

False branching and sheath-structure in the Myxophyceae, with special reference to the Scytonemataceae^{1).}

By

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(With 9 figures in the text.)

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1. Introduction.

In a species of *Aulosira* (*A. pseudoramosa*), recently described by the writer (4), reproduction takes place by means of hormogones which, after undergoing a resting period within the sheath of the parent-filament, germinate *in situ*, the first step being the secretion of a new sheath which entirely surrounds them. Hormogones adjacent to the open end of the sheath of the parent grow out direct, whilst intercalary hormogones pierce the parent-sheath which

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at this stage has become hard and brittle. Short hormogones always ultimately emerge completely from the sheath, but long ones remain to a large extent enclosed within it, although their free ends project more or less markedly. The latter condition is found especially when the hormogone has already grown to some extent within the parent-sheath before its tip pierces the latter; such growth is possible when there is an empty space adjacent to the hormogone resulting from the death of certain cells of the parent-trichome. If a germinating hormogone of the *Aulosira* emerges in this way at the side of a heterocyst, an appearance resembling the branching of a *Tolypothrix* is obtained, while when two such hormogones emerge on either side of a dead cell or of a disc of intercellular substance, we have the appearance of a branching *Scytonema*. The germinating hormogones in this species thus simulate the appearance of a typical member of the Scytonemataceae and, without a knowledge of the mode of development, the alga would have been regarded as a form showing false branching.

As previously stated, the hormogones become completely enveloped by a new hyaline sheath before germination commences. It seemed desirable to compare such hormogones with the pseudobranches of the Scytonemataceae and with this object in view a large number of forms showing false branching were examined. The primary object was to determine whether the individual sheaths of the false branches completely enveloped them as in the hormogones of the *Aulosira* just described or, alternatively, how far they could be traced back into the parent-filament. It was found in all cases that the sheath of the false branch only extends back a short distance into the parent-filament and that, after thinning down gradually, it always ends blindly. This observation gave a further impetus to study in greater detail the origin and mode of development of the false branches and of their sheaths in the Scytonemataceae and certain other falsely branched Myxophyceae, as well as the formation and germination of hormogones and hormocysts. I am indebted to Prof. F. E. FRITSCH for suggesting this line of investigation.

The literature hitherto published does not contain any account of the mode of origin and development of the branch-sheaths, nor are there any clear illustrations showing its relative position with respect to the sheath of the parent-filament. AGARDH (1 and 2) who established the genus *Scytonema* and KÜTZING (27) who established *Tolypothrix* give no figures that afford information on this point.

The same is true of the figures to be found in LYNGBYE (30), HASSALL (26), WOOD (39), RABENHORST (32), BORZI (8), COOKE (11), WOLLE (38) and many others, as well as in the more recent works of TILDEN (34), WEST and FRITSCH (37), etc. BORZI's figures of *Spelaeopogon*, *Seguenzaea* and *Diplonema* which are published much later (9) show the same lack of detail. BORNET and THURET (7) at one or two points in Pl. 34 Fig. 1 show the backward continuation of the sheath of the branch into the main filament as far as the next heterocyst, but there is no reference to the origin and position of the branch-sheaths in the text. The figure of *Scytonema amplum* published by W. et G. S. WEST (36) shows branch-sheaths quite clearly in the main filament, but it is not large enough to allow one to recognise how far they extend; the same is true of *S. mirabile* as depicted by LEMMERMANN (29, p. 198, Fig. 9).

GEITLER (23, p. 741) describes the formation of pseudobranches in *Scytonema*, but does not deal with the development of the new sheath and its relation to that of the parent-filament. The same lack of detail is found in ERCEGOVIĆ's (13) account of the formation of the looped branches in *Kyrtuthrix dalmatica* ERCEG. GONZÁLEZ-GUERRERO (25) deals only with the growth of the trichome in the pseudobranches of Scytonemataceae.

It thus appears that all workers have so far practically ignored the characters presented by the sheaths in the false branches of Myxophyceae. The facts here presented thus fill a gap in our knowledge of the morphology of Myxophyceae and are at the same time of some value in relation to their taxonomy.

2. Materials.

The subsequent observations were made mainly on a number of species of *Scytonema* and *Tolypothrix*, though a few other falsely branched forms were examined. The material was all collected in the Tropics or Subtropics, except for *Tolypothrix distorta* KÜTZ. var. *penicillata* THUR. which was gathered by Prof. FRITSCH from rocks on the shore of the Lake of Geneva in 1923. It included a few forms collected by the writer from North India, some collected by Prof. M. O. P. IYENGAR¹⁾ from South India, a number of species from Natal in Prof. FRITSCH's possession, and a large number of Scytonemataceae and certain other forms collected in Ceylon in 1903

¹⁾ I am indebted to Prof. IYENGAR for kindly handing over this material to me for investigation.

by Prof. FRITSCH. I am indebted to him for placing this rich collection at my disposal. All the material was preserved in weak formalin and was in excellent condition. A well-preserved slide (No. 903 B) of *Scytonema amplum* W. et G. S. WEST (collected from Dominica, West Indies), made by the WESTS and in the possession of the British Museum (Natural History) was also examined.

Although a very large number of forms has been examined, only a few are cited in the subsequent matter for the sake of brevity¹⁾.

3. The general characters of the sheath and the method of investigation.

The sheaths were coloured in most of the species examined. A permanently hyaline and comparatively thin sheath is found in forms floating in waters of some depth (e. g. *T. nodosa* and *S. simplex*), while aquatic species subjected to casual or periodic changes in the environmental conditions (e. g. *S. mirabile* f. *minor*) have hyaline sheaths which are occasionally slightly coloured. On the other hand forms growing in subaerial habitats never have a permanently hyaline sheath, as the latter always becomes coloured to a varying extent at an earlier or later stage. The pigmented sheath in these cases is fairly hard and it is likely that during dry periods it protects the contained trichomes from desiccation. In certain forms, moreover, hormogones pass through a period of rest within the parent-sheath. It is probable too that in all such cases the pigmented sheath acts as a light screen, as suggested by LEMMERMANN (29, p. 6).

The pigmentation either appears simultaneously throughout the thickness of the sheath (e. g. *S. myochrous* forma and *S. Fritschii*) or it originates in the inner layers and gradually extends to the

¹⁾ The forms investigated and referred to in this paper are as follows. *Calothrix ramosa* sp. nov.; *Fischerella anomala* sp. nov.; *Scytonema amplum* W. et G. S. WEST; *S. Bewsii* FRITSCH and RICH; *S. dilatatum* sp. nov. and f. *major*; *S. Fritschii* GHOSE, *S. Geitleri* sp. nov. and var. *tenuis* var. nov.; *S. guyanense* (MONT.) BORN. et FLAH., var. *prolifera* var. nov.; *S. Hofmanni* AG., var. *crassa* var. nov.; *S. Millei* BORN. forma; *S. mirabile* (DILLW.) BORN. and f. *minor*; *S. multiramosum* GARDNER, var. *ceylonica* var. nov.; *S. myochrous* (DILLW.) AG. and forma; *S. Pascheri* sp. nov.; *S. pseudoguyanense* sp. nov.; *S. pseudohofmanni* sp. nov. and forma; *S. saleyeriensis* WEBER-VAN BOSSE, var. *indica* var. nov.; *S. simplex* sp. nov.; *S. tolypothrichoides* KÜTZ. f. *terrestris*; *Tolypothrix distorta* KÜTZ. var. *penicillata* THUR. and var. *samoensis* WILLE; *T. magna* sp. nov.; *T. nodosa* sp. nov.; *T. tenuis* KÜTZ. forma. The descriptions of new species and varieties will follow in paper to be published in the Rev. Algologique.

outer ones. In the latter case the mature sheath may ultimately become coloured throughout (*S. saleyeriensis* var. *indica*, *S. Geitleri* var. *tenuis*) or a thin outer layer remains uncoloured (e. g. *S. pseudoguyanense*, *S. Millei* forma). The colour is yellow, yellow-brown or golden-brown and in some cases pure brown or dark brown. The nature of the pigment is not known, but it does not appear that iron compounds are concerned as no reactions have been obtained with the usual iron-tests.

Whenever a branch, hormogone or hormocyst are formed or when the terminal portion of a filament resumes growth after a period of rest or after it has been accidentally ruptured, a new sheath is secreted and this is always hyaline. The interval that elapses before the pigment appears varies in different cases. In a form of *S. myochrous*, described by FRITSCH and RICH (19), pigment appears immediately after the secretion of the new sheath so that even very short branches, which have just pierced the parent-sheath, have a yellow-brown or sometimes even a dark brown sheath. This, however, is the only case of the kind that has come to my notice.

The sheath in all cases shows affinity for basic aniline dyes and is readily stained with aqueous methylene blue, aqueous safranin, ruthenium red and other pectic stains (cf. 28). A hyaline sheath always assumes a much deeper colour than a pigmented one which in fact sometimes appears not to stain at all; it may be, however, that the pigment masks the stain. As has long been known, chlor-zinc-iodide stains the sheath in some forms but not in others. It thus appears that the sheath always contains pectic substances, but in some cases these are accompanied by cellulose probably in a combined state (cf. 28). Sheaths, which stain blue or violet with chlor-zinc-iodide, do so as soon as they are formed, so that the cellulose-constituent is present in them from the very beginning. The capacity to take up stains gradually decreases as the sheath becomes pigmented.

Since in most cases the sheath was coloured and sometimes deeply coloured, it was often so opaque that the new hyaline sheaths of branches, hormogones etc. lying within that of the parent could not be distinctly observed even after staining. It was therefore necessary to find a means to remove the pigment without otherwise affecting the sheath. Several reagents, such as acetic acid, caustic potash, hydrogen peroxide, dilute mineral acids and Eau de Javelle, were tried, but the only effective one was the last. Even this acted very slowly in most cases, since even after several

weeks immersion there was still some trace of colour left. After treatment with Eau de Javelle the material was thoroughly washed with water and stained with either aqueous methylene blue or aqueous safranin which coloured the new hyaline sheath deeply, while the parent-sheath was only slightly coloured. In this way the new sheaths could be distinctly seen through the parent one. Where the part of the branch-sheath situated within that of the parent was also coloured, the same treatment gave satisfactory results in most cases, for the two sheaths showed some differentiation after staining owing to their originally possessing different depths of pigmentation. In those few cases, where branch- and parent-sheath were both deeply pigmented, treatment with Eau de Javelle removed most of the pigment and after staining the two could be distinguished.

Differentiation between the old and new sheaths was further facilitated by the usual presence in the preserved material of a space of diverse width between sheath and trichome, as well as between the sheaths of the parent and of the branch or hormogone, especially in filaments which were rather old and in an unhealthy condition. In many cases further the cells in such filaments contracted when treated with chlor-zinc-iodide, so that the sheaths became more distinct.

Prolonged treatment with Eau de Javelle has the one disadvantage that it gradually dissolves the cell-contents and ultimately even the cell-walls, leaving the filament empty. The walls of heterocysts are not affected, though the contents are dissolved. This difficulty was overcome by examining the material periodically during its immersion in the Eau de Javelle. In some cases, however, it was necessary to destroy the trichomes in order to make the sheaths clearer. It was sometimes difficult to distinguish distorted and compressed heterocysts from degenerate cells of similar shape, especially when the former had relatively thin walls and lacked terminal granules, but after treatment with chlor-zinc-iodide (with or without previous treatment with Eau de Javelle) the inner walls of heterocysts assumed a deep violet colour in all cases (cf. 21, p. 227). The only alga in which this result was not obtained in spite of several trials was *Scytonema mirabile* f. *minor*.

4. General data on the mode of growth of the sheath.

In the terrestrial forms here considered the apical growth of the filaments does not appear to be continuous, but no doubt takes place periodically with intervals of rest. These may be of shorter

or longer duration, corresponding either merely to the hot period of the day or to an interval of several days, while during prolonged dry spells they may be of much longer duration. When the filament (Fig. 1 A) starts growth after a brief interval of rest, the elongating apex of the trichome ruptures the closed end of the sheath (Fig. 1 C s) and, as it emerges, secretes a new sheath (to be called lamella) of its own. In some cases the new sheath is formed before it ruptures the old sheath (Fig. 1 B n). The new sheath or lamella (Fig. 1 D n) not only covers the apex of the new extension of the trichome, but also continues backwards for some distance into the old filament, internal to its sheath, thinning down gradually and ultimately ending blindly. With each period of elongation of the trichome the same events occur and each time a new lamella is formed. There is thus an interval between the secretion of two successive lamellae. The successive lamellae of the increments diverge from the trichome and lie successively within the next older ones which have been ruptured apically by the elongation of the trichome (Fig. 1 E). Eventually they become compressed to form the different layers of the firm thick sheath which surrounds the older portions of the trichome and which is therefore compound in origin. The layers (lamellae) in the sheath are thus in large part at least an expression of successive periods of growth and each extends for a varying distance

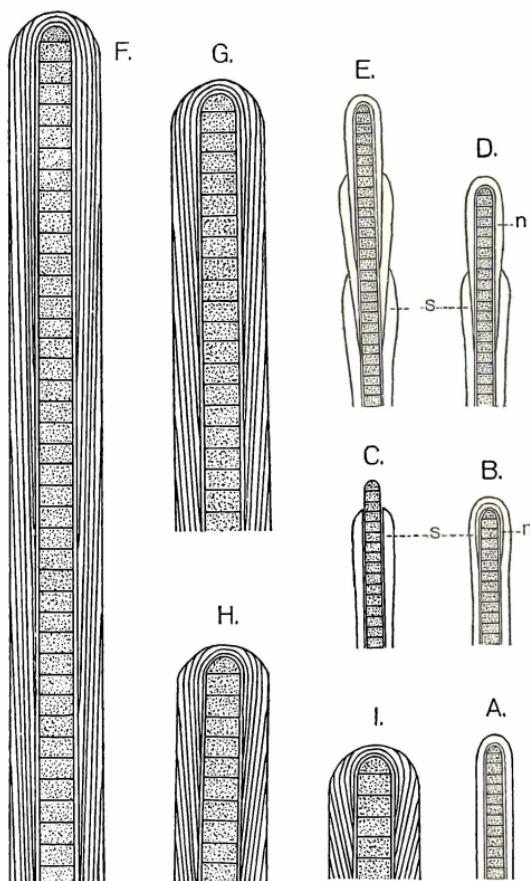


Fig. 1. A—E diagrams illustrating the growth of a filament and the formation of the new sheath at the apex; F—I diagrams illustrating different degrees of divergence of the strata of the sheath in relation to the rate of growth of the filament.

n new sheath or lamella; s parent-sheath.

to end blindly on the one hand at the surface of the sheath, on the other hand at its inner margin.

When during active periods the cells divide rapidly and growth is considerable the new increments of the trichome are long, and successive lamellae of the sheath are of appreciable length, while when growth is slow both may be very short. In the former case the successive lamellae which form the internal strata of the compound sheath in the older parts of the filament extend for long distances and appear to be parallel (Fig. 1 F), while in the latter case they constitute short strata which present a markedly divergent appearance (Fig. 1 H and I). In reality the lamellae of the sheath diverge in both cases and each corresponds to a period of growth. Even in the sheath with apparent parallel strata, if the lamellae are traced towards the apex of the filament, they are found successively to terminate at the surface, the next underlying lamella then becoming the external layer of the sheath. A cursory observation of the case shown in Fig. 1 F would lead to the conclusion that the stratification of the sheath was parallel, especially if only a short portion of the filament were examined, but the stratification is really divergent, though not as prominently so as that seen in Fig. 1 H and I. Fig. 1 F and I are drawn on the same scale, the rate of the growth of the filament in F being supposed to be eight times that of the filament in I, and this leads to the difference in the angle of divergence of the lamellae in the two cases. Sometimes when filaments possessing an apparent parallel stratification in the sheath are bent so that layers are split (*Scytonema saleyeriensis* var. *indica*, Fig. 2 B) the divergent nature of the stratification becomes apparent.

Not uncommonly in the filaments of certain forms one observes occasional points where the filament narrows quite abruptly, so that two distinct portions, narrow and broad, are recognisable (e. g. *S. saleyeriensis* var. *indica*, Fig. 2 C and *S. myochrous*, Fig. 2 H) (cf. also 23, Fig. 498 a). Though the sheath of the broader part usually extends over the narrower one in such a way as to make the outer surface more or less smooth, a swelling or joint of varying magnitude is evident, especially in forms with thick sheaths. There may also be a distinct line of demarcation between the two portions, as in Fig. 2 J. If the sheath is comparatively thin a distinct rupture of the sheath of the older portion is sometimes recognisable (*Tolypothrix distorta* var. *samoënsis*, Fig. 2 F). The narrower portion is clearly emerging from the broader part as a new extension. The trichome has recommenced growth after a period of rest, secreting a new sheath

of its own and bursting through the apex of the old sheath; the original rounded contour of the latter is still distinctly recognisable at some joints (*Scytonema myochrous*, Fig. 2 H). Moreover, in forms with coloured sheaths (except *S. myochrous*) the new extension at first always possesses a hyaline sheath. The joints thus produced are very conspicuous when the extensions are newly formed, but as the latter grow in thickness the former gradually disappear (*S. multiramosum* var. *ceylonica*, Fig. 2 L). Quite the same features are seen where growth is resumed by a trichome after one or more cells at its apex have degenerated and died, which in terrestrial forms is probably a result of desiccation (Fig. 2 E of *S. pseudohofmanni*).

All the species examined, moreover, occasionally show places where the filament narrows down suddenly without the formation of a swollen joint, the narrower portion again appearing as the extension of the broader one, with the same difference in colour of the sheaths in forms with coloured sheaths. It appears that the broader portion has been broken across accidentally before giving rise to the new extension, since its sheath clearly shows a ruptured end and does not cover that of the new growth so as to smooth over the difference in thickness between the two (e. g. Fig. 2 G; cf. also 7, Pl. 34 Fig. 1 and 19, Fig. 23 E); in such cases the line of demarcation is often wavy and irregular (Fig. 2 M and K). Such joints do not usually subside altogether, though in later stages the projecting edge of the sheath of the main filament becomes more or less rounded (e. g. *S. Hofmanni* var. *crassa*, Fig. 2 A; cf. also Fig. 2 G).

In the various cases just considered the terminal portion of the trichome when it starts to grow afresh secretes a new lamella either before breaking through the tip of the parent-sheath (*Tolypothrix distorta* var. *samoënsis*, Fig. 2 F, 1; cf. also Fig. 4 G, 1) or after it has grown out of the confines of the parent-sheath (*Scytonema dilatatum*, Fig. 2 I and D), and the sheath of the new extension subsequently develops in the way described at the outset of this section.

The sheath is therefore in all cases formed by apposition of successive layers and each stratum represents an individual sheath or lamella, as was described by CORRENS (12) in *Petalonema alatum* BERK. (cf. also 23, Fig. 507). Although the growth of the filaments is mainly apical, some division of cells in the older parts also takes place; at such points it is possible that enlargement of the sheath takes place also by intussusception. Since the rate of growth of the filament determines the appearance of the stratification in the sheath many intermediate stages between a distinctly divergent sheath

and one with apparent parallel stratification may be found (cf. Fig. 1G). The degree of divergence will depend on the amount of growth made in successive periods of activity and may vary in different

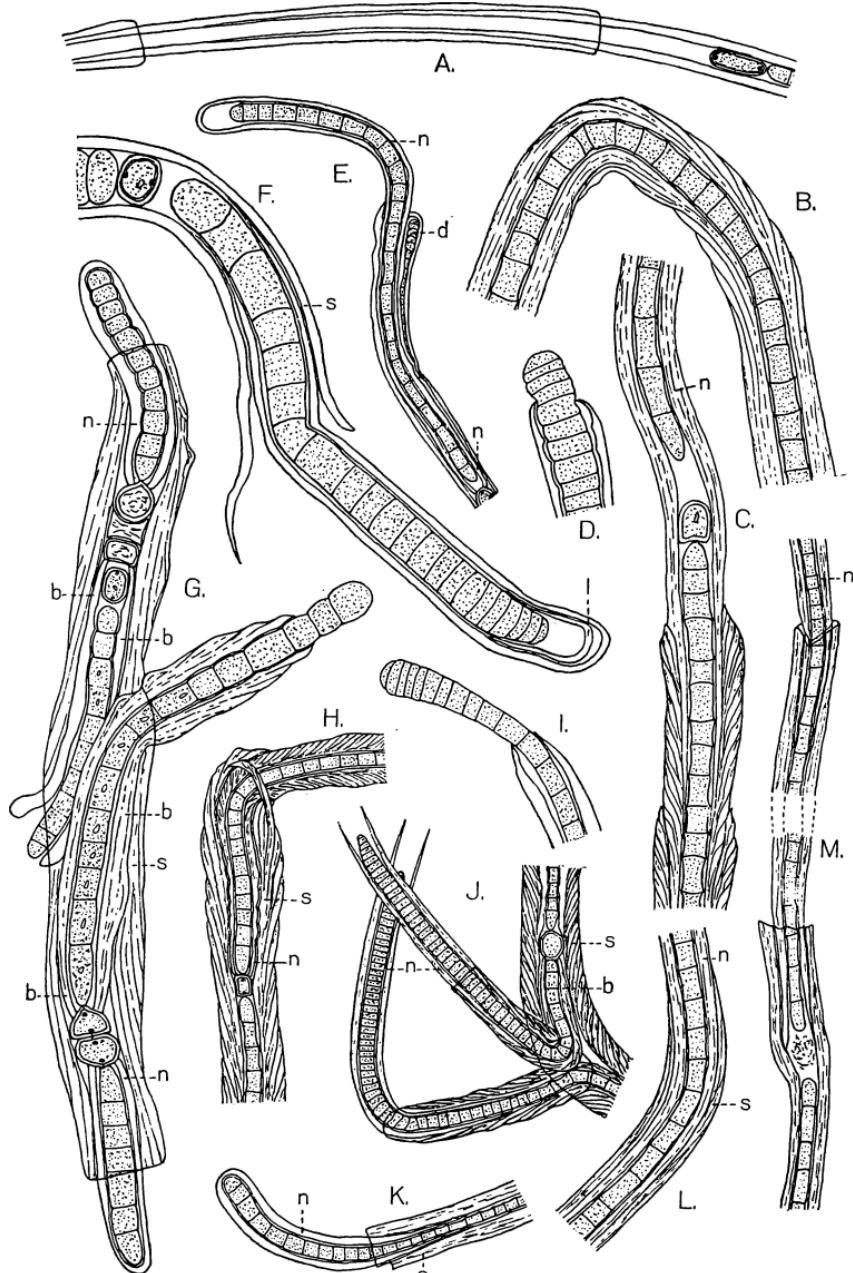


Fig. 2. A empty filament of *Scytonema Hofmanni* var. *crassa* showing renewed growth of the sheath after two successive periods of rupture. B and C, *S. saleyiensis* var. *indica*; B with divergent stratification only at the bend, C with new

growth possessing a sheath with parallel stratification, also two joints, produced after successive prolonged resting periods. D and I apices of filaments of *S. dilatatum* showing growth of trichome beyond the confines of the parent-sheath. E the same of *S. pseudohofmanni* showing renewed growth of trichome after the death of a number of apical cells (d). F the same of *Tolypothrix distorta* var. *samoënsis* showing rupture of parent-sheath and formation of a new lamella (l) at the apex. G *Scytonema mirabile* showing renewed growth after rupture and two pseudobranches arising on opposite sides. H *S. myochrous* showing a swollen joint produced on renewal of growth after a period of rest. J *S. myochrous* forma showing renewed growth with indistinct parallel stratification of the sheath of branches after a period of rest. K and L *S. multiramosum* var. *ceylonica*; K renewed growth after rupture; L showing disappearance of joint as a result of thickening of the sheath of the new growth produced after a period of rest. M. renewed growth of a filament of *S. amplum* after two periods of rupture, the joints displaying the broken edges of the successive older sheaths. b branch-sheath; d dead cell; l lamella; n new sheath; s parent-sheath. A—F, I, K and L $\times 430$; G $\times 590$; H, J and M $\times 270$.

parts of a filament. When environmental conditions become adverse divergent stratification becomes evident.

The lamellae or sheaths of the successive new extensions in all cases continue backwards into the main filament for some distance, thinning down gradually and ultimately ending blindly. If there is a heterocyst near at hand the lamella may extend up to it, but it never encloses it (Fig. 2 E, G and H, n.). The same is true of the sheaths of pseudobranches which will be described later. The heterocysts are, therefore, incapable of secreting a sheath around themselves. If a heterocyst (terminal or intercalary) is found to be covered by a sheath it may be taken for granted that it was differentiated from a vegetative cell of the trichome after the latter had become enveloped by the sheath, i. e. the sheath was secreted prior to the formation of the heterocyst. These observations will be substantiated in the subsequent account.

The concept that the layering of the sheath is related primarily to successive growth of the trichome requires to be verified by an observation of living material which it has not yet been possible to undertake. The hypothesis, however, fits in with all the ascertained facts and, whether the suggested explanation is correct or not, there is no doubt that a stratified sheath in the heterocystous forms here considered is always divergent in nature.

5. The stratification of the sheath.

The sheaths of Scytonemataceae are either thin or thick, those of the latter type varying in thickness not only in different forms but also, in some cases, in different parts of the same plant. Old

filaments with unhealthy trichomes usually possess thicker sheaths than normal healthy ones. Thick sheaths are either stratified or unstratified. Unstratified sheaths are usually met with in submerged forms. In some of these the sheath is differentiated into an inner firmer and an outer diffluent portion (*Tolypothrix helicophila* LEMM., *T. polymorpha* LEMM.), as the writer (4) has observed to be the case in unbranched forms like *Aulosira Fritschii* and *A. prolifica*. In a form of *Scytonema Millei*, growing on roots projecting into water, the hyaline sheath is at first homogeneous and rather soft, but sooner or later a thin outer layer becomes firm (Fig. 5 B, o.), whilst much later the same change affects the thick inner portion which at the same time becomes pigmented from the inside towards the outside and develops parallel stratification (Fig. 5 C, i.). Even in some subaerial forms no stratification is recognisable in a hyaline sheath or in hyaline portions of the sheath, but as soon as the latter show pigmentation stratification becomes evident. In the opinion of the writer thick sheaths are always stratified and formed in the way described in the last section, but in some cases the stratification is not visible, probably owing to the more or less diffluent nature of the layers. Pigmentation is accompanied by hardening of the sheath and it is probably this change that makes the stratification evident in pigmented sheaths.

The thick sheaths of subaerial forms are usually stratified and such sheaths are also met with in some of the aquatic forms. The stratification is distinguished as having either parallel (cf. Fig. 1 F) or divergent (cf. Fig. 1 H and I) layers according as the latter run approximately parallel to the outer surface of the sheath or form a more or less pronounced angle with the margin. Much diagnostic value has been attached to this feature, BORNET and FLAHAULT (5, pp. 86—89) classifying the species of *Scytonema* into the sections *Euscytonema* with sheaths which are unstratified or show parallel stratification, *Myochrotes* with sheaths showing divergent stratification, and *Petalonema* with thick sheaths having highly divergent funnel-shaped layers. The same classification has been adopted by LEMMERMANN (29) and GEITLER (23), except that they have followed MIGULA (31, p. 131) in regarding *Petalonema* as a distinct genus.

Among the described species of *Scytonema* and *Tolypothrix* the majority having stratified sheaths possess parallel stratification. Distinct divergent stratification is only found in *Scytonema myochrous* (DILLW.) AG., *S. crassum* NAEG., *S. crustaceum* AG., *Tolypothrix scytonematoidea* GARDNER, *T. byssoides* (HASS.) KIRCHN. var. *polycladus* FRÉMY, *T. arboricola* FRÉMY, and *T. fragilissima* ERCEG. all of which are

terrestrial forms. The species of *Petalonema* are all likewise terrestrial, with the exception of *P. involvens* (A. Br.) MIGULA. This species, found on aquatic plants in marshes, possesses indistinct layers in the outer portion of its sheath and is scarcely quite comparable to the others. Among the forms examined by the writer only two (i. e. *Tolypothrix magna* and *Scytonema myochrous* forma) possess distinctly divergent sheaths and these are likewise terrestrial. There is in fact no record of a purely aquatic form showing distinct divergent stratification in the sheath.

Parallel stratification on the other hand appears in forms growing both in aquatic and terrestrial habitats. It may therefore be inferred that distinct divergent stratification is related in some way to the conditions realised in more extreme terrestrial habitats and that under other less extreme conditions parallel stratification results. The frequent high temperature and the repeated scarcity of water in terrestrial habitats, particularly in the Tropics, must undoubtedly often check the growth of the forms in question and this is believed to cause the development of the divergent stratification which would thus be conditioned by slow and repeatedly checked growth. The data on the distribution of the two types of stratification thus confirm the view put forward in the last section that it is the rate of growth of the filament that determines the type of stratification of the sheath. A sheath, which is markedly divergent throughout (*S. myochrous*), is only to be expected in forms which occupy permanently an extreme terrestrial habitat. This view is further supported by the presence of intermediate stages between a distinctly divergent sheath and one possessing apparent parallel stratification. Such are seen in *S. mirabile*, collected from stone-work during the rainy season in one of the wettest parts of Ceylon and also in a form of *S. mirabile* described by FRITSCH and RICH (19, p. 366), growing on rocks in a quiet pool in a stream and presumably subjected to a varying water-level; in both the sheaths possess only slightly (yet distinctly) divergent strata (Fig. 3 B and C and Fig. 2 G; cf. also Fig. 1 G).

Divergent stratification may sometimes appear quite suddenly at the apices of terrestrial forms or at other points in a filament which for the rest has a sheath with distinct or indistinct parallel stratification. For example, in *Scytonema saleyeriensis* var. *indica* the sheath usually shows parallel stratification (Fig. 3 H), but at the apices a very distinct divergent stratification is seen (Fig. 3 A). Similar divergent stratification has also been observed at the apices

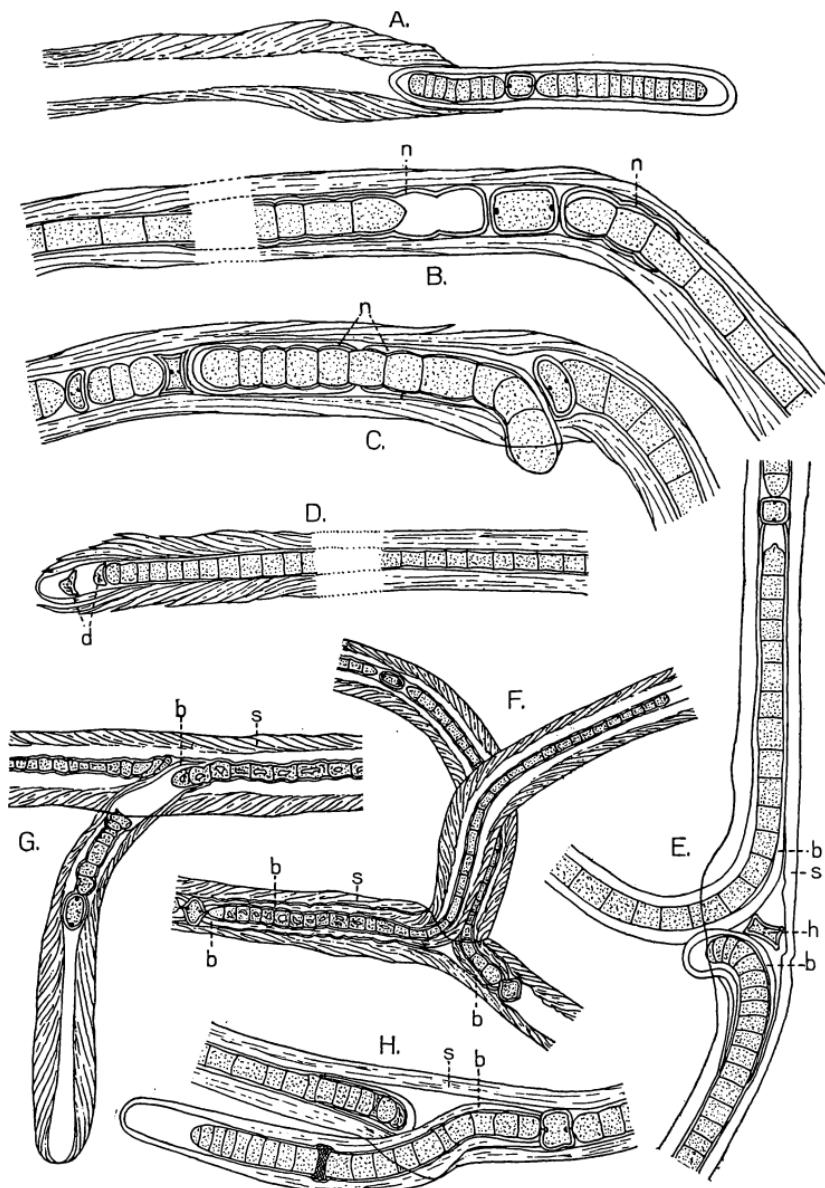


Fig. 3. A and H *S. saleyeriensis* var. *indica*; A with divergent stratification and emerging hormogone; H with parallel stratification in the sheath. B and C *S. mirabile*; B showing formation of a new sheath over the free ends of the segments before growth commences; C showing a stage before the fusion of the new sheaths has occurred. D *S. pseudohofmanni* forma showing divergent stratification at the apex only. E *Tolyphothrix distorta* var. *samoënsis* showing production of pseudo-branched on either side of a two-pored heterocyst. F and G portions of branching filament of *Scytonema myochrous* forma. b branch-sheath; d dead cell; h heterocyst; n new sheath; s parent-sheath. A, G and H $\times 430$; B-D $\times 590$; E and F $\times 270$.

of a form of *S. pseudohofmanni* (Fig. 3 D). Such cases can also be found in the literature. Thus GARDNER (20, p. 81) records the presence of faintly divergent layers at the growing apices of old plants of *Scytonema multiramosum*, as well as in a form described as *S. catenulum* (l. c. Pl. 17 Fig. 34) in which the sheath is normally slightly gelatinous and unstratified. These cases illustrate the presence of occasional divergent layers at the apices of the sheaths and are probably to be explained as resulting from a period of slow growth of the alga, probably as a result of unfavourable conditions (drought in a terrestrial form) which usually are first experienced at the apices.

It is probable that, as a result of very acute conditions, a thick and highly divergent sheath may be formed at the apices before apical growth stops altogether. Such apices are sometimes associated with the presence of one or more dead terminal cells (Fig. 3 D, d) which indicate how extreme the attendant conditions must have been. Such threads no doubt undergo a period of prolonged dormancy, contrasting sharply with the short periods of rest that are believed to occur between the formation of successive lamellae in the ordinary sheath. With the advent of conditions favouring rapid growth, the trichome recommences to elongate and the sheath of the new extension, narrower than the old, may either possess a (distinct or indistinct) parallel (cf. Figs. 2 C and 23, Fig. 298 a) or a marked divergent stratification according to the conditions under which this resumed growth takes place.

Similarly parallel stratification may also appear in the new growth of a filament which possesses a distinctly divergent sheath. An example is afforded by a form of *S. myochrous* which normally possesses distinctly divergent layers both in the main filament and in the branches (Fig. 3 F and G), but when the apex of a branch recommences growth the sheath of the newly formed portion shows indistinct parallel stratification (Fig. 2 J).

It is quite clear from the above discussion that the same form may exhibit different types of stratification in its sheath when growing under different conditions or that two plants differing only in the nature of the stratification of the sheath may be merely habitat-forms of the same species. This leads to the inference that the character of the stratification in the sheath of a particular form may not always be a constant feature and therefore not always a reliable diagnostic character.

It was stated above that submerged forms do not possess divergent stratification, but in *Scytonema Bewsii* FRITSCH and RICH (19, p. 364) and *S. tolypothrichoides* KÜTZ. the occasional presence of divergent layers has been recorded. A careful examination of the former, which is aquatic and therefore shows no divergence at the growing apices, indicates that divergence of strata appears at places where the filament restarted growth after a period of rest, especially where the edge of the old ruptured sheath becomes amalgamated with the new one (cf. Fig. 2L). Such divergence is, however, merely due to the gradual narrowing down of the sheath of the new growth which extends for some distance into the main filament. KÜTZING (27) does not figure *S. tolypothrichoides* and the only drawing that appears to correspond to his description is that of FRÉMY (16, Fig. 267; cf. also GEITLER 23, Fig. 500)¹⁾. Here the growing apices show practically no stratification and the indistinct divergence is again only recognisable in the older parts of the filaments. The former feature, as in the case of *S. Bewsii*, is quite in conformity with the aquatic habitat, while the faintly divergent strata in the older parts scarcely differ from what can occasionally be observed in other forms with mainly parallel stratification.

6. Methods of false branching.

The formation of false branches is usually initiated by the degeneration of an occasional cell of the filament whose trichome thus becomes divided into two segments, the free ends of which grow out of the parent-sheath and develop as branches. Both segments may grow out simultaneously or one after the other, or only one of them may develop into a branch. Sometimes in place of a single degenerating cell there may be several, forming a short row and either fused together or separate from one another. The form of such cells varies in different cases and appears to be largely dependent upon the amount and the direction of the pressure exerted on them by the adjacent growing segments of the original trichome. A degenerating cell between two segments which are growing equally is at first usually somewhat biconcave, but later as the segments grow out to form branches the margin adjacent to them undergoes compression and the cell in optical section comes to be roughly triangular. Such cells which have slightly thickened

¹⁾ The *S. tolypothrichoides* drawn by BRÜHL and BISWAS (10, Fig. 19c) is so unlike KÜTZING's description that it almost certainly belongs to another species.

walls and usually indistinct granular contents, sooner or later disintegrate and disappear.

In other cases the trichome becomes segmented by the secretion of biconcave discs of intercellular substance of a dark green colour between two cells; such discs usually take on a deeper stain with dyes than the adjacent cells. More rarely it is the formation of intercalary (two-pored) heterocysts (usually single, rarely more than one) that conditions the breaking up of the trichome into segments, one or both of which may then grow out to form branches (*Tolypothrix distorta* var. *samoënsis*, Fig. 3 E, h; cf. also GARDNER 20, Pl. 20 Figs. 47—50). Such heterocysts occurring at the points of branching are never in a healthy condition and it is probable that the trichome separates from them only when their contents begin to degenerate. Like the degenerating cells they may assume different forms when compressed by the outgrowing branches. Not uncommonly trichomes become segmented as a result of the degeneration of a cell or cells adjoining such heterocysts, which may be in a healthy or unhealthy condition; in this case the heterocysts may remain more or less firmly attached to one segment, while the other grows out into a branch.

In some cases, when the segments are formed by the degeneration of a cell, the free end of one segment may develop into a branch, while the adjacent end-cell of the other becomes transformed into a one-pored terminal heterocyst (e. g. *Tolypothrix tenuis* forma, Fig. 4 A; cf. also 23, Fig. 461, d and e; and 15, Pl. 14 Fig. 49). When no remnants of the original degenerating cell are left in the parent-filament, such a branch appears to have arisen by the side of a terminal heterocyst which has, however, in reality been formed secondarily, as for example in *T. nodosa* (Fig. 4 C). In the material studied in the present investigation no instance has been found of the development of a one-pored heterocyst in the middle of a trichome before the latter has undergone segmentation; in other words such heterocysts, when present, always showed either an adjoining biconcave intercellular disc or a dead cell or at least a smaller or larger space formed by the dying away of such cells before the segment adjoining that terminating in the heterocyst had grown out to form a branch. A similar observation has been made by the writer (4, Fig. 7 B) in unbranched forms like *Aulosira prolifica* and *A. pseudoramosa*. FRÉMY's figures (15 and 16) of various forms of *Tolypothrix* (incl. *Hassallia*) showing one-pored heterocysts immedia-

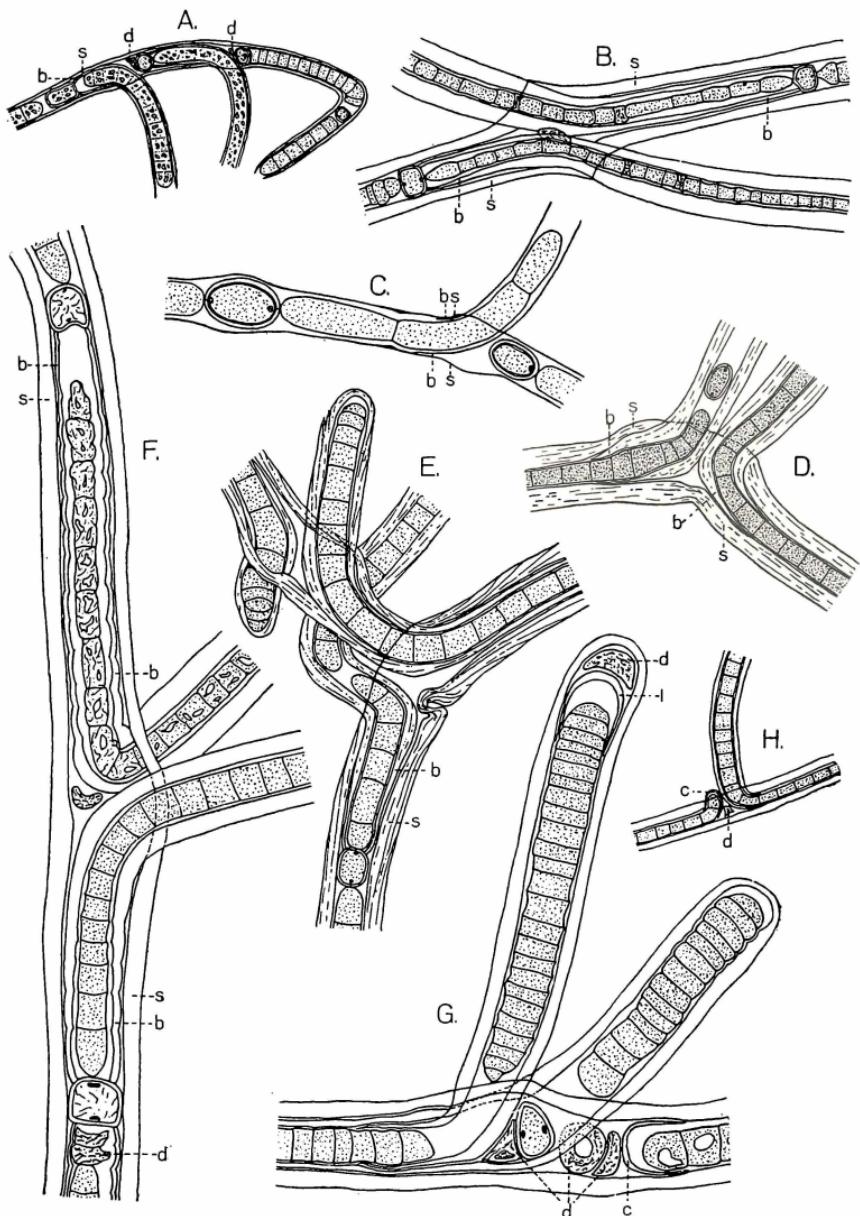


Fig. 4. A *Tolyphothrix tenuis* forma, with single branches arising at the side of dead cells adjacent to one-pored heterocysts; B *Scytonema pseudoguyanense* with two pseudobranches arising on opposite sides at about the same level; C *Tolyphothrix nodosa* showing a pseudobranch adjacent to a one-pored heterocyst; D *Scytonema dilatatum*, geminate branching; E *S. mirabile*, with one of the geminate branches forming secondary branches in the manner shown in B; F *S. Pascheri*, geminate branches arising through separate adjacent apertures in the parent-sheath; G *Tolyphothrix distorta* var. *samoënsis*, single branch producing a secondary branch from the part inside the parent-sheath; H *S. Hofmanni* var. *crassa*, formation of mucilage-cap over the free end of an emerging branch; b branch-sheath; c mucilage-cap; d dead cell; l lamella; s parent-sheath. A, B and H $\times 340$; C $\times 730$; D-G $\times 470$.

tely adjoining branches probably represent, in view of the above observations, advanced stages in which the dead cells between the heterocysts and the growing branches have disappeared. GEITLER'S figure of *Scytonema chiastum* (23, p. 751, Fig. 478 b), showing two one-pored heterocysts with an intervening dead cell, lends further support to this view. Similarly, in *Calothrix ramosa* the trichome becomes broken into two segments by the degeneration of a cell (Fig. 7 E, d) which ultimately disappears and, while the lower segment grows out to form a branch, the lowermost cell of the upper segment is transformed into a terminal heterocyst; or, if the first heterocyst happens to die the adjoining cell becomes a heterocyst and this may be repeated (Fig. 7 C, d, h; cf. also 4, Fig. 6 D).

The trichomes thus become segmented owing to the appearance of degenerating cells, biconcave intercellular discs or two-pored heterocysts, after which the free ends of the adjacent segments grow out as single or geminate branches. When formed singly the branch may in its turn produce a branch a little way beyond its point of emergence from the sheath of the parent-filament. In rare cases it may even form a branch from the part inside the parent-sheath, in which case an appearance somewhat resembling that of geminate branching may be realised (e. g. *Tolypothrix distorta* var. *samoënsis*, Fig. 4 G). In the case of geminate branching both branches may emerge on the same side of the parent-filament through a single split in the sheath (*Scytonema dilatatum*, Fig. 4 D; *S. simplex*, Fig. 5 A). They may, however, grow out through separate openings adjoining one another, either emerging directly (*S. Pascheri*, Fig. 4 F) or after growing for a little distance within the main filament in opposite directions so that the two branches cross each other. More rarely the two branches emerge from the main sheath on opposite sides at about the same level (*S. pseudoguyanense*, *S. mirabile*, Fig. 4 B and E; cf. also Fig. 2 G; and 25, Fig. 16). As previously mentioned, both branches may grow out simultaneously or one of them may be delayed in its emergence, so that one branch is shorter than the other (*Tolypothrix distorta* var. *samoënsis*, Fig. 3 E and *Scytonema Hofmanni* var. *crassa*, Fig. 4 H). Occasionally one or other of the two branches may produce a single or geminate branch soon after breaking through the parent-sheath (*S. mirabile*, Fig. 4 E). No one type of branching among those just described has been found to be distinctive of a particular species in the material examined; consequently the method of branching can scarcely serve as a reliable taxonomic character.

Another mode of formation of geminate branches is by the development of loops (cf. 23, p. 741), as in *S. Millei*, *forma* and *S. Bewsii*. Here any one of the cells between two heterocysts may gradually enlarge, whilst the colour of its cell-contents changes to dark green and the contained granules become smaller (Fig. 5 B, e; cf. also 23, Fig. 484 a and b). This larger cell is then gradually pushed out on one side by the growth and division of the adjoining cells so that a short loop is formed in the trichome. The enlarged cell then divides into two which remain situated in the middle of the loop as the latter gradually becomes longer and narrower by the division of its other cells (Fig. 5 C). The loop then pierces the parent-sheath and the two cells at its apex begin to degenerate; ultimately they separate from one another, as well as from the adjoining healthy cells, so that the loop breaks at its apex and its two limbs become a pair of branches (Fig. 5 E). The two degenerating cells resemble the similar cells found within the trichomes. In some cases the enlarged cell does not divide into two until the loop touches the sheath or has actually pierced it (Fig. 5 D, e).

Occasionally, in forms of *S. Millei* and *S. myochrous* and usually in *S. pseudoguyanense*, the loop is produced by rapid division of the cells at certain points in the main trichome without previous formation of any special cell in the middle (Fig. 5 J). When such a loop breaks through the parent-sheath it consists of similar cells throughout (Fig. 5 K), and it may grow to a varying length (sometimes 400 μ , Fig. 5 H) before a cell at the tip begins to degenerate (Fig. 5 I and L) or an intercellular disc is secreted (Fig. 5 F) whereby the two limbs are separated as two branches. The two limbs may even before they separate from each other form secondary branches by the degeneration of certain cells. The origin of geminate branches by the formation of loops has, however, not been found to be a specific character in any species examined, since such branches may also be produced by any of the other methods described above. GEITLER (23, p. 741) regards the origin of geminate branches by the formation of loops with enlarged cells at their apices as typical for *Scytonema*, but since only one example of this kind of branching has been met with in a very large quantity of material examined this conclusion does not appear to be justified.

In loop-formation the separation of the two limbs is usually accomplished by the degeneration of two special cells formed before the loop emerges from the parent-sheath, while in other cases of false branching the degenerate cell or cells appear and break up

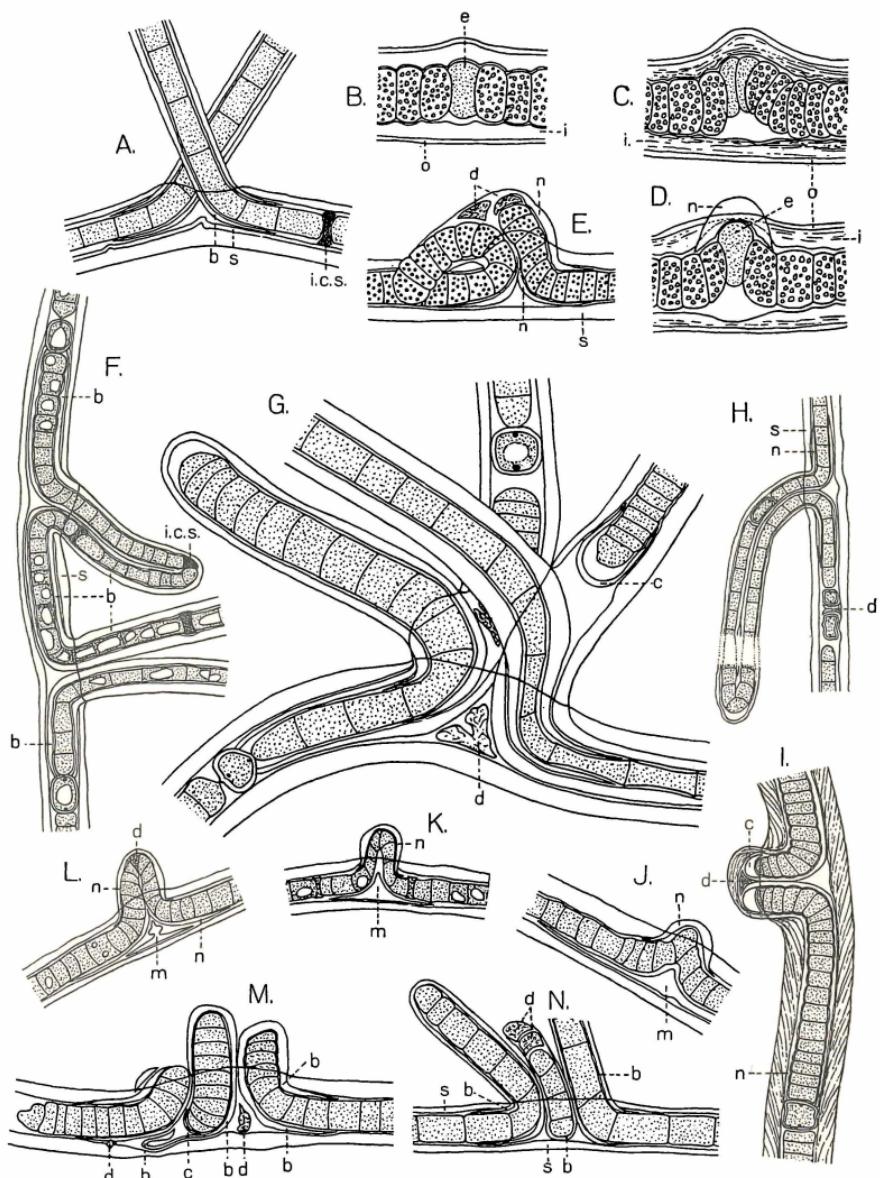


Fig. 5. A *Scytonema simplex*, geminate branching; B—E and H *S. Millei* forma, geminate branching by loop-formation; F and J—L *S. pseudoguyanense*, the same; G *Tolyphothrix distorta* var. *samoënsis*, four pseudobranches arising at the same point; I *Scytonema myochrous* forma, geminate branching by loop-formation; M *S. dilatatum* forma, three pseudobranches arising at the same point; N *S. mirabile* forma, three branches arising at the same point, the middle one a true branch. b branch-sheath; c mucilage-cap; d dead cell; e enlarged cell; i inner portion of sheath; i. c. s. disc of intercellular substance; m mucilage-pad; n new sheath; o outer portion of sheath; s parent-sheath. A, F, H, I, K—M $\times 340$; B—D and N $\times 730$; E, G and J $\times 470$

the trichome while the latter is still within the parent-sheath, formation of outgrowing branches taking place subsequently. The process is therefore much the same in the two cases, except that in the former the separation of the degenerating cells from the adjoining living ones is much delayed. The formation of loops not containing any degenerating cells before emergence from the parent-sheath, although such cells are formed later, marks a still further postponement of the process of splitting.

The geminate branches, formed in any of the ways described above, either grow more or less parallel to each other and at right angles to the main filament or bend and diverge to a varying degree. They may thus form an acute angle with the main filament, or sometimes even an obtuse one so that they cross each other, as in *S. simplex* (Fig. 5 A) and *S. myochrous* forma (Fig. 3 F). In still other cases both become inclined in the same direction. Similarly single false branches may grow out at practically all angles with respect to the parent-filament.

In *Scytonema mirabile* forma *minor* (Fig. 5 N) three branches have occasionally been observed arising together from the same point in the filament. In such cases the middle branch is formed by outgrowth of a single cell which was present in the parent-filament between two degenerating cells, one or both of which may ultimately disappear. The middle branch is therefore a true branch, while the two lateral ones develop in the usual way from the free ends of the two adjoining segments of the trichome. In *S. dilatatum* forma *major* one of the two geminate branches sometimes produces a secondary branch immediately after emergence from the parent-sheath from the part within the latter, so that three branches appear to arise at the same place (Fig. 5 M; cf. with the case described on p. 261). A similar instance was observed in *S. saleyeriensis* var. *indica*. In *Tolypothrix distorta* var. *samoënsis* (Fig. 5 G) both of the geminate branches occasionally produced similar secondary branches, so that four branches appeared to arise from one place.

7. The origin and development of branch-sheaths.

In the case of geminate false branches produced from loops (*Scytonema Millei* forma) the new sheath is secreted after the loop of the trichome has pushed out the parent-sheath to a slight extent or has actually pierced it. At first it appears as a covering only on the outer side of the loop (Fig. 5 D, n) and to begin with is rather

diffluent, although later becoming dense and firm. As the loop grows out of the parent-sheath all its cells gradually become enveloped by the new sheath which can then be recognised even on the inner (concave) side (Fig. 5 E, n). As long as the loop is short, the new sheath can only be traced into the main filament as far as the point where the two limbs of the loop bend outwards, but as the latter elongates the new sheath gradually extends further along the main filament as a result of its secretion by more and more cells of the trichome. It can then be traced back from the point of origin of the loop in both directions along the main filament to thin down gradually and end blindly (Fig. 5 H); if there is a heterocyst near at hand the new sheath may extend up to it and terminate there, as in Fig. 5 I (n). When a second loop develops from the part of the branch-trichome situated within the parent-sheath, this loop does not form a new sheath since it takes with it that which already surrounds the trichome (Fig. 5 F, b).

In *Scytonema pseudoguyanense*, as soon as the formation of the loop commences, a pad of diffluent mucilage is secreted on its inner concave side and, as the loop enlarges, this pad grows and fills up the space between the loop and the parent-sheath (Fig. 5 J and K, m); this appears to help in the protrusion of the loop. A little later, when the usual covering of mucilage is secreted on the outer side of the loop, further enlargement of the primary pad of mucilage stops and, as the former gradually envelopes the whole loop, the original mucilage-pad becomes denser and undergoes contraction. It then becomes gradually dissolved (Fig. 5 L, m) and ultimately disappears, though this usually takes a long time and remnants have often been found at the base of loops which have grown to a considerable length.

In the case of single or geminate branches which are separate from the first and produced in the way described in the last section, the new sheath is first secreted as a mucilaginous cap over one or two of the terminal cells at the free end of the segment. This may happen only after the segment begins to grow and to bend to the outside, sometimes only when it touches the parent-sheath (*S. Milleiforma*, Fig. 6 I, c) or even only after it has emerged through the latter (*S. Hofmanni* var. *crassa*, Fig. 4 H, c; cf. also 24, Fig. 6¹). In other

¹) GONZÁLEZ-GUERRERO describes the alga as *S. Cuatrecasasii* which GEITLER (23, p. 787) considers to be a form of *S. myochrous*. While agreeing with GEITLER that GONZÁLEZ-GUERRERO's figures show disorganised filaments, the writer thinks it improbable that the alga is a form of *S. myochrous* since its sheath, for the most

cases, however, the mucilaginous cap is secreted before the free end of the segment commences to grow and before it shows any sign of bending outwards (Fig. 4 and 5 G, c; cf. also Fig. 6 F, c). In one and the same plant (e. g. *S. guyanense* var. *prolifera*) the cap may sometimes be secreted before (Fig. 6 D, c) and sometimes after outgrowth of the segment.

During the outgrowth of the free end of the segment into a branch the cap extends backwards towards the main filament as more and more cells of the trichome secrete mucilage, and in this way a new and extensive sheath is gradually formed around the branch-trichome. This branch-sheath usually extends into the main filament very gradually, but in some cases it develops quickly so that when a branch has grown to only a short length outside the parent-filament its sheath may already be traced backwards into the latter for a considerable distance. This latter condition is well marked in *S. mirabile* and occasionally in *S. dilatatum* forma *major*, where the new sheath may be of considerable length even before the free end of the segment commences growth and bends to the outside (Fig. 3 B, n), while, when the segment is very short, the new sheath may be formed along its whole length before it grows out into a branch (Fig. 6 C, n).

When both ends of a segment consisting of one or more cells are free, as in *S. mirabile*, mucilage-caps may be formed over both (Fig. 6 F, c). Such cases could also be interpreted as representing the growth of a segment accompanied by splitting across of a sheath which at first completely surrounded it. I have not, however, observed any case in which a short segment was completely surrounded by a sheath of its own and do not consider such an interpretation justified. Subsequently the caps over the ends of such free segments extend backwards in opposite directions, as the segment grows, and develop into branch-sheaths which ultimately meet at the middle of the segment and form a common sheath around the latter, one or both ends of which may have already emerged as branches. Stages have been observed in which the two new sheaths have not yet fused and are still separated by a small space, thus showing their distinct origin quite clearly (Fig. 3 C, n). Without a knowledge of the mode of development of the sheath it is difficult after fusion has occurred to distinguish the enclosed segment from a hormogone

part, shows distinct parallel stratification. The occasional divergent layers in the sheath of this alga do not differ from those which are commonly found in forms showing apparent parallel stratification.

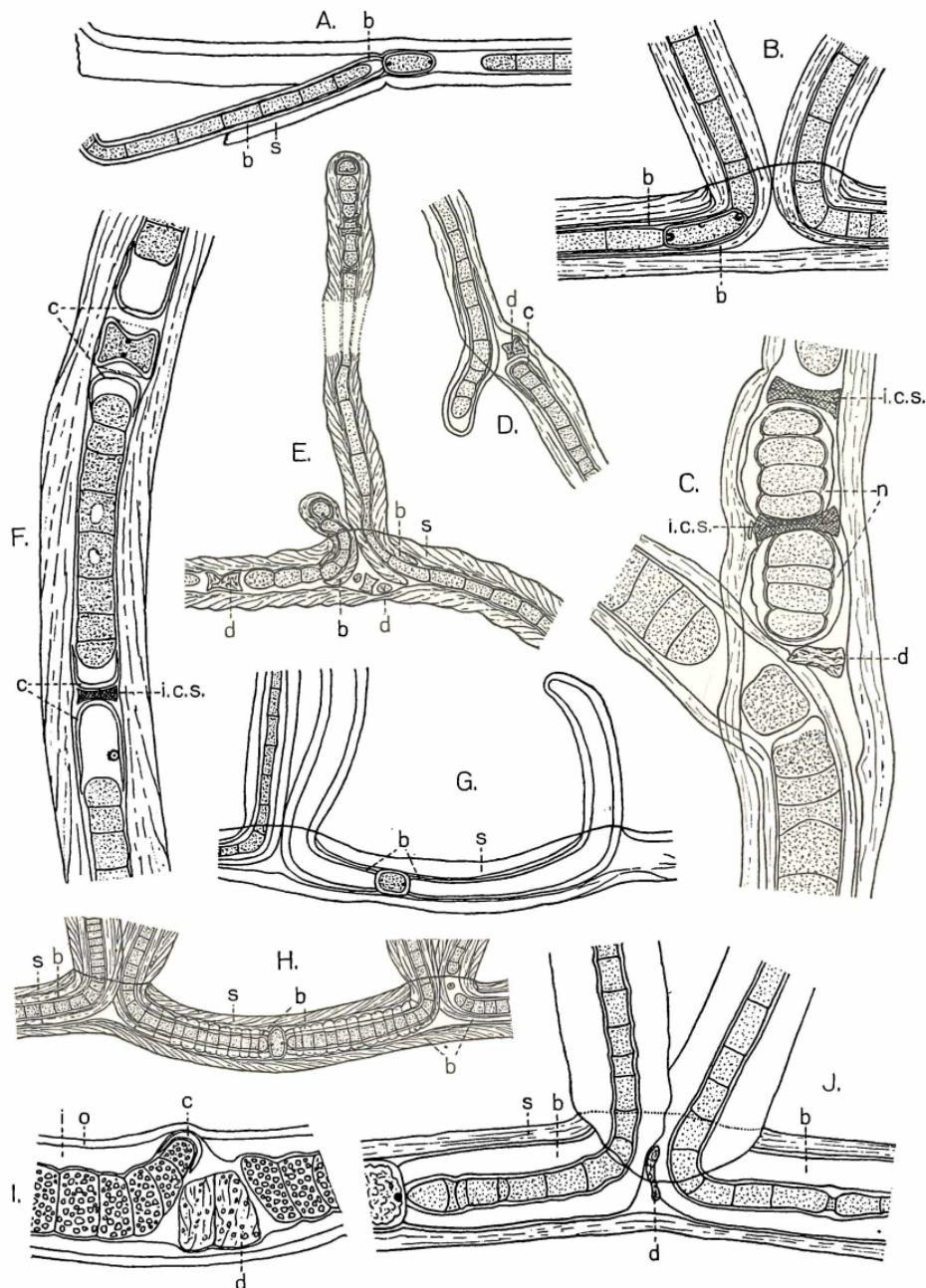


Fig. 6. A *Scytonema Hofmanni* var. *crassa*, sheath teased out to show the branch-sheath terminating at the heterocyst; B *S. Bewsii*, branch-sheath enclosing a newly formed heterocyst, C *S. dilatatum* forma *major*, showing new sheath formed over the whole length of short segments before they grow out into pseudobranches; D *S. guyanense* var. *prolifera*, secretion of mucilage-cap before the free end of the segment commences to grow; E *S. Geitleri*, sudden termination of branch-sheath

within the parent one; F *S. mirabile*, formation of mucilage-caps at either end of a segment before its growth; G *S. pseudohofmanni* forma, showing sheaths of two branches terminating at a median heterocyst; H *S. myochrous*, showing the same; I *S. Millei* forma, formation of mucilage-cap over the free end of a segment after the latter has reached the parent-sheath; J *S. pseudoguyanense*, branch-sheath of even thickness terminating at the heterocyst. b branch-sheath; c mucilage-cap; d dead cell; i inner portion of sheath; i. c. s. disc of intercellular substance; n new sheath; o outer portion of sheath; s parent-sheath. A, D and E $\times 430$; B, C, F, G and J $\times 590$; H $\times 265$; I $\times 910$.

which is germinating *in situ* and has secreted a new sheath (cf. p. 271), especially when only one end of the segment has emerged to form a branch. When such segments include a heterocyst, the two new sheaths extend only as far as the latter and therefore do not fuse (*S. pseudohofmanni* forma, Fig. 6 G, b and *S. myochrous*, Fig. 6 H, b). GONZÁLEZ-GUERRERO (25, Fig. 16) in *S. myochrous* shows a segment, with a median heterocyst, both ends of which have grown out into branches, the whole being enclosed in a common sheath. This appears to me to require further verification since I have not found any such case in this or in any other species, the two branch-sheaths in such cases always ending at the median heterocyst and never covering the same (Fig. 6 H; cf. also Fig. 6 G). Such a state of affairs would only be possible if the median heterocyst were differentiated after the sheaths of the two branches have fused to form one, but this has not been observed in *S. myochrous*.

When three branches grow from the same point, as in *S. mirabile* forma *minor* (Fig. 5 N; cf. p. 264) the sheaths of the two lateral branches are developed in the usual way, but the middle cell becomes completely enveloped in a new sheath before growing into the third branch, so that the latter is entirely surrounded by its sheath. In *S. dilatatum* forma *major* (Fig. 5 M) where one of the geminate branches gives rise to a secondary branch within the parent-filament, the lower end of the upper segment thus cut off may be covered by the secretion of a new mucilage-cap.

The distance to which the branch-sheath can be traced backwards into the main filament varies in different forms and sometimes even in the same form. Ordinarily it extends some way into the main filament and then terminates blindly after thinning down gradually, and it never extends beyond the next heterocyst (Fig. 6 A, b). In *S. myochrous* (Fig. 6 H, b), *S. Pascheri* (Fig. 4 F, b) and *Calothrix ramosa* (Fig. 7 C, b) the branch-sheath of the mature branch can generally be traced to the next heterocyst; in extreme cases this may mean a length of 250 μ . When no heterocyst is near at hand the

branch-sheath can usually be followed a considerable distance within the main filament and in such cases sometimes becomes so thin that it is distinguishable under the microscope only as a delicate line. In some cases, however, the branch-sheath remains of more or less even thickness and ends suddenly (*Scytonema Geitleri*, Fig. 6 E, b) or at the next heterocyst (*S. mirabile*, Fig. 2 G, b and *S. pseudoguyanense*, Fig. 6 J, b).

In *S. dilatatum* (Fig. 4 D, b) and *Tolypothrix nodosa* (Fig. 4 C, b) the branch-sheath cannot be traced backwards beyond the point of origin of the branch from the main filament, unless a heterocyst is situated near at hand in which case it extends up to it. In *T. distorta* var. *samoënsis* and in a form of *S. myochrous* it can be traced as far as the point of origin of the branch as long as the latter is short (Fig. 3 E and G, b), but as the branch inceases in length the sheath gradually extends up to the next heterocyst (Fig. 3 E and F, b).

In all cases, therefore, if a branch-sheath extends up to a heterocyst, it terminates there. On the other hand, if a herterocyst is formed subsequently in a part of the branch which is already covered by the new sheath, the latter envelopes it, as in *S. Bewsii* (Fig. 6 B). The same features are found in *Calothrix ramosa* (Fig. 7 D). Here the elongating terminal portion of the main trichome, which is not included in the sheath, secretes a new lamella which only extends for a very short distance into the main sheath. The new growth becomes cut off from the lower portion by the death of an intermediate cell, while the next cell above becomes transformed into a one-pored heterocyst which therefore appears included in the sheath. The new filament thus constituted ultimately separates and becomes an independent plant. If, however, the secretion of the new sheath is delayed until a basal heterocyst has been formed in the new length of trichome, the former envelopes the vegetative cells but does not extend round the heterocyst (Fig. 7 B).

The apex of the lower segment also elongates and emerges from the parent-sheath, secreting a new lamella of its own which can be traced backwards into the main filament, if the latter be long, for a considerable distance, ultimately terminatiug blindly in the usual way. If, however, the lower segment is comparatively short the new sheath may terminate after reaching the next heterocyst. Figure 7 A shows successive formation of new heterocysts as the older ones degenerate and here the different lamellae of the sheath are seen to terminate at the respective heterocysts, after the formation of which they were secreted.

The new extension (i. e. the upper part) of the original trichome may in its turn be segmented in the same way and the process may be repeated indefinitely. The upper segments, provided with a basal heterocyst

and a new sheath, become successively detached from their respective parent-filaments and may develop into independent plants. In such cases, as stated above, the basal heterocyst would not be covered by the sheath, since the former was differentiated before the latter

was secreted¹⁾. But when a new plant develops from a hormogone in which the basal heterocyst is formed after the secre-

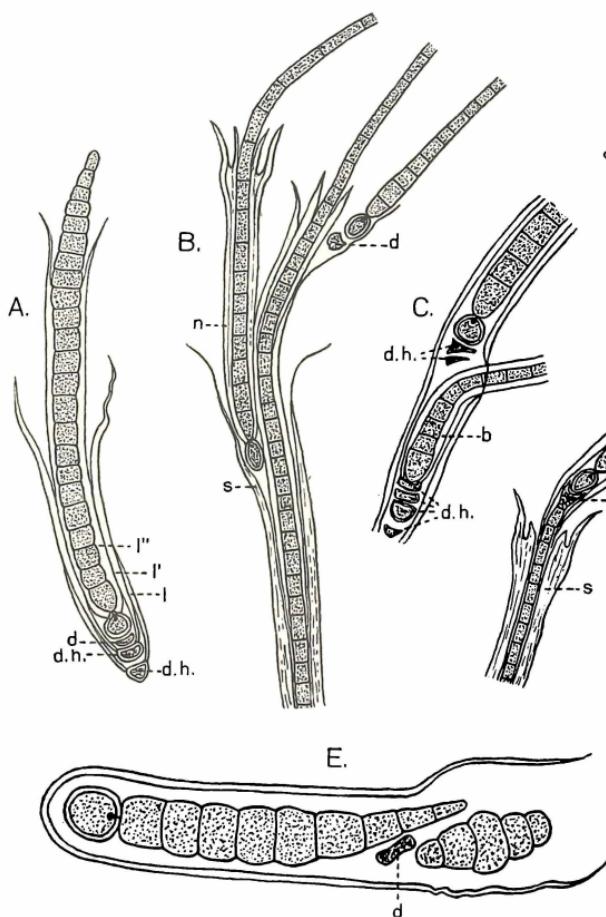


Fig. 7. *Calothrix ramosa*. A abnormal filament showing different lamellae of sheath ending at successive heterocysts; B and C typical filaments showing pseudobranching; D formation of a new filament from the terminal portion of the old one; E germination of a hormogone and subsequent branching of the trichome. b branch-sheath; d dead cell; d. h. dead heterocyst; l, l' and l'' different lamellae of the sheath; n new sheath; s parent-sheath. A—D $\times 570$; E $\times 1210$.

tion of the sheath, the latter envelopes the heterocyst (Fig. 7 E)²⁾. It thus appears that in *Calothrix* the basal heterocyst is outside or

¹⁾ Cf. the germinating hormogones of *Gloeotrichia punctulata* THUR. (7, Pl. 42, Figs. 3 and 4), and also *Calothrix Flahaultii* FRÉMY (14, Fig. 1) and *C. Braunii* BORN. et FLAH. (16, Fig. 230).

²⁾ Cf. also *Calothrix confervicola* AG. (6, Tab. 3, Figs. 6 and 7).

enclosed within the sheath, according as the former was differentiated before or after the latter is secreted. Both cases may occur in the same plant (cf. *C. intricata* FRITSCH (18, Pl. 3 Figs. 158—160)). The same features are sometimes shown by *Microchaete investiens* FRÉMY (16, Fig. 249 a).

8. Hormogones and hormocysts.

Multiplication in the Scytonemataceae is accomplished mainly by means of hormogones and sometimes by hormocysts. The hormogones are formed by fragmentation due to the death of occasional vegetative cells which may assume a biconcave shape, to the secretion of biconcave intercellular discs, or sometimes to the degeneration of an intercalary heterocyst. They may consist of from one to many cells. They perennate inside the parent-sheath and on the return of favourable conditions emerge from it and develop into new plants.

In a form of *Scytonema pseudohofmanni*, as appears to be the rule in many families of Myxophyceae, the hormogones escape through the open ends of the parent-sheath as naked trichomes and subsequently secrete a sheath of their own, after which they commence to grow into new filaments. In most of the cases examined (e. g. *Scytonema guyanense* var. *prolifera*; Fig. 8 I and *S. pseudoguyanense*; Fig. 8 J), however, the hormogones become completely enveloped in a new sheath before liberation. Under these circumstances they may either emerge through the open end of the parent-sheath (*S. saleyeriensis* var. *indica*, Fig. 3 A and *S. guyanense* var. *prolifera*, Fig. 8 H and I; cf. also Fig. 8 F, or, if they occupy an intercalary position, may break through the sheath which at this stage is usually brittle (Fig. 8 F). In either case the hormogones begin to germinate *in situ*. Those which break out laterally from the parent-sheath, while a considerable part is still enclosed within the latter, are liable to be mistaken for pseudobranches unless they are carefully examined and the presence of a complete enveloping sheath is recognised.

The germinating hormogones usually differentiate a single median heterocyst (rarely two at some little distance from each other) before they grow to any appreciable length; in a few instances the heterocyst is terminal. Sometimes the heterocyst is differentiated before the hormogone grows out of the parent-sheath (Fig. 3 A), while in other cases such heterocysts are formed only after emergence,

both conditions being occasionally met with in the same plant (Fig. 8 H and I). Homogones with median heterocysts have been figured by BORNET and THURET (7, Pl. 35 Fig. 4) in *Scytonema Hofmanni* KÜTZ. and by WEBER-VAN BOSSE (35, Pl. 1 Fig. 3) in *S. saleyeriensis* WEBER-VAN BOSSE, and similar hormocysts by BORZI (9, Taf. 10 Fig. 58) in *Leptopogon intricatus* (A. BRAUN) BORZI, and by FRÉMY (17, p. 176 Fig. 16) in *Westiella intricata* BORZI. Occasional hormogones with two intercalary heterocysts have been observed in *Scytonema tolypo-thrichoides* forma *terrestris* and are also shown by BORNET and THURET (7, Pl. 35 Fig. 4).

When a hormogone differentiates a median heterocyst it grows at both ends, but when a terminal heterocyst is formed growth is confined to the opposite end (cf. 7, Pl. 35 Fig. 4 and 9 Taf. 10 Fig. 58).

In *Scytonema guyanense* var. *prolifera*, apart from the normal hormogones just described, structures of a special type have been observed. After fragmentation of the trichome in the usual way, one end-cell of certain segments develops into a one-pored heterocyst. When the new sheath forms, it surrounds all the vegetative cells but not the terminal heterocyst. As these structures grow within the parent-sheath they may overlap one another. Later they grow out of the filament through its open end or by breaking through the parent-sheath like ordinary branches (Fig. 8 E). No structure of this nature has been observed wholly free from the parent-filament and it is possible that they produce new filaments *in situ* within the disorganising parent-sheath. They differ from hormogones with terminal heterocysts in the fact that such are entirely surrounded by the new sheath and develop into new filaments only after complete emergence. These structures, therefore, appear to be hormogones which have been arrested by the formation of terminal heterocysts before the secretion of the new sheath, and are perhaps intermediate between branches and hormogones. They resemble the homogones of *Stigonema pulvinatum* BRÉB. drawn by BORZI (8, Taf. 12 Figs. 28, 29), except that they have not been observed outside the filaments.

The formation of hormocysts has been studied in detail in a form of *Scytonema pseudohofmanni*, as well as in *S. Geitleri* and *Fischerella anomala*. In the first the segment of the trichome after becoming enveloped by a sheath develops a terminal heterocyst and is set free by disorganisation or rupture of the brittle parent-sheath (Fig. 8 A). The hyaline sheath of the hormocyst later becomes firm

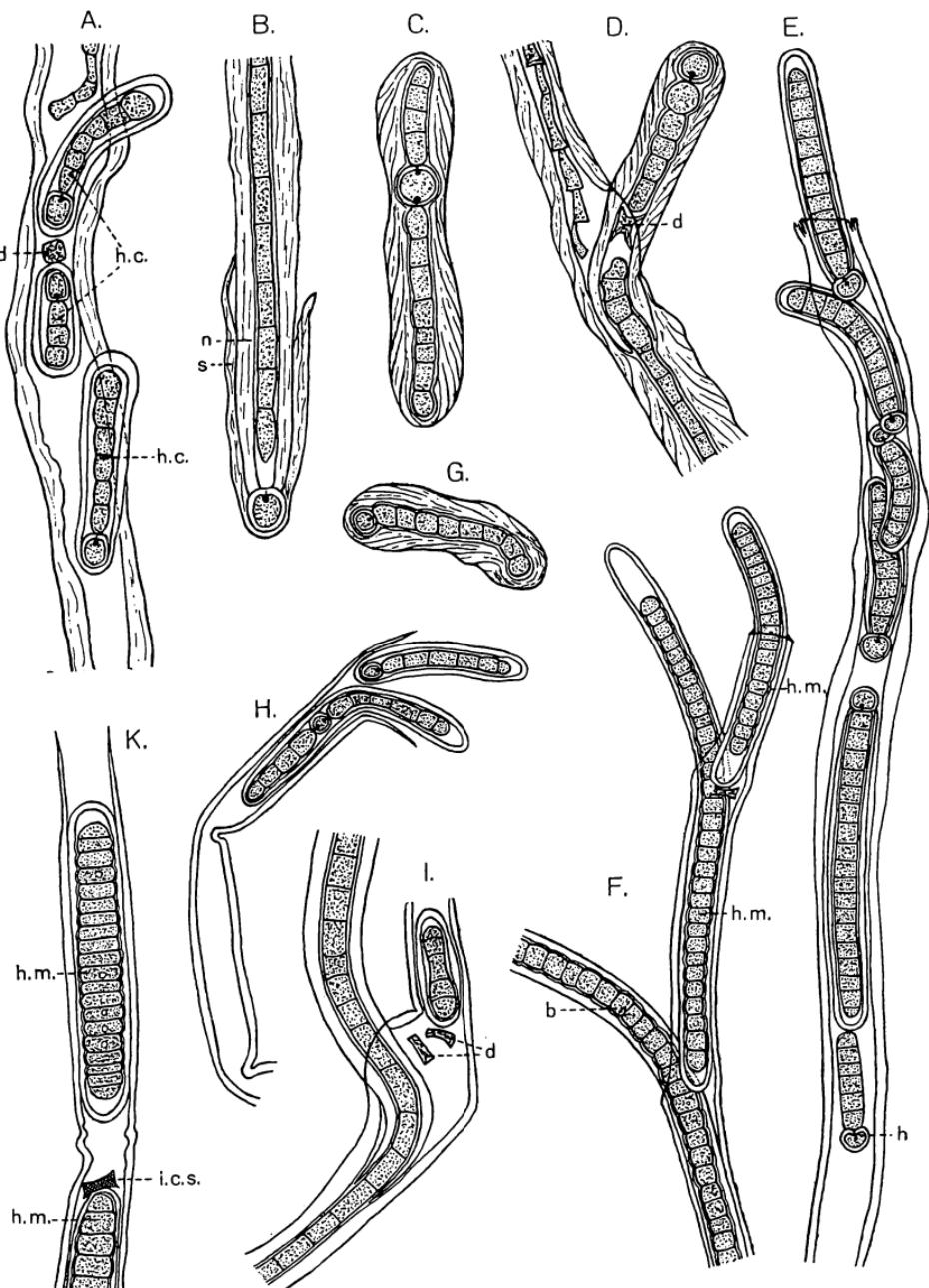


Fig. 8. A and B *Scytonema pseudohofmanni* forma; A development and emergence and B, germination of hormocysts. C, D and G, *S. Geitleri*; C and G, hormocysts; D short branch with a terminal heterocyst. E, H and I *S. guyanense* var. *prolifera*; E filament containing structures intermediate between hormogones and pseudobranches (cf. text p. 272); H and I emergence of hormogones. F *Tolypothrix distorta* var. *penicillata*, emergence of hormogones. J *Scytonema pseudoguyanense*, hormogones. b pseudobranch; d dead cell; h heterocyst; h. c. hormocyst; h. m. hormogone; i. c. s. disc of intercellular substance; n new sheath; s parent-sheath. A and B $\times 780$; C-E and G-J $\times 570$; F $\times 360$.

and brown and in that condition it passes through a resting period. When germination commences the hormocyst grows into a filament with the heterocyst at the basal end. As the short trichome of the

hormocyst lengthens, it pierces the tip of the brown sheath and secretes a new hyaline sheath which extends within the parent-sheath down to the basal heterocyst (Fig. 8 B), but, as in other cases, never envelopes it.

In *Scytonema Geitleri* the formation of hormocysts takes place in another way. Here the pseudobranches are short and club-shaped, the cells at the tip being broader than at the base; they usually have a fairly thick hyaline sheath which extends backwards only as far as the bend. Sooner or later the end-cells of these branches become transformed into heterocysts (Figs. 6 E and 8 D), after which the branches become detached from the main filament by the death of one or more cells at their base. The open end subsequently becomes covered up by the secretion of a mucilaginous cap which completes the original sheath, so that the whole branch is enveloped in a sheath which ultimately becomes thick and firm and yellow-brown or brown in colour (Fig. 8 G). In this condition the branch functions as a hormocyst, which germinates in the same way as that of

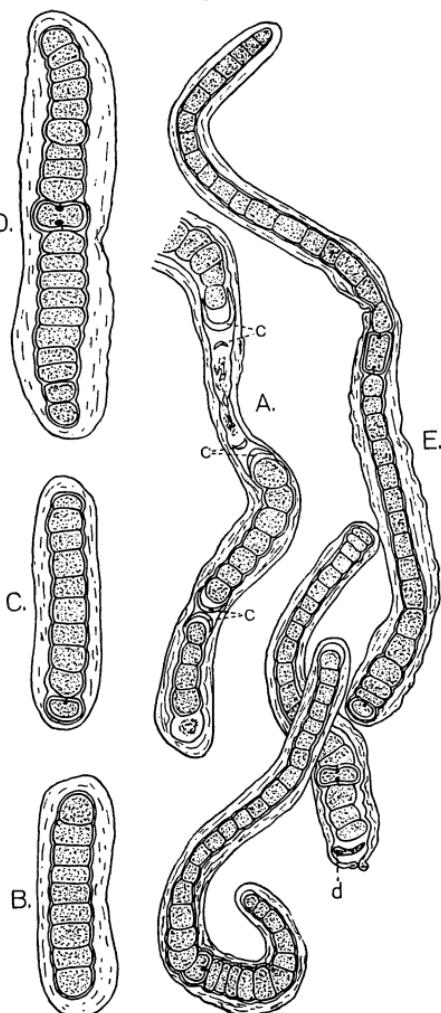


Fig. 9. *Fischerella anomala*. A trichome broken into segments, prior to the formation of hormocysts; B—D hormocysts; E germination of hormocysts. c mucilage-cap; d dead cell. A and E $\times 430$; B—D $\times 590$.

S. pseudohofmanni above described. In rare cases, however, the branches break off from the main filament before terminal heterocysts are formed. Under these circumstances, prior to perennation, they differentiate median (intercalary) heterocysts (Fig. 8 C) as in some of the hormogones

described above, and in the hormocysts of *Westiella intricata* Borzi and *Leptopogon intricatus* (A. BRAUN) Borzi (cf. also p. 271), though in the last two cases the median heterocysts are formed only when the hormocysts begin to germinate. SCHMIDLE (33, Taf. 10 Figs. 2—4) has also described formation of hormocysts in *Camptylonema indicum* by the detachment of short branches or of the apical portions of the main filaments, and here too median heterocysts may be formed before the hormocysts perennate.

In *Fischerella anomala* the hormocysts are formed in a similar manner, being either complete short branches or formed by segmentation of the filament (Fig. 9 A). Before separation, the free ends of their trichomes secrete a new sheath in the form of a cap which later becomes very much thickened and eventually closes over the ruptured end completely. In due course the sheaths become light yellow, deep yellow or sometimes yellow-brown. The hormocysts may (Fig. 9 C and D) or may not (Fig. 9 B) differentiate a heterocyst (terminal or intercalary) before perennation. The germination of these hormocysts takes place in the same way as in *Scytonema Geitleri* (Fig. 9 E), *Leptopogon intricatus* (A. BRAUN) Borzi and *Westiella intricata* Borzi.

9. General remarks.

The preceding account has shown that hormogones may be formed which are completely enveloped by a new sheath before they grow out of the parent-filament and, moreover, that they may first grow within the sheath of the latter to a considerable length before they break through it like pseudobranches. The pseudobranches, on the other hand, possess a sheath which can only be traced into the main filament for a certain distance, the termination being either abrupt or taking place at the first heterocyst. Without a knowledge of these differences certain forms (especially those growing in terrestrial habitats), having hormogones germinating in the way above described, might be regarded as branched. Apart from contributing these new facts relating to the morphology of the Myxophyceae, the present investigation has brought out certain other points which have an important bearing on the taxonomy of the class.

The diverse stratification of the sheath, already fully discussed, has been shown probably to depend on the habitat and it may be doubted whether it is always a reliable diagnostic character, especially in the case of subaerial forms. Until, however, it has been shown experimentally that one and the same form may show either divergent

or „parallel“ stratification according to its habitat, it will remain useful to distinguish between species with marked divergent and ill-defined divergent or „parallel“ stratification.

The genus *Petalonema* of BERKELEY (3) was reduced to a section of *Scytonema* by BORNET and FLAHAULT (5) and BORZI (8). The main reason for its retention by other workers is the possession of a very thick sheath with highly divergent stratification and the mode of formation of this sheath which, however, has only been studied in *P. alatum* BERK. and *P. velutinum* (RABENH.) MIG. The thickness of the sheath is in no way distinctive since, except in *P. alatum* BERK. and *P. pulchrum* (FRÉMY) GEITLER (*Scytonema pulchrum* FRÉMY), the sheaths do not differ in respect of thickness to any appreciable extent from those of certain species of *Scytonema* and *Tolypothrix* (e. g. *S. myochrous* (DILLW.) AG., *S. crassum* NAEG., *Tolypothrix epilithica* (EREG.) GEITLER). In a form of *Scytonema myochrous* having a divergent sheath with a smooth inner margin the lines of stratification run through the whole thickness of the sheath in normal filaments. In old and unhealthy filaments, in which the thickness of the sheath and trichome may be $10.5\ \mu$ and $4.2\ \mu$ respectively, however, the lines of stratification cannot be traced right through the sheath, since there is an inner unstratified pigmented portion, added subsequently and increasing the thickness of the sheath as a whole, the inner surface of which follows the contour of the degenerating trichome and is consequently uneven (Fig. 3G). This type of sheath does not differ from that shown in FRÉMY's figure of *Scytonema densum* (A. BR.) BORN. et FLAHL. which GEITLER (23, Fig. 509) refers to *Petalonema*; here the trichome is likewise degenerating and the divergent strata are recognisable only in the outer part of the sheath. The sheath of this plant hardly differs from that of *Scytonema crustaceum* AG. (23, Fig. 504, 3).

GEITLER (22, p. 262) at first followed LEMMERMANN (29, p. 214) in placing *Scytonema crustaceum* AG. in *Petalonema*. Later (23, p. 782), however, he included this species in *Scytonema*, while *S. pulchrum* FRÉMY (16, Fig. 270) is referred to *Petalonema*. FRÉMY's figure of *S. pulchrum* shows that the growth of the filament was interrupted by frequent periods of rest, since the sheath presents a jointed appearance like that occasionally observed in *S. saleyeriensis* var. *indica* (Fig. 2C, lower portion) and certain other forms. Except for this jointed appearance there is hardly any difference from terrestrial species of *Scytonema* with a distinct divergent stratification in the sheath. The sheath of *Petalonema involvens* (A. BR.) MIG. (23, Fig. 508) also

shows no special feature which would justify its separation from *Scytonema* (cf. p. 255).

The method of growth of the sheath is essentially the same in *Petalonema* and in the forms here examined. GEITLER's figure of *Petalonema velutinum* (RABENH.) MIG. (23, Fig. 507) shows that the development of the successive layers of the sheath takes place in exactly the same way as in the forms of *Scytonema* and *Tolypothrix* described in this paper. The only species of *Petalonema* which appears to differ in some respects from an ordinary terrestrial species of *Scytonema* and *Tolypothrix* is *P. alatum* BERK. in which the layers of the thick sheath are funnel-shaped. The latter feature is evidently due to the different layers of the sheath diverging rather abruptly after running parallel for some distance and to the great thickness of the diverging portions (cf. 12, Taf. 15 Fig. 19). In view of the facts just presented it appears scarcely desirable to maintain *Petalonema* as a distinct genus and it would be best to re-establish it as a section of *Scytonema*.

BORNET and FLAHAULT (5, p. 118) have used the thickness of the sheath as a diagnostic character in classifying *Tolypothrix* and this has been followed by LEMMERMANN (29, p. 216) and GEITLER (23, p. 711). The species are grouped in two sections, one with „a thin sheath (distinctly thinner than the trichome)" and the other with „a very thick sheath (as thick or almost as thick as the trichome)"¹⁾. It is difficult, however, to maintain a line of demarcation between the two sections and attention may be drawn to the fact that *Tolypothrix Letestui* FRÉMY (16, Fig. 252) and *T. conglutinata* BORZI (18, Fig. 145) which are placed respectively in one and the other section by GEITLER (23), hardly differ from each other with respect to the thickness of the sheath in relation to that of the trichome. It must also be recalled that the sheath of the same species may possess varying thickness at different stages of its life.

In measuring the thickness of the sheath, moreover, it is necessary to take into consideration the branch-sheaths. Ordinarily when a branch-sheath extends inside that of the parent for some distance, the thickness of the filament is not appreciably increased

¹⁾ In spite of the importance given to this character the actual thickness of the sheath is never stated. The thickness of the sheath can be approximately gauged from the difference between the thickness of filament and trichome, but some figures show a space between trichome and sheath, due to contraction in preserved material.

because the parent-sheath gradually undergoes compression and becomes thinner as the branch-sheath develops within it; the latter also gradually narrows down. In some cases, however, the branch-sheath is not only as thick or almost as thick as that of the parent, but also it may not thin down to any appreciable extent, or even may retain the same thickness up to the next heterocyst. In such cases the parent-sheath may likewise remain more or less of the same thickness, though the trichome becomes slightly narrower and its cells more elongate. These different conditions may even occur in the same plant (cf. *Scytonema pseudoguyanense*, Figs. 4 B and 6 J). In the cases last mentioned the breadth of the filament would be increased considerably owing to the trichome being surrounded by branch- and the parent-sheaths (cf. *Tolypothrix Saviczii* KOSSINSK. 23, Fig. 475, 10), and under these circumstances the thickness of the branch-sheath must be excluded in measuring the sheath of the filament. In order to obtain an accurate measurement of the sheath of the filament and of the filament itself it is advisable in all cases to measure the thickness in a region between two heterocysts which is not producing any branch. The thickness measured at any other point may not be reliable, especially in terrestrial forms with pigmented sheaths, in which the branch- and the parent-sheaths are not distinguishable from each other without special treatment.

The presence of hormocysts or hormogones has also been used to distinguish one genus from another. GEITLER (23, p. 679), for instance, distinguishes *Seguenzaea* from *Spelaeopogon* by the presence of hormogones in the former and of hormocysts in the latter. This also does not appear to be a sound basis of classification since I have found both homogones and hormocysts in two different samples of a form of *Scytonema pseudohofmanni* (cf. pp. 271, 272). The formation of hormogones requires more moisture than that of hormocysts so that, when different parts of the same terrestrial stratum experience different conditions of moisture, they may produce hormogones and hormocysts respectively. In other words the production of hormogones and hormocysts may be dependent upon environmental conditions in the same way as some of the other characters previously discussed.

In view of these remarks it appears that terrestrial Myxophyceae may be very plastic in their behaviour, and experimental treatment will be necessary to determine in how far their features may undergo modification according to the character of the habitat.

10. Summary.

The paper deals with the structure of the sheath and the methods of pseudobranching, as well as with the mode of formation and germination of hormogones and hormocysts in the Myxophyceae, with special reference to the Scytonemataceae. The following are the principal conclusions:

1. The sheaths in aquatic forms are permanently hyaline, except in those species which are subjected to casual or periodic changes of water-level in which the sheaths are occasionally slightly coloured. Subaerial forms always develop pigmented sheaths at an earlier or later stage, so that pigmentation may be regarded as a result of a subaerial mode of life. The pigment either appears first in the inner layers and gradually spreads to the outer ones or appears simultaneously throughout the thickness of the sheath. In practically all cases a freshly secreted sheath is hyaline. Iron-compounds do not appear to be responsible for the pigmentation. The sheaths consist of pectic substances which are sometimes combined with cellulose and, when the latter is present, it is found in the sheath from the very beginning. Thickness of the sheath is not always a reliable character in classification, since the sheath tends to thicken in old and unhealthy filaments and may vary in thickness in different parts even of a healthy filament.

2. Growth of the filaments takes place in the following way. As the apical portion of the trichome ruptures the sheath and emerges from it, it secretes a new sheath or lamella which not only surrounds the new length of trichome but also extends backwards along the old part of the trichome gradually thinning down and ultimately ending blindly. With each fresh elongation of the apex a similar lamella is formed and the various lamellae compose the thickness of the sheath which is therefore a compound structure. The successive lamellae diverge from the trichome, each lying within the next older one which has been ruptured at the tip to allow of the extension of the trichome. The different layers of a mature sheath therefore represent a number of individual sheaths in the same way as CORRENS described it for *Petalonema alatum* BERK.

3. The stratification of the sheath is thus always divergent and never mathematically parallel. So-called parallel stratification is due to the fact that the successive lamellae extend for long distances owing to prolonged periods of rapid growth. When growth is slow (probably as a result of drought in a terrestrial form) the divergent

nature of the stratification becomes evident. Forms showing distinct divergent stratification are always terrestrial, while purely aquatic forms never show such a stratification. The stratification of the sheath is thus probably in the main determined by environmental conditions. Some forms exhibit parallel and divergent stratifications in different parts of the same plant. Moreover, there are all gradations in the angle of divergence of the lamellae between a sheath showing „parallel“ stratification and one with a highly divergent stratification. The type of stratification of the sheath may therefore not always be a reliable diagnostic character.

4. The formation of branches is usually initiated by segmentation of the trichome in various ways (cf. pp. 258, 259) after which the free ends of the adjacent segments grow out as single or geminate branches. In some cases, when only one segment grows out into a branch, the end-cell of the other segment may become transformed into a one-pored terminal heterocyst and, when the intervening cell has disappeared, the branch appears to have arisen by the side of this heterocyst which has, however, in reality been formed secondarily. No instance has been observed in which a one-pored heterocyst develops in the middle of the trichome before the latter undergoes segmentation.

5. Geminate branches may also in rare cases arise by loop-formation, the separation of the two limbs of the loop being accomplished in various ways (cf. p. 262). No particular method of formation of branches has been found to be distinctive of any one species, so that the method of branching cannot serve as a reliable taxonomic character.

6. In the case of geminate branches produced from loops the new sheath at first appears as a covering only on the outer side of the loop, but as the latter lengthens the sheath gradually envelopes the whole and extends in both directions into the main filament. In the normal method of production of false branches from segments the new sheath is at first secreted as a mucilaginous cap over one or two of the terminal cells at the free end of the segment. This may happen either before or after the segment begins to grow to the outside. The branch-sheath usually extends back into the main filament very gradually, but in some cases it develops quickly and may be of considerable length before the free end of the segment commences growth. When the segment is very short, the new sheath may be formed along its whole length before it grows into a branch.

7. In all types of branching the branch-sheath extends into the main filament for a varying distance, either ending blindly after thinning down gradually or terminating at the next heterocyst. In no case does the branch-sheath extend beyond a heterocyst. This is also true of sheath-formation when a filament recommences growth after a period of rest or after it has been ruptured so that heterocysts are evidently incapable of secreting a sheath. If a heterocyst is covered by a sheath it may be taken for granted that it was differentiated from a cell already surrounded by the sheath.

8. Apart from the usual type of hormogone, in which a new sheath is secreted after emergence from the parent-filament, instances are described in this paper of hormogones which secrete a new sheath while still within the parent-filament. Such hormogones may begin to grow *in situ* and emerge by breaking through the parent-sheath like pseudobranches. In most cases these hormogones, either before or after emergence, differentiate a single median heterocyst or occasionally a terminal one.

9. Hormocysts may be either segments of a trichome enveloped by a new sheath or complete short branches detached from the main filament or segments of the filament broken across. They may differentiate a median or terminal heterocyst before perennation.

10. Like other features in terrestrial Myxophyceae the formation of hormogones and hormocysts is dependent upon external conditions, the former being produced under more favourable conditions of moisture than the latter. It would not, therefore, be surprising if different parts of the same stratum, experiencing different moisture-conditions, should produce both kinds of structures. This has been observed in *Scytonema pseudohofmanni* (cf. pp. 271, 272). A distinction of genera based upon the formation of hormogones or hormocysts may therefore not be a reliable one.

11. Since the growth of the sheath in the forms examined has been found to correspond to that of *Petalonema* and thick sheaths with divergent stratification are not confined to this genus alone, it is suggested that it is advisable to regard *Petalonema* merely as a section of *Scytonema*.

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