of the plate.

does not mention their shape. The photograph further shows, at a higher level, in particular to the right, groups of darker cells which might possibly be identical with the generative cells mentioned above and their derivates.

In examining the germination of the monospores, Chemin observed the first stages of the young plants which I have not seen. He found that the germinating spore produced a short articulate cell-filament giving rise at its distal end to a disc which after two weeks might consist of some twenty cells. Though the smallest discs observed by me were only slightly larger than these, I have not observed any trace of such a germinating filament. The rare hyaline hairs observed in my cultures have nothing in common with it. It is remarkable that Chemin did not meet with any trace of chromatophores or phycoerythrine in the spores, while I found a distinct yellowish chromatophore. After one month the greatest discs measured 40 μ in diameter and were thicker in the middle than at the border. After two months the discs were only slightly more developed but they had multiplied by proliferation. Chemin concludes that the discs are probably the beginning of *Ahnfeltia*.

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Forelagt paa Mødet den 14. November 1930.
Færdig fra Trykkeriet den 28. Februar 1931.

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