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Studies on *Cyanophyceae.*

By

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II. Structure of the investment and spore-development in some *Cyanophyceae.*

(With Plate VII.)

1. General remarks.

In the course of the examination of stained filaments of the *Anabaena*, which formed the subject of the first paper of this series (Fritsch 04), my attention was attracted by the curious structure, presented by the immediate cellular investment. The detailed structure seemed to indicate, that the cells of a filament of *Anabaena* retain their individuality to a greater extent, than appears at first, and although this structure is most emphasized in filaments, which are proceeding to form spores, it occurs also in the purely vegetative stage. A number of further genera of *Cyanophyceae* were examined and the interpretation of the features there observed in the light of those, discovered in *Anabaena*, leads to some interesting comparisons; a large number of genera still remain univestigated, but I have purposely omitted the more elaborate heterocystous forms for the present.

The immediate investment of the *Cyanophyceous* cell has received little attention and those, who have examined it, came to very varying results. Like the cell-contents the cellular envelope of the blue-green Algae differs very markedly from the same structure in other Algae. In the first place (and this applies to *Anabaena* amongst others) it is often extremely difficult to recognise in the unstained vegetative condition. This led some observers such as Kützing (43, p. 48 and 180) and Borzi (86, p. 82) to consider, that the protoplast was merely bounded by a plasmic membrane in most cases; thus within the mucilaginous investment of a *Nostoc* Borzi distinguishes a further envelope ('parete'), but this is regarded as being merely a peripheral portion of the protoplasm ('tutto inseparabile dal

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corpo protoplasmatico"), and the same conclusion is arrived at in the case of *Oscillaria*. Much the same view is held by Bornet and Flahault in their „Revision des *Nostocacées* hetérocystées" (86), where the protoplasm of the cell is considered to be in direct contact with the sheath. Much the most important contribution on the subject is Gomont's „Recherches sur les enveloppes cellulaires des *Nostocacées* filamenteuses", based on the examination of 11 genera. Whilst a large part of the paper is concerned with the sheath, the conclusions arrived at with regard to the immediate envelope of the cell are summarised by Gomont as follows: „La membrane propre de la cellule est toujours mince, étroitement appliquée contre le plasma, mais elle peut être cependant mise en évidence par la dissolution et la contraction de celui-ci; elle est insoluble dans les acides et ne se colore jamais en bleu par les réactifs iodés". Gomont thus considers that a definite membrane is present in all cases and this view is also adopted by Kirchner (98, p. 46). I refrain from citing further literature, as Gomont has done so fully up to the time of his publication.

On the grounds of my investigations I have come to the conclusion, that each protoplast in the *Cyanophyceae* is provided with two investments of its own in the mature condition independently of the external mucilaginous sheath; the inner of these investments forms an actual membrane right round the protoplast, whereas the outer takes the form of a small cylindrical sheath enveloping the cell. These will be described more fully in the course of the detailed consideration of the genera and I wish at this point only to make a few remarks on the nature of the inner investment, which corresponds to the cell-membrane of the two observers just mentioned. I have already mentioned above that it is difficult to distinguish the immediate envelope of the *Cyanophyceous* cell in many cases; this however only applies to the lateral portion of this envelope, for adjacent cells are separated from one another in *Anabaena* (or *Nostoc*) by a well-marked colourless patch, representing the transverse septum, but the limits of this latter with reference to the protoplast are mostly difficult to define. Gomont (88, p. 209) successfully devised a method, by which the cell-wall of *Cyanophyceae* could be rendered evident und by means of which he attained the above-mentioned results; he employed a 33 % solution of chromic acid, which in the course of an hour or so dissolves away the greater part of the protoplasmic contents, leaving the cell-membrane perfectly intact, although a slight contraction seems to me to be involved. Here therefore we meet with a second peculiarity of the cell-wall of the blue-green Algae, viz. its resistance to strong oxidising agents; in this respect it differs very markedly from most other plant-membranes [1]). According

[1]) According to Gomont (loc. cit. p. 212) similar reactions are shown by the membranes of some other Algae (e. g. a *Protococcus*, a *Conferva*, and a *Cladophora*); these membranes are however quite different physically.

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to Gomont (loc. cit. p. 212) its chemical behaviour is midway between that of the cuticle of higher plants and the membrane of the Fungi, being more resistant than this latter. But by far its most important peculiarity seems to me to lie in its great elasticity, which is well exemplified by Brand's (03, p. 303) recent experiments on plasmolysis in this group; according to him (p. 303) „deuten die Erscheinungen auf eine größere Elastizität der *Cyanophyceen*-Membran und auf eine festere Verbindung zwischen ihr und dem Plasma. Eine so vollständige Ablösung des letzteren, wie solche an Grünalgen leicht erzielt werden kann, kommt bei den *Cyanophyceen* nur an besonders günstigen Objekten vor, ... In der Mehrzahl der Fälle folgt die Membran auf größere oder kleinere Strecken dem sich kontrahierenden Plasma, und es findet oft nur an ganz kleinen, vereinzelten Stellen Ablösung statt".

In its physical properties therefore the membrane of the *Cyanophyceae* is quite unlike that of other Algae. I am inclined to regard it as a modified plasmic membrane of a more or less viscous mucilaginous nature and, if we choose to apply to it the term cell-wall, we must keep in view the fact, that it differs very markedly from the structure, usually so called. It is probably a membrane of a rudimentary type of development and we need not be surprised to find it in a group, in which cytological differentiation is on so low a basis. The heterocysts appear in some respects to have a better differentiated membrane, but a detailed comparison with the membrane of the vegetative cell is yet wanting. — I shall have occasion to mention further examples, illustrating the elasticity and viscous nature of the cellular envelope in the course of this paper.

A few words must be added here on the subject of the protoplasmic connections between the individual cells in *Cyanophyceae*; such connections have been described and figured by a number of different authors (Borzi 86, p. 74, Tab. III: Nadson 95, Tab. V, fig. 55), and were especially characterised by their remarkable size. In the first paper of this series I have myself (04, p. 93) described and figured (loc. cit. fig. 3, 6, 7) such cases, but I am now inclined to place an entirely different interpretation on them. In correspondence with its viscous character the cell-membrane will frequently become more or less compressed or drawn out between adjacent cells, which may either be merely due to mechanical strain and is especially liable to be caused by the various staining reagents, used by the above-mentioned investigators. If filaments of *Anabaena* for instance are stained with methyl blue[1]) we get appearances, such as those in figs. 1 and 2. All these cases of so-called protoplasmic continuity therefore are probably merely due to contraction of the intercellular portion of the cellular

[1]) The filaments have to be retained in the stain for about two days to produce an appreciable result.

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investment. This by no means does away with the probability of interchange between contiguous cells (cf. Fritsch, loc. cit. p. 92, 93), for, as explained above, I regard the membrane of the *Cyanophyceous* cell as being of a somewhat plasmic nature, and in that case a gradual diffusion from cell to cell is very probable. We might compare a *Cyanophyceous* filament with a continuous protoplasmic tube, certain portions of which at definite intervals are somewhat modified to constitute transverse septa.

At the present day we are acquainted with spores or resting cells in a considerable number of blue-green algal genera and in a recent treatise of Brand's (03, p. 37) a synopsis of the same is given. Yet if we refer to the literature on the subject, — and I abstain from doing so in detail, as Brand carefully discusses it in the just-mentioned treatise, — we find very little information as to the mode of development and the ultimate fate of these spores. In most cases the statements are confined to a more or less careful description of the fully mature spore. Borzi practically alone in his 'Note alla morfologia e biologia delle Alghe ficochromacee' (78, p. 257) enters into the subject in somewhat greater detail. His description of the development of the spores in *Anabaena Flos-Aquae* Ktz. is as follows (loc. cit. p. 260): „As in *Nostoc* the spores are metamorphoses of the more internal vegetative cells of each thread. . . . . This transformation is manifested in the first place by a slight increase in volume of the cell, destined to be changed into a spore. Its contents become by degrees finely granular, whilst the wall grows more and more in thickness. The mature spores have a globose or ovoid form; they are double the size, — or a little larger — than the normal vegetative segments, are more or less intensely bright yellowish-gold in colour and are filled with innumerable small granules, which Iodine tincture stains blue. The exosporium is much thicker than the endosporium and is provided with very delicate and scarcely distinct ridges".

I have mainly studied the development of the spores in the species of *Anabaena*[1]), whose general features were already described in the first paper of this series (Fritsch 04); but their development is so closely connected with the features of the cellular investment, that I propose in the following to describe the two phenomena side by side. Filaments, which are going to develop spores, show some signs of this tendency at a rela-

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[1]) There seems good evidence for this species being *Anabaena Azollae*. Large quantities of the same Alga have arisen in a vessel, containing *Azolla*, which was collected in Brittany last April, and in this material heterocysts are also quite abundant (cf. Fritsch 04, p. 89, foot-note 2).

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tively early stage and for the sake of brevity I shall designate them sporogenous filaments as a contrast to the purely vegetative filaments.

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2. Detailed considerations.

(a) *Anabaena.* When purely vegetative filaments are examined microscopically, as already stated, an enveloping membrane is readily evident only between adjacent cells. Sporogenous filaments on the other hand exhibit well-marked lateral walls to the cells, which appear as a fairly thick dark line, when focussed so as to be seen in optical section (fig. 4 and 5). If such filaments are stained with an aqueous solution of Iodine the following peculiar structure appears (fig. 5). The longitudinal (lateral) walls of each cell are sharply marked off from one another in adjacent cells (fig. 4, 5, c. s.) and appear separated from one another by the colourless area, which represents the transverse wall between the two cells concerned (fig. 5, t. s.). This latter is bounded laterally by a faint, slighlty concave limit (cf. fig. 3b, t. s.). Careful examination reveals the fact, that the free ends of the lateral walls are connected with one another transversely by a very delicate line (l in Fig. 5), running apparently right round each end of the protoplast, the transverse wall (t. s.) between adjacent cells, separating these lines from one another. In other words, looking at such stained sporogenous filaments under a high power, their appearance is such as to give one the impression that the lateral walls of each cell form part of a hollow sheath-like cylinder around the same, the open ends of which give rise to the above-mentioned line, connecting the free ends of the lateral walls. Each cell of the filament is thus surrounded by a special cylindrical sheath of its own (= cell-sheath, fig. 5 and 8, c. s), which, when division of the cells takes place, is simply split into two fresh sheaths by the development of a colourless intercellular mass (fig. 3a, b). When a cell of *Anabaena* is about to divide an indentation of the lateral walls (= cell-sheath) appears at about the middle of their length, giving rise to a constriction, running round the middle of the mother-cell (fig. 3a). At the same time a very thin colourless strip (cf. fig. 3a, t. s.), appears in the cell-contents on the same level as the constriction of the cell-wall (cylindrical sheath) and, as this strip gradually increases in width (fig. 3b) and develops into the intercellular colourless area, the new cells move apart from one another and the individual cylindrical sheath of each becomes distinct. The details of this process are difficult to observe and I am not at present prepared to say, whether the splitting of the sheath is a purely physical process or whether it is the result of some special structural change. In his recent preliminary paper on the cell-structure of *Cyanophyceae* Wager (04, p. 406) describes this

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process in the following words: „The division of the cell is brought about by the formation of a transverse wall, which grows inwards from the lateral wall and divides the cytoplasms and nucleus into two equal or nearly equal parts". I was not able to observe the exact point of origin of the separating mass, but it is very probable that it is formed from without inwards as in the specimens, studied by Wager. In accordance with the views, which I have expressed above on the nature of the cellular envelope of *Cyanophyceae*, I consider that this intercellular substance, which arises between the new daughter-cells, is only a modified portion of the protoplasm.

Internal to the cell-sheath sporogenous filaments of *Anabaena* however exhibit a further investment in the form of a narrow colourless strip of similar appearance to the intercellular substance and which like it takes on a faint brown colouration with Iodine (fig. 5, S i. i.). This apparently abuts directly on the coloured peripheral portion of the cell-contents and is continuous with the intercellular mass, separating adjacent cells. That is to say each protoplast of a sporogenous filament of *Anabaena* is surrounded on all sides by a thin strip of colourless substance (fig. 5 and S, i. i.), which I shall refer to below as the inner investment; laterally this envelope is bounded by the cell-sheath, already described, whilst terminally it forms the intercellular substance between adjacent cells. This inner investment I regard as the actual membrane of the cell, which is possibly alone present during the commencement of the vegetative phase and to which all the remarks on the nature of the investment, made above (p. 32) apply; as filaments pass over to the sporogenous condition the cell-sheath begins to develop on the outside of the inner investment.

If filaments of the *Anabaena* in question are treated with a 33 % solution of chromic acid according to Gomont's method the cell-contents are slowly dissolved and the envelope, surrounding each cell, becomes more distinct. Each cell is then seen to be surrounded by a definite membrane, constituted by the above-mentioned inner investment, whilst the cell-sheath is now by no means so easy to recognise or has disappeared; a certain amount of contraction is, as already stated, involved in this process. As the spores reach maturity however this treatment has no effect on the cell-sheath and leaves the two investments of the protoplast well-defined. This seems to point to the fact, that the cell-sheath is a specialised inner portion of the mucilaginous envelope, for according to Gomont the sheath is far more readily soluble, than the actual cell-membrane (loc. cit. p. 214, 215). Its differentiation probably commences at a very early stage and its rudiments are probably developed, although not sharply marked, in filaments, which are in a purely vegetative condition. It is not visible in these cases however without the help of stains, whereas sporogenous filaments admit of the recognition of all the above structural features in the ordinary

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living condition, although stains make them show up more prominently. In young stages the much smaller size of the cells makes the determination of details a great difficulty; nor is the inner investment very strongly developed at that period and consequently it is very difficult to distinguish between it and a possible rudimentary cell-sheath. The two investments of the protoplast only become sharply defined in well-advanced sporogenous filaments, — a fact, which is not surprising, when we consider, that their origin (as an excretion from the protoplast) is the same. It is natural to expect that the cell-sheath will become more defined, as the protoplast becomes older, and will reach its most marked differentiation, when the spore develops, i. e. when the necessity of a firmer outer covering is fully realised.

As the cells of a filament pass over into the sporogenous condition the transverse limits of the cell-sheaths of adjacent cells become better defined (cf. fig. 5 and 8). Gradually also by the increase of the colourless intercellular septum the cells move further apart, whilst the cell-sheath increases in extent and closes in round the open ends, so that the outer investment ultimately forms a complete sheath round the mature spore (fig. 6). As the sheath closes in it envelopes a portion of the intercellular septum so that the sheath or exospore of the spore (fig. 6, ex) surrounds a complete inner investment or endospore (fig. 6, en). The remainder of the intercellular septum has swollen up considerably and has become invisible: it is the cause of the now more or less wide separation of the spores. The spores thus exhibit two well-marked membranes, as in the cases, described by Gomont and Borzi. With regard to the spores the former (loc. cit. p. 233) remarks: „La spore enfin, là où elle existe, est bien, comme on l'admet généralement, produite par l'encystement d'une cellule végétative. Elle possède un exospore où se retrouvent les enveloppes de celle-ci, et un endospore produit au moment de la maturité, et identique par ses propriétés à la membrane cellulaire végétative." Brand (03, p. 34) also considers that „das Endospor . . . erst bei der die Keimung einleitenden Zellverjüngung entsteht, . . . nur an ganz reifen Exemplaren vorhanden ist". Gomont and Brand thus regard the endospore as produced at the moment of maturity; in *Anabaena* both the envelopes of the spore are however present long before maturity is reached and. if either. it is certainly the exospore in my opinion, which is newly formed. The process is scarcely one which comes under the name encystment. During the development of the spores the cells increase very much in size and the fully-developed spore is 2—3 times larger than the ordinary vegetative cell; there is however very little change in colour[1]) in the species. which I

[1]) The cell-contents are slightly yellowish-green, but could scarcely be called coloured (cf. Brand 03, p. 33).

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studied, — a point of difference from the cases, described by Borzi (cf. p. 33). The latter author does not describe the way, in which the two walls of the spore develop in *Anabaena*. I leave a further discussion of the spore and its relation to the „gonidia" of Brand (03, p. 44 et. seq.) to the next paper of this series [1]).

In the examination of well-advanced sporogenous filaments numerous stages are met with (fig. 7, 8), which seem to me to quite plainly support the theory of structure of the investment, propounded in the preceding pages. Specimens, such as that represented in fig. 8 are of quite common occurrence; here the uppermost spore is about to liberate its contents and the terminal (transverse) portion of the inner investment is more or less papillosely developed on one side and this papilla quite visibly protrudes through the open end of the cell-sheath. Again in fig. 7, which represents the contents of a sporogenous cell in course of protrusion, one end of the cylindrical cell-sheath quite visibly surrounds the equator of the protoplast, which is enveloped in a new inner investment. Such cases will be further discussed in the third paper of this series.

I still wish to add a few words on the behaviour of the external mucilaginous investment of the *Anabaena* towards stains. Treated with Vesuvin it turns brown and is seen to consist of a number of successive layers. The innermost, and therefore most recent, of these closely follows the outline of the cell-sheaths of the individual protoplasts and thus presents a moniliform appearance, indicating the excretive activity of each cell. These investments do not include the heterocysts (cf. Brand 03. p. 44). It is very instructive to watch the behaviour of a filament, when Vesuvin is slowly added under the microscope. A very wide mucilaginous investment, which was quite invisible before, becomes indicated by its margins contracting slightly and taking on the brown stain. The contraction goes on very slowly but evidently, and at the same time the mucilage acquires a darker and darker brown colour; ultimately it encloses the filament as quite a narrow sheath, showing one or more layers of stratification. In all probability many of the layers discernible during the process of contraction are due to folds. As soon as any cell of a filament becomes transformed into a heterocyst excretion of mucilage from this cell ceases and the stratification of the mucilaginous envelope seems in the main to

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[1]) The spores of certain *Cyanophyceae* (e. g. *Nostoc microscopicum* Carm. *N. commune* Vauch., *Gloeocapsa alpina* Näg.) differ in the lack of an exospore, which is replaced by a thick and consistent mucilage sheath (cf. Brand 03, p. 35, 36). These are all aerial species. These forms are interesting, as to my thinking they show, that in certain cases the spore does not develop a special cell-sheath (which is regarded as a modified innermost layer of the external mucilage), but that this structure is replaced by the whole of the outer mucilage becoming more consistent, — a pure case of homology.

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be due to such changes. When a filament has a row of heterocysts one behind the other (cf. Fritsch 04, p. 89) the distal one has no mucilage envelope whatsoever: the next heterocyst is surrounded by a layer of mucilage, formed before its transformation, the third has two such layers, and so on — The cell-sheath, as in the case of the filaments treated with Iodine, becomes better defined, when stained with Vesuvin: the inner investment however remains practically uncoloured. In young filaments, in which a cell-sheath is not yet recognisable, staining with Vesuvin makes the inner investment (then the only one ?) particularly prominent: for the protoplast is separated from the brownly stained external mucilage by a narrow colourless area, representing the inner investment.

(b) *Nostoc*. It is scarcely necessary to give many details here, as the structure practically agrees with that of *Anabaena*. I was not able to obtain sporogenous filaments and therefore the recognition of many of the points was of considerable difficulty. With the help of Iodine or Vesuvin however the cell-sheath was brought out prominently and especially the lateral parts are then well defined. There can be no doubt in such stained specimens, that the lateral portions of the outer envelope (cell-sheath) are only proper to the individual cells (cf. fig. 3b). In many cases too the thick dark line, which marks the lateral portion of the cell-sheath extends round on to the terminal portion of the cell for a little way, which is probably due to a slight thickening of the margin of the open end of the cylindrical sheath: the cell-sheath then appears [ ] in optical section.

(c) *Gloeocapsa* and *Gloeothece*. An interesting case is furnished by *Gloeocapsa*: in most cases (especially in the large-celled forms) two envelopes are quite readily distinguishable around the cell-contents viz. the colourless inner investment (fig. 9, i. i.) and surrounding that a well-marked cell-sheath (fig. 9, c. s.), which here extends right round the cell. Division takes place in a manner quite similar to that described above for *Anabaena*; the cell becomes constricted at its middle, whilst the separating colourless mass (transverse wall) gradually appears (fig. 9). Ultimately however it develops to a far greater extent than in the previous cases, so that the daughter-cells become more or less widely separated and the open cell-sheath gradually closes in right round each daughter-cell. We thus see that the normal vegetative condition in a *Gloeocapsa* or *Gloeothece* presents the same structure as do the spores of an *Anabaena*, i. e. in its reproductive cells this latter genus reverts to the primitive type of structure, which probably appertained to its ancestors. The fact that the spores of an *Anabaena* divide so as to form a filament is due in part to a condensation of the intercellular septum, in part to the loose diffluent character of the external sheath (cf. p. 45, 46).

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At the same time young stages of *Gloeocapsa* are always to be found in which the cell-sheath is unrecognisable and in these the demonstration of the inner investment is a very difficult matter; even with the help of chromic acid I was not able to render it visible in a satisfactory manner, owing apparently to the very considerable contraction in this case. Brand has already (00, p. 4) commented on this difficulty. but mentions a case, in which „ganz frische Teilungsprodukte einer Zelle . . . . . abnormer Weise durch eine farblose schlauchähnliche Brücke zusammenhingen", which is probably due to special development of the inner investment in the case in question; I have met with similar phenomena (i. e. cases, in which two adjacent cells were connected by the much drawn out transverse septum) in *Anabaena*, and in my opinion they tend to confirm the gelatinous nature of the investment.

The portion of the investment, that I have called the cell-sheath in *Gloeocapsa*, was also recognised by Nägeli (49, p. 47, 48), for he says: „Die Zellwandung (i. e. the entire investment) ist sehr dick und in der Regel das Zelllumen mehrmals übertreffend, selten demselben bloß gleichkommend. . . . . An der Wandung kann meistens die schmale Zellmembran und die breite Hüllmembran unterschieden werden". Nägeli's „Zellmembran" corresponds to the cell-sheath and the „meistens" indicates, that he already observed its occasional absence; the „Hüllmembran" refers to the external mucilage. Brand (00, p. 7) also came to the conclusion, that Nägeli's „Zellmembran" was not the actual cell-membrane, for he says: „jene öfters bemerklichen Zonen, welche Nägeli im Auge zu haben scheint, gehören aber der Gallerte an, und die eigentliche Zellhaut von *Gloeocapsa (alpina)* ist, wie bereits angedeutet, mit den gewöhnlichen Hilfsmitteln überhaupt nicht zur Anschauung zu bringen". In the case of *Chroococcus helveticus* Klebs (86, p. 391) states that: „Jede intensiv blaugrüne feinkörnige Zelle besitzt eine äußerst zarte, dünne Zellwand" and here also I have no doubt that the cell-sheath is meant.

When the colonies of a *Gloeocapsa* or *Gloeothece* are subjected to a 33 % solution of chromic acid the external stratified sheath is first attacked and gradually dissolved away; it takes some little time before the acid reaches the cell, but then, as in *Anabaena*, the cell-sheath slowly disappears, unless the cells have reached the mature size. The inner investment, as already mentioned, is very difficult to discern afterwards.

A few words may be added on the genus *Merismopedia*, in which a large number of cells are bound together by thin transparent mucilage to form flat plates; owing to the small size of the cells specimens, stained with Vesuvin, were examined. The cell-sheath in these is well marked in contrast to the inner investment; it is either confined to pairs of cells or surrounds larger groups of them, when rapid division is taking place. The former state of affairs is by far the commonest and it is noti-

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ceable that all the individual pairs of cells, which are thus each enveloped by a common cell-sheath, lie in one direction: this shows that division is prevalent in this direction. The mucilage investment of the whole colony is well-marked in stained material and projects only very slightly beyond the general contour of the aggregate of cells.

(d) *Oscillaria* and *Lyngbya*. In the genus *Oscillaria*, which is of considerable interest from the point of view of the present paper, it was found convenient to examine a species with fairly broad filaments, as such tend to make the recognition of details of structure in the investment rather more easy; the following observations therefore in the main refer to *Oscillaria Fröhlichii*. The cells which constitute the filaments of this species are flat, generally several times broader than they are long (cf. fig. 11) and the colourless septum between adjacent cells is only of very slight width; when the cell-contents are very granular it is almost impossible to recognise the delimitations of the individual protoplasts, as the granules tend to aggregate about the region of the septa. The whole row of cells or filament is here enclosed in one general sheath, which is however quite evidently merely due to the coherence of the individual cell-sheaths of an *Anabaena* or *Nostoc*. In correspondence with the slighter development of the transverse septa the sheath is not split during division, but remains as one continuous whole round the entire row of cells. However the sheath still shows its composite origin, in that it is slightly constricted at each point of separation of two contiguous cells (fig. 11, c. s.); these contrictions run transversely right round the filament and give rise to a rough stratification in surface view. The colourless inner investment of each cell (fig. 11, i. i.) is rather better seen laterally (i. e. on the inner side of the sheath) and is generally very readily visible at the apex of the filaments.

In the year 1897 two papers, dealing with the structure of the cell-membrane and the movements of *Oscillaria* were published (Correns 97, Kolkwitz 97), but the subject-matter contains very little bearing on the present paper. The outer walls (i. e. the coherent cell-sheath) show a reticulate structure according to Correns, when treated in a certain way, and in connection with this, the following statement of this observer is of some interest here: „Bei weit geöffneter Irisblende sieht man ein rotes Netz auf farblosem Grunde, schmälere oder breitere farblose Streifen laufen den Ansatzlinien der Scheidewände entlang“ (p. 139). That is to say the parts of the coherent cell-sheath, which lie opposite the lines of separation of the protoplast (the region, where the cell-sheath splits on division in *Anabaena*!), show a different structure to that of the remainder of the sheath.

Treated with Vesuvin the cell-sheath of an *Oscillaria* becomes very prominent and the inner investment also seems to take on a faint brown colouration, although this appearance

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may be due to colouration of the cell-contents. There is no trace of external mucilage. When placed in a 33 % solution of chromic acid the cell-contents, as in other *Cyanophyceae*, are slowly dissolved. For some time the sheath still remains visible as a faint line outside the inner investment, but ultimately it disappears completely and there only remain the cavities of the protoplast, surrounded by the inner investment.

The usual distinction between *Oscillaria* and *Lyngbya* depends on the absence of a sheath in the former and its presence in the latter, but it has long been asserted that this is a difference which is scarcely tenable. As Gomont (loc. cit. p. 222 footnote) points out, practically all species of *Oscillaria* are provided with a delicate sheath and it may be questioned whether by suitable conditions of cultivation the few exceptions might not also be shown to have a very delicate one, for the demonstration of the cell-sheath is always a matter of difficulty in small-celled species of *Anabaena* or *Nostoc* for instance. In the present state of our knowledge of species of *Oscillaria* it also seems very probable, that some of these naked forms may be merely young stages of sheathed species. There is no doubt however, that there is a series of forms, in which the sheath is a prominent feature and in which it is markedly thickened, but this sheath does not correspond to the cell-sheath of an *Anabaena*, nor to the above-described sheath of *Oscillaria Fröhlichii*, but finds its homologue in the external mucilage of the former. In a marine species of *Lyngbya* (*L. salina* Ktz.?), which I collected recently on the coast of Brittany, a considerable number of filaments (diam. 12 μ) merely present the structure above described for *Oscillaria*, but the majority have a further envelope outside the (cell-) sheath (Fig. 16, c. s.); this external sheath (fig. 16, e. s.) is limited towards the exterior by a well-marked line, which is separated from the filament by a narrower or wider space, filled with invisible mucilage and it quite evidently corresponds to the external mucilage of an *Anabaena*. When this sheath is of considerable thickness (it often attains 30 μ in diameter) the outer limit is itself thick (diam. 3 μ about), whilst the remainder of the sheath presents numerous layers of stratification. Again in a species of *Lyngbya* from near Trincomalie in Ceylon all the filaments are surrounded by a well-developed and consistent sheath, which is more uniform than in the last-discussed species and encloses a filament with a thin coherent cell-sheath, resembling the structure of an *Oscillaria* in all respects. External sheath and cell-sheath are here in close apposition and the two might easily be overlooked as distinct structures.

We thus see, that in one series of forms the external mucilage of *Anabaena*, *Nostoc* etc. has been discarded altogether and the only investment common to the whole filament is the coherent cell-sheath; these are the species of *Oscillaria*, which are thus capable of movement during the whole of their life.

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In another series of forms however an external sheath is present as well as the coherent cell-sheath — during a part of the life-history at least — in consequence of which motion has disappeared except in the hormogonial stage; these are the species of *Lyngbya*. If this difference is kept in mind there is no difficulty in keeping the two genera distinct except in the hormogonial stage. Of course it still remains to be seen whether all species of *Oscillaria* cannot under certain conditions excrete external mucilage and so acquire the characters of a *Lyngbya*: for in the case of *Oscillaria caldariorum* Hauck Gomont describes how (contrary to herbarium-specimens at his disposal) the filaments showed no trace of a sheath (NB. the cell-sheath was surely present), when first collected, but after some weeks cultivation, on sable de rivière stérilisé et simplement humecté they acquired. de gaînes solides ne différant en rien de celles que présentent les échantillons placés par les auteurs dans le genre *Lyngbya*. What I have endeavoured to emphasize is that the sheath of an *Oscillaria* is quite a different thing to the sheath of a typical *Lyngbya*.

As in *Oscillaria*, the transverse portion of the inner investment in a *Lyngbya* (and the remarks of this and the ensuing paragraph apply also to *Tolypothrix*) vary in thickness and may be very much obscured, by the granular cell-contents. Inside the external sheath the cell-sheath is often not well-developed, but as soon as the filament is liberated as a hormogonium the cell-sheath begins to thicken laterally: in fact whenever the filament comes into contact with the exterior such thickening takes place. It often happens that a hormogonium is partly liberated from a filament, when the process of liberation ceases: the free portion then not only forms a well-marked cell-sheath, but outside this forms a fresh strip of external sheath (fig. 14): this may happen repeatedlyand thus we get appearances like fig. 14. The tendency to produce a thickened investment, as soon as exposed, is also illustrated by fig. 12; here a small part of the filament has died away, having left the transverse septa still persistent; the two ends of the filaments thus exposed, are covered by a very much thickened portion of the cell-sheath. In the same way, in an exposed termination of a filament in *Anabaena*, we always find the cell-sheath, extending right round the exposed surface (fig. 5).

The contraction of the immediate cellular envelope is well illustrated, when a typical *Lyngbya* is treated with chromic acid: after some time we find a row of more or less emptied cells (i. e. with the cell-contents dissolved away) lying loosely within the outer sheath (cf. fig. 4, Pl. IV. Gomont. loc. cit. and my fig. 15). Ultimately however the sheath becomes entirely dissolved away and there only remains a row of empty cells with the inner investments (cf. *Oscillaria* above). When treated with Vesuvin the sheath of a *Lyngbya* of course develops a well-marked brown colour (cf. *Anabaena*).

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(e) *Tolypothrix.* The species of *Tolypothrix* are always provided with a well-developed external sheath of the same tough consistency, as in *Lyngbya*; and at first sight one very easily overlooks this and the cell-sheath as distinct structures. As soon however as the filaments are treated with Iodine no doubt can remain, for the filament of cells with their immediate investments contracts away from the external sheath (fig. 13), at the same time becoming stained so that inner investment and cell-sheath show up quite well. There is however one point, which distinguishes these contracted filaments from those of an *Oscillaria* or a *Lyngbya*; the cell-sheath is much more pronouncedly moniliform than in either of the latter genera (fig. 13, c. s.) and if the filaments are examined carefully, it will be found that here and there it is split between adjacent cells. That is to say the structure of the actual filament (i. e. independent of the external sheath) in *Tolypothrix* recalls that of *Anabaena* or *Nostoc* to some extent, and, in that the cell-sheath is not entirely coherent, is less specialised than in *Oscillaria* and *Lyngbya*.

The effects of different reagents on filaments of *Tolypothrix* are similar to those in *Lyngbya* and it only remains to draw attention to the fact, that in the former genus the heterocysts are included in the general external sheath, — a point of difference from *Anabaena* and from the genus, next mentioned.

(f) *Rivularia* furnishes a particularly interesting case; I examined *Gloeotrichia natans* (Hedwig) Rabenh. from the Plankton of Ceylon. Here the basal end of the filament is almost invariably occupied by a heterocyst and if this is absent the lowest cell exhibits distinct modifications, as evidenced by its behaviour towards reagents[1]); the other end of the filament is produced into a longer or shorter, generally much-attenuated hair-like structure. The base of the filament, exclusive of the heterocyst[2]). is surrounded by a mucilaginous sheath, the external limits of which are sometimes well-marked even in unstained material, although just as often invisible; emanating from the proximal portion of the cell, immediately adjacent to the heterocyst, the limit of the sheath arches outwards aud thus comes to be separated from the following cells by a considerable interspace. The sheath can generally only be followed up a little way and is unrecognisable in the upper portion of the filament; this is undoubtedly due to the fact, that it is only excreted by the

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[1]) Whereas all the cells of the filament take on a brown colour with Iodine the basal heterocyst or, if this is absent, the lowermost cell remains unstained (cf. Fritsch 04. p. 90).

[2]) The heterocysts of this species (fig. 10h) are very peculiar. Under a low power one can distinguish the following structure. On the exterior of the heterocyst is a thin membrane, which encloses a rounded slightly flask-shaped cell, which is provided with inner investment and cell-sheath. Between the cell-sheath and the above-mentioned thin membrane is a clear space of considerable width, which is apparently empty. The actual cell on the other hand is occupied by deep blue-green homogeneous contents, which fill its entire lumen. I shall publish further details subsequently.

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lower cells of the filament, those situated more apically having lost this power with their tendency to develop into hair-cells. This differentiation of apex and base of the filament, which thus also finds its expression in the external sheath and is of course likewise exhibited by the strictly basal development of the single large spore, is also noticeable in reference to the immediate investments of the cell. In the basal cells of a filament the cell-sheath is readily visible outside the colourless inner investment of each protoplast (fig. 10, c. s.); in most filaments it is however less and less easy to recognise as one advances towards the apex and the cells, which make up the hair-like termination of the filament, are invariably devoid of a cell-sheath and only possess the inner investment. As in the case of the external sheath, mentioned above, is is very difficult to fix the precise point, at which the cell-sheath is no longer evident, nor is this point by any means constant in different filaments; in one case the greater number of cells of a filament are without the cell-sheath, whilst in another the majority is provided with this latter investment. The cell-sheath presents the same marked moniliform structure, as in the filaments of a *Tolypothrix* and for whole stretches the cell-sheaths of the individual cells may be quite distinct from one another, as in *Anabaena*; in such regions the structure of the filament is identically that of this latter genus. On the whole however the cell-sheaths are more commonly found united, although such a coherent cell-sheath differs from that of *Oscillaria* and agrees with that of a *Tolypothrix*, in its very marked moniliform constrictions.

The single large basal spore develops from a single vegetative cell by great increase of size of the latter; as development proceeds the external mucilage at the base of the filament. becomes more and more distinct, and ultimately forms a rather closely-fitting sheath round the mature spore. It is noticeable that. whereas the ordinary vegetative cells are only stained faintly brown by Iodine, the sporogenous cell and often also one or two of the following cells take on a deep brown colour. I hope to be able to furnish further details of the development of the spores in this genus subsequently, but as yet I have not been successful in finding many stages.

General conclusions.

In the following paragraphs I shall attempt to put some interpretation on the above-discussed phenomena and endeavour to sketch out the line. along which the filamentous forms developed from the unicellular. Much of what follows is not new. but I consider its recapitulation necessary for a full understanding of the facts.

The simplest form, that has been examined, is *Glococapsa* and there seems no reason to suppose that its structure differs

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from that of the related unicellular forms in any essential respects. It is of especial interest because it is one of the unicellular *Cyanophyceae*, from which the higher filamentous forms were in all probability derived. In this genus the cells are capable of dividing in three directions at right angles to one another, and if we suppose, as seems most likely, that the ancestor of such unicellular forms was capable of dividing along all directions (a parallel for which is found in *Aphanocapsa*) *Gloeocapsa* represents a fairly primitive type, — more primitive probably than a form like *Merismopedia*, which is only capable of division along two directions. If we imagine the capacity for division along one of these planes to become lost (*Aphanothece, Gloeothece*), we reach the conditions, necessary for the development of the filamentous stage and with that pass on to the higher forms; in correspondence with this tendency for division solely along one direction we find that the spherical cell of a *Gloeocapsa* or *Merismopedia* acquires a more or less pronounced cylindrical form (in *Gloeothece*, etc.). In *Gloeothece* and *Aphanothece* however the filamentous tendency is still opposed by the consistency of the ellipsoidal or spherical mucilage envelopes, which effectively prevent the formation of a row of cells by this uniaxial division. The phenomenon, which we have before us here, is well described by Nägeli (49, p. 57) in the following passage: „In der Mutterblase (i. e. the enveloping layer of mucilage) liegen die beiden Tochterzellen nach der Teilung hintereinander. Sie dehnen sich dann in die Länge; ist die Blase weich, so folgt sie anfänglich dem Drucke, reißt aber, wenn die Tochterzellen ihre eigenen Blasen bilden (fig. 2c). Besitzt dagegen die Mutterblase zweier Individuen nicht so viel Elastizität, um dem Drucke der Ausdehnung dieser letzteren folgen zu können, so werden dieselben mechanisch von der ursprünglichen Richtung abgelenkt (fig. 2b; fig. 3b, c). Mit dem weiteren Wachstum und der Bildung der eigenen Hüllmembranen weichen sie zuletzt so sehr von der anfänglichen Stellung ab, daß sie mehr oder weniger parallel neben einander liegen (fig. 3d, e)." — The same applies to *Aphanothece*. — In the genus *Synechococcus* we have a stage, which takes us onwards a little way towards the filamentous series. As in *Aphanothece* and *Gloeothece* we have cylindrical cells, dividing in one direction only, but the colonies are only surrounded by a loose diffluent mucilage. As a rule division apparently follows the lines of that in *Gloeocapsa*, *Gloeothece* etc., mucilage being formed abundantly between the products of division and the cell-sheath no doubt forming a complete envelope round each individual cell: occasionally however the intercellular mucilage is less developed and the products of division form short rows of cells. It remains to be seen whether the cell-sheath is then individual to each cell or coherent. I have not been able to obtain *Synechococcus* for this investigation, but judging from memory and the published figures, it seems probable that the former will be the case. The

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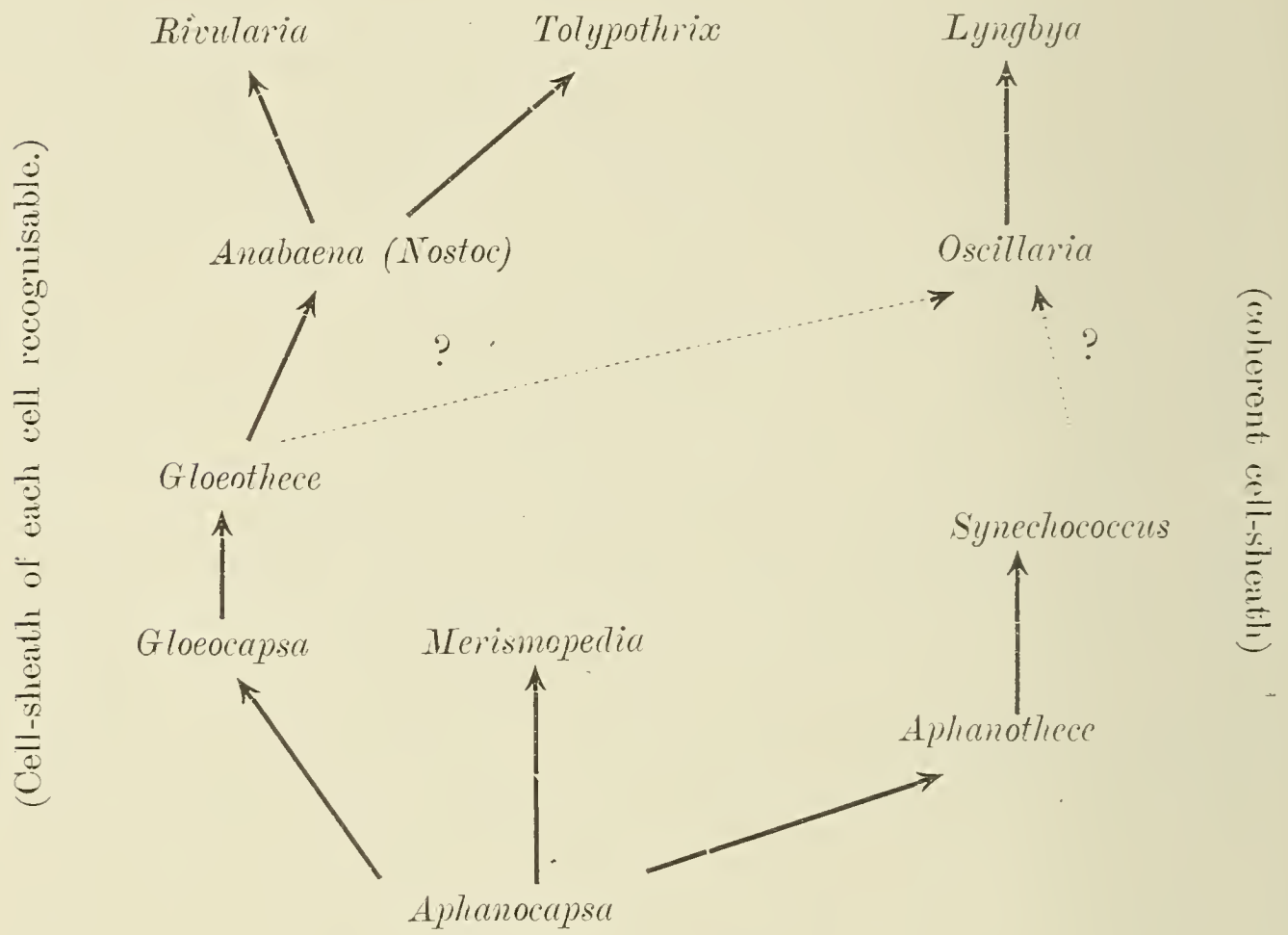
short rows of cells of *Synechococcus* otherurse recall *Oscillaria* to a great extent.

Dangeard (99) in his exceedingly instructive paper on the evolution of sexuality has shown conclusively, that the filament or row of cells is the most advantageous from the nutritive point of view; and quite in correspondence with this we find that in the *Cyanophyceae*, as in other algal phyla, the filament is the most successful form. The cell-sheath, which in *Gloeocapsa* and other unicellular forms, constitutes a firm investment around the whole cell, is only necessary laterally, when the filamentous stage is attained. By the rapid succession of divisions all in one direction no time is given for the closure of the gap, left in the cell-sheath, whilst by a suppression of the mucilage, excreted between the products of division, a consistent trans-



verse septum originates, which completely replaces the cell-sheath at this point. In this way the state of affairs, occurring in *Anabaena*, is attained. It should be noted that each cell of the filament still retains its individuality to some extent, in so far as it has its own peculiar cell-sheath, probably excreted primarily by each individual cell, and, in so far as in the course of division of a cell, already provided with such a cell-sheath, the latter is split into two portions, appertaining to the daughter-cells. It seems probable that this splitting is merely due to the relatively strong development of the intercellular septum, which is certainly more strongly developed here than in a form like *Oscillaria*, — a point of resemblance to *Glococapsa* etc.

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It should be noted that (as exemplified by *Aphanothece* and *Glocothece*) a change in the character of the external mucilage was a necessity for the formation of the filament. In *Oscillaria* the external investment has been discarded altogether and the necessary rigidity is obtained by the coherence of the cell-sheath; in other forms however *(Lyngbya)* this was not sufficient and a more or less consistent outer sheath was further developed. The heterocystous forms studied have all retained an outer sheath and perhaps it is owing to this that coherence of the cell-sheath is not so marked in any of these forms[1]). The scheme on p. 46 is meant to show the way, in which the higher filamentous *Cyanophyceae* arose from the unicellular forms, as far as can be gathered from present day forms; but although it indicates relationships it must not be regarded as a phylogenetic series. As will be seen two main series of forms are to be distinguished: the series *Gloeocapsa — Gloeothece — Anabaena*, in which the cell-sheath can always be recognised as individual to each cell, owing to its very marked constriction, even when coherent; and the series *Oscillaria — Lyngbya*, which probably developed from a form like *Synechococcus*, and is characterised by the uniform cell-sheath around the whole filament. *Lyngbya* represents a return to the old conditions, in as much as it possesses a well-marked external sheath, which is lacking in *Oscillaria*.

Summary.

It may be well to briefly summarise the conclusions of the present paper:

(I) Each cell of the sporogenous filament (and probably also of mature vegetative filaments) of an *Anabaena* has two envelopes, — an inner investment, which completely encloses the protoplast, and outside this a special cylindrical sheath, which has been designated the cell-sheath; when division of the cells takes place this cell-sheath is simply split into two fresh sheaths by the development of an intercellular septum.

(II) The inner investment, which is possibly the only one in young stages, is regarded as a modified plasmic membrane of a viscous, gelatinous nature; the cell-sheath is probably a modified innermost layer of the external mucilaginous sheath and unlike the inner investment is dissolved by chromic acid, except in the almost mature spore.

[1]) As already mentioned the higher heterocystous forms have not been fully examined, but it may be well to point out that the heterocystous forms in Kirchner's *Scytonemataceae* (98, p. 78, fig. 57 C and D for instance) appear to have the same moniliform structure of the cell-sheath of the filaments inside the external sheath as *Tolypothrix*. *Plectonema* (loc. cit. fig. 57 A), which is devoid of heterocysts on the other hand appears to exhibit a structure like that of *Lyngbya*. All these forms will be treated of subsequently in greater detail.

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(III) Exospore and endospore of the spore are merely the fully developed cell-sheath and inner investment respectively. both of which in the mature condition completely envelope the protoplast. This does not agree with previous accounts of the development of the spore. In the spore of an *Anabaena* we find the same structure of the investment reoccurring, as we get in *Gloeocapsa* etc.

(IV) In *Oscillaria* the transverse septa are less developed than in *Anabaena* and consequently the cell-sheath is not split during division, but forms a coherent whole round the entire filament. Its composite character is still indicated by a slight constriction at each transverse septum.

(V) The sheath of an *Oscillaria* and *Lyngbya* are two entirely different structures, the former as just stated being the coherent cell-sheath, whilst the latter is homologous with the external mucilage of *Anabaena* etc. Within this latter sheath the filaments of *Lyngbya* present a structure, identical with that of *Oscillaria*.

(VI) In *Tolypothrix* and *Rivularia* on the other hand the actual filament (within the external sheath) is provided with a cell-sheath, which is only in part coherent and shows a very marked moniliform structure.

(VII) The intercellular protoplasmic connections of many observers are due to changes, produced in the gelatinous transverse portion of the inner investment during staining. Protoplasmic connection is unnecessary, as diffusion can probably take place through the cell-membrane.

University College London
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Description of the figures on plate VII.

(It was found necessary in many cases to use high magnifications. — Zeiss's apochromatic 3,0 mm, Apert 0,95 and compensation eye-piece 12 or 18 being mostly employed. All the figures were drawn with the help of an Abbè drawing apparatus. The following symbols are made use of to denote different points in the figures; *c. s.* = cell-sheath: *i. i.* = inner investment: *e. s.* = external sheath: *t. s.* = transverse septum: *ex* = exospore; *en.* = endospore: *h.* = heterocyst).

Fig. 1 and 2. Small portions of filaments of *Anabaena*, stained with methyl blue: the transverse septa are curiously contracted, so as to resemble protoplasmic connections. (× about 2300.)

Fig. 3. Two young cells of a species of *Nostoc* in process of division: the inner investment is not indicated, *a* transverse septum (*t. s.*) just appearing and cell-sheath constricted: *b* Division complete: cell-sheath of each cell evident, being separated by the thick colourless transverse septum. (× about 2500).

Fig. 4. An ordinary vegetative filament of *Anabaena* in the unstained condition. The cells are separated by well-marked transverse septa. (× 1450.)

Fig. 5. Portion of a vegetative filament of *Anabaena*, stained with Iodine. The cells are separated from one another by well-marked transverse septa (*t. s.*) and the cell-sheaths (*c. s.*) are seen to be individual to each cell. Within these latter is a well-defined inner investment (*i. i.*), continuous with the transverse septa. Note that at the lower end. which represents the termination of a filament, the cell-sheath extends right round the one end of the cell. (× 2300 about.)

Fig. 6. Three spores of *Anabaena*, showing exospore (cell-sheath) and endospore (inner investment), and separated from one another by a well-marked space. (× 1450.)

Fig. 7. Sporogenous cell of *Anabaena* with contents in process of protrusion. The liberated portion is surrounded by a new inner investment, whilst the outline of the open end of the cylindrical cell-sheath runs round the approximate equator of the protoplast. (× 1450).

Fig. 8. Small portion of the sporogenous filament of *Anabaena* (with almost mature spores): the uppermost cell has the inner investment produced into a papilla terminally, which is plainly surrounded by the one end of the cell-sheath. (× 1450).

Fig. 9. Division of a cell of *Gloeocapsa*, showing the transverse septum and the contricted cell-sheath, which is as yet not split. (× about 1600.)

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Fig. 10. Basal portion of a filament of *Gloeotrichia natans* (Hedwig) Rabenh., showing the coherent. but markedly constricted cell-sheath and the basal heterocyst (*h*). (× about 1600).

Fig. 11. Part of a filament of *Oscillaria Fröhlichii*, showing the coherent cell-sheath. The constrictions are rather exaggerated. (× 1450.)

Fig. 12. Part of a filament of *Tolypothrix* in the living, unstained condition, in which no cell-sheath is visible within the external sheath (*e. s.*). A small portion of the filament has died away through injury, leaving the prominent transverse septa (*t. s.*). The exposed apices of the filament are covered by the much-thickened cell-sheath. (× 1450).

Fig. 13. Small portion of a filament of *Tolypothrix*, treated with Iodine. The central filament has contracted away from the external sheath and its coherent, but moniliform cell-sheath and the inner investments of the protoplasts are now quite visible. (× about 1600).

Fig. 14. Living, unstained filament of *Tolypothrix*, illustrating repeated sheath-formation; see text p. 42. (× 1450.)

Fig. 15. Portion of a filament of *Tolypothrix*, treated with chromic acid. The filament has contracted away from the external theath (*e. s.*): the cell-sheath has been dissolved away and only the inner investment remains (*i. i.*). The protoplasmic contents have all disappeared except for a few globules in each cell. (× 1450.)

Fig. 16. Small portion of a filament of *Lyngbya salina* Ktz.. showing the wide hyaline external sheath, the coherent cell-sheath and the delicate inner investments around the protoplasts. (× 600 about.

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