# MYXOPHYCEÆ (OR CYANOPHYCEÆ)

## (Blue-green Algæ)

THE Myxophyceæ (which are also known as the Cyanophyceæ[1] and as the Schizophyceæ[2]) are the lowest and most primitive of Algæ, having in their general organization a certain resemblance to the Bacteria. They combine two outstanding features: first, the copious secretion of mucilage, which often becomes very tough; and secondly, the characteristic blue-green colour of the cells. The latter feature may, however, be partially or wholly masked owing to the presence of other pigments, either in the cells or in coloured sheathing envelopes. Some are unicellular, some filamentous, and many are colonial. They occur everywhere in damp and wet situations; and quite a large number exist in subaërial habitats. Owing to the bright colours of the cells and sheaths, the Myxophyceæ furnish in moist climates many of the richest tints of the landscape, and as they occur in profusion on rocks, stones, and the trunks of trees, they sometimes impart a decided character to the country.

The Blue-green Algæ are mostly freshwater and subaërial, although a few inhabit brackish waters, and some are marine. Many forms exist in quantity in the freshwater plankton, and a few in the plankton of the warmer oceans. They also constitute the principal vegetation of hot springs.

[1] The group-name 'Cyanophyceæ' is a fairly good one, but it is being gradually superseded by the name 'Myxophyceæ,' which is perhaps a little better. Some 15 per cent. of the species of this group are not of a blue-green colour at any period of their life, and about 30 per cent. of the remainder have their cells so lodged within sheaths and gelatinous envelopes of a yellow, orange, red, brown, or purple colour that they also do not appear blue-green in the mass. The name 'Myxophyceæ' is now in general use except in the British Islands where it has been thought more advisable to retain a 'colour name.'

[2] The name 'Schizophyceæ' is a very inappropriate one, as 70 per cent. of the known species are propagated by hormogones and spores, and do not multiply by fission. Moreover, in the large group of the Hormogoneæ cell-division is accompanied by the laying down of a new transverse wall, and does not occur by 'fission' (consult p. 9).

Apart from their interest as very primitive organisms, with a world-wide distribution and a capacity for existence under the most varied conditions of environment, the Myxophyceæ present a cytological problem which as yet cannot be regarded as entirely solved. Much labour has been expended on the cytology of this group by many skilled investigators, but the conflicting opinions which have been expressed render it a matter of the greatest difficulty to give in a brief space a reasoned account of what might be regarded as our present knowledge of the minute structure of the Myxophycean cell.

Several summaries of this work were given during the years 1903—6, notably those of Kohl ('03), Phillips ('04), Olive ('05), and Guillermond ('06). Subsequently these four papers formed the subject of a critical article by Zacharias ('07). Since then many more investigations have been made with a view to elucidate the rather obscure structural details of the Blue-green Algæ, and some of these have been summarised by Pavillard ('10).

THE CELL-WALL. The cell-wall may be regarded as the definite layer immediately surrounding the protoplast. It is composite in character, and consists in its earlier stages largely of cellulose. Later, it ceases to give any cellulose reactions, offers much resistance to the penetration of reagents, and according to some authors has much in common with fungus-cellulose. Its resistance to reagents caused both Borzi and Hegler to state that there is much resemblance between it and the cuticle of higher plants. Hyams and Richards ('02) have shown that it sometimes contains silica.

In the adult cell of *Oscillatoria* and *Lyngbya*, and in the cells and spores of *Anabæna*, the cell-wall consists, according to Fritsch ('05), of an 'inner investment,' which is a modified plasmic membrane of a viscous gelatinous nature, and a 'cell-sheath,' which is probably the modified innermost layer of the external sheath of mucilage (fig. 1). Unlike the inner investment, the cell-sheath is soluble in chromic acid except in the mature spore. The cell-sheath would appear to form a coherent whole around the filaments of the Oscillatoriaceæ, but in the heterocystous forms it is split at each cell-division.

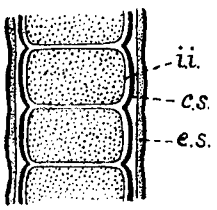


Fig. 1. Small portion of filament of *Tolypothrix* sp. after treatment with iodine. × about 1600 (slightly modified from Fritsch). *i. i.*, inner investment; *c.s.*, cell-sheath; *e.s.*, external sheath.

All Blue-green Algæ secrete mucilage to a greater or less extent. Most of the colonial unicells, and many of the filamentous forms, are embedded in a more or less extensive mass of mucus, the external surface of which may be covered with a thin cuticle. The gelatinous mass is frequently lamellose (fig. 2, *B*—*E*), and some or all of the layers may be coloured. In the filamentous forms the mucus is in the form of a sheath, which is often readily diffluent, as in *Anabæna*, many species of *Phormidium*, etc.; or it may attain various degrees of toughness and not infrequently become chitinized, as in *Lyngbya*, *Scytonema*, etc. Sheaths of this kind are the secretion of the enclosed cells of the filament, and all stages can be observed between a hyaline mucous investment and a tough, lamellose sheathing tube. The strong sheaths of some forms are therefore the homologues of the copious mucous integuments of others. All the gelatinous investments and sheaths originate as lamellæ, although this is sometimes scarcely evident, and they should really be regarded as portions of the cell-wall, in some cases undergoing gelatinization and in others a toughening to form a hard sheath. The gelatinous mass consists mostly of pectose compounds, and in certain species of *Glœocapsa* is brilliantly coloured. The investments of the unicells as well as those of the filamentous forms are often chitinized. In a few species of *Schizothrix* the sheath consists partly of cellulose and colours blue with chlor-zinc-iodine.

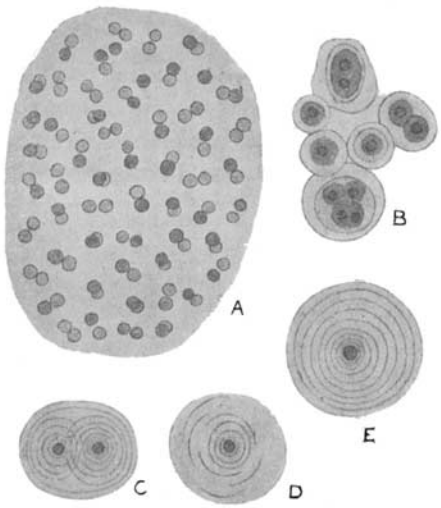

Fig. 2. Unicellular Blue-green Algæ embedded in mucus and showing the colonial habit. *A*, *Aphanocapsa Grevillei* (Hass.) Rabenh.; *B*, *Glœocapsa magma* (Bréb.) Kütz.; *C—E*, *Gl. montana* Kütz. All × 450.

The general function of the sheaths and gelatinous investments of the Myxophyceæ is undoubtedly to enable the plants to withstand periods of dryness, as the water is but slowly evaporated from such investments, and is very readily absorbed. They thus form a kind of water-reserve.

THE PROTOPLAST. Much controversy exists regarding the structure of the protoplast. It can readily be seen, sometimes even in the living cell, to consist of two parts, a peripheral coloured zone surrounding a colourless 'central body.' Both portions are generally granular, the granules of the central body being larger and as a rule only observable by appropriate staining. During the last thirty years this so-called *central body* has received much attention from cytologists, largely with the view of determining whether or not it should be considered as a true nucleus with functional activities of a similar nature to those exhibited by the nuclei of more highly organized cells. It occupies in most cases about one-quarter or one-third the volume

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of the cell, and its external form is largely determined by the shape of the cell; as for instance, in the numerous forms with disc-shaped cells where it is much compressed. The evidence brought forward concerning the precise nature of the central body is very conflicting, but most of the recent investigators agree that it differs considerably in its structural details from the nucleus of higher plants. The various authors come mostly within three categories: those who state that the central body is not a nucleus; those

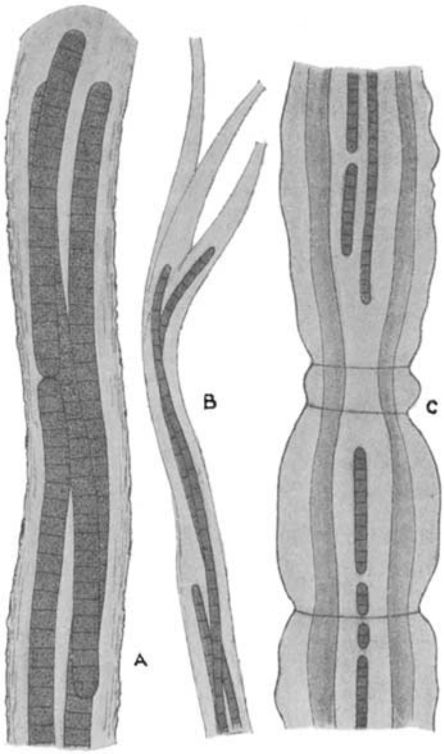


Fig. 3. Filamentous forms of Blue-green Algæ with conspicuous sheat
*Mülleri* Näg.; *B*, *S. lardacea* (Ces.) Gom.; *C*, *Dasyglœa amorpha* Berk. All ×460.

who regard the central body as a definite nucleus, comparable with that in higher types of cells; and those who hold the view that it is a nuclear structure of a somewhat primitive type.

I. Borzi ('86) failed to demonstrate the presence of a nucleus, and both Stockmayer ('94) and Zukal ('92) have declared that the central body has no relation to the nuclei of higher plants. Marx ('92), whose work was largely micro-chemical, concluded that it was not possible to demonstrate the existence of a nucleus. Zacharias ('90—'92) found that the central body differed in all respects from a true nucleus, and that there was no proof that it had the same function as the nucleus of higher plants. Deiniga ('91) did not assign to the central body the function of a nucleus, because, like Zacharias, he could not demonstrate its presence in all the cells of a filament. Palla ('93) found no chromatin in the central body, and regarded it as questionable whether it should be regarded as a nucleus or not; but he also added that the direct division may be more complicated than it appears to be. Massart ('02) affirmed that there was no reason to consider it as a nucleus owing to its vacuolation and indefinite outline. Macallum's investigations ('99), were mainly negative, and he believed that there was no cell-nucleus or any structure resembling one. Fischer ('05), in a very suggestive paper, also denies the existence of a nucleus. He describes, however, what he terms a 'carbohydrate mitosis' (or 'pseudomitosis of anabænin') which is an equal division of carbohydrate reserves by means of simple mitotic dispositions, but this interpretation of any of the structures described as occurring in the myxophycean cell has never been supported, whereas there is much evidence to the contrary.

II. In contrast to the opinions just enumerated, Wille ('83), Zacharias (in one of his earlier papers in 1885, the views in which he afterwards repudiated) and Scott demonstrated to their own satisfaction the presence of a body of a nuclear character. Hegler ('01) considered that his investigations conclusively proved that the central body was a nucleus. It consisted of a faintly stainable ground substance in which small granules were loosely embedded. The granules he regarded as chromatin because their behaviour during division, and towards stains and reagents, agreed in all respects with the behaviour of the chromatin of the nuclei of more highly organized cells. The nucleus, he stated, differs from that of higher types in the absence of a nuclear membrane and a nucleolus. Kohl ('03), as the result of some very careful work, states that the Blue-green Algæ possess a nucleus which differs from that of higher plants not only in the absence of a nuclear membrane and nucleolus, but also in its remarkable form. It possesses numerous radiating outgrowths of a pseudopodium-like character, which sometimes extend as far as the cell-wall and are retracted if the fixation is slow. It also contains a number of granules of albuminous material, the 'central granules,' and chromatin is always present distinct from other inclusions. Phillips ('04) regarded the central body as a true nucleus with chromatin in the form of hollow vesicles in the resting cell. Olive ('05) also stated that the central body was a true cell-nucleus.

The three last-named authors have each described a mitotic division of the declared nucleus during which a rudimentary spindle and rudimentary chromosomes can be demonstrated.

Gardner ('06) also considered the central body as a nucleus consisting of granules and chromatin embedded in an achromatic ground substance. He described three types of nuclear structure: (1) some forms (*e.g.* the large, short-celled species of *Oscillatoria*) in which the chromatin is disposed in the ground substance in the form of disconnected masses; (2) others (*e.g. Symploca muscorum*) in which it is partially united into a coarse, thread-like mass; and (3) still other cases (*e.g. Dermocarpa*) in which the chromatin is united into a definite network (fig. 4). The division of the nucleus was in all cases amitotic, with the possible exception of *Synechocystis* (fig. 8).

III. Between the extreme views of the above-mentioned authors there are the carefully considered opinions of those who regard the central body as a nucleus of a primitive or rudimentary kind. Hieronymus ('92) demonstrated the presence of granules in the central body, which, although not identical with chromatin, performed the functions of chromatin, and he also described the presence of vacuoles. He was the first to point out the absence of a nuclear membrane, and he suggested that the central body might well be regarded as an 'open nucleus' in contradistinction to the 'closed nucleus' of higher plants. Nadson ('95) considered the central body only as an aggregation of the middle alveoli of an alveolar protoplast, distinguished from the outer portion of the protoplast by the fact that it is the region where the so-called chromatin granules are exclusively or especially concentrated. He concluded that the central body corresponded to the nucleus of other organisms, but differed in its morphological peculiarities. Wager ('02) stated that the central body was vacuolated, and possessed granules which stained deeply with nuclear stains, resisted the action of digestive fluids, and gave strong reactions for phosphorus and masked iron. He considered that the granules had all the characters of nuclein and were comparable to the chromatin of a true nucleus.

Guillermond ('06) stated that the central body consists of a hyaloplasm in which there is an achromatic reticulum containing granules of chromatin. He regards it as a true chromatic network and compares it to the 'chromidial apparatus' described in

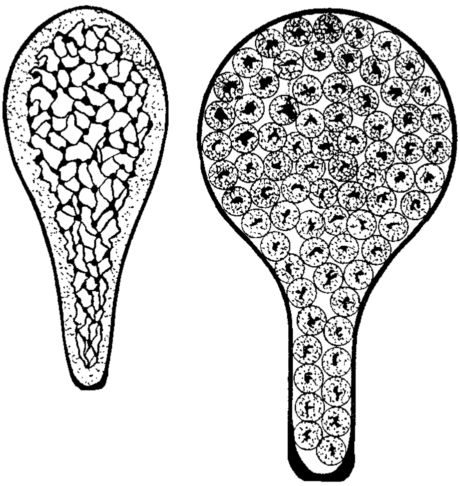

Fig. 4. *Dermocarpa fucicola* Saunders. Left figure, section of mature cell in vegetative condition, showing a thin layer of cytoplasm surrounding a definite network of 'chromatin.' Right figure, section of cell containing mature gonidia. Very highly magnified (after Gardner).

certain of the Protozoa. There is no spireme; there are no chromosomes, nor is there any division of the chromatin granules; and the division is amitotic. Swellengrebel ('10), from observations on only one species of *Calothrix*, found an alveolar achromatic ground substance in which were embedded granules and filaments of chromatin, with a more or less uneven distribution. He also stated that the distinction between the groundwork of the central body and the surrounding cytoplasm is somewhat slight, and sometimes the chromatin granules are diffused throughout the cell. The latter condition was observed by Guillermond, but only in vacuolated cells, and he therefore considered it merely as a pathological condition. Brown ('11) found in a species of *Lyngbya* a nuclear body consisting of a mesh of fine fibres embedded in a clear substance resembling nuclear sap. Small granules were scattered along the fibres, the latter staining like linin and the former like chromatin.

Still more recent work carried out by Miss Acton on various members of the Chroococcaceæ is largely confirmatory of Nadson's view that the protoplast is alveolar and that the 'central body' is a slight concentration of the alveoli in the meshes of which certain distinctive granules occur. This central concentration of the alveoli is really only apparent, as it is due to the absence of vacuoles from the 'central body,' whereas vacuoles cause a considerable breaking-down of the peripheral alveoli (consult fig. 5).

From this mass of conflicting evidence it is possible to sift out certain facts which hardly admit of dispute, and, if the whole question be carefully considered in the light of probable misinterpretations due to optical illusions and other causes, it is possible to arrive at conclusions which may not be far removed from the truth. The majority of recent workers agree that there is in the Myxophycean cell a structural differentiation (the so-called

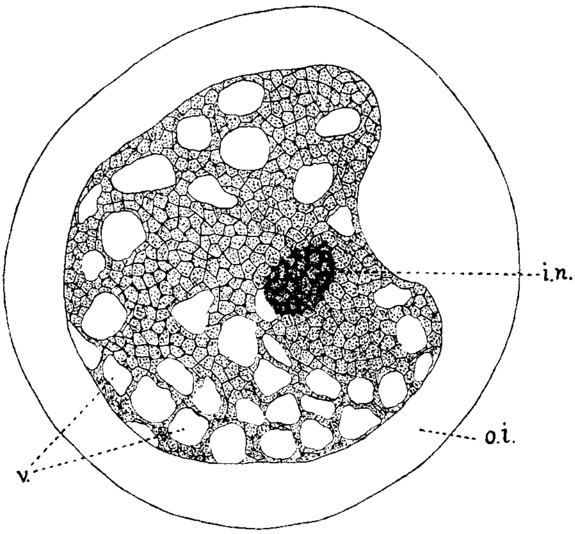


Fig. 5. Section through cell of *Chroococcus macrococcus* Rabenh. showing the incipient nucleus (*i.n.*) and the small vacuoles (*v.*) in the cytoplasm. The fine reticulation of the protoplast is also well shown. The outer line marks the limit of the outer integument or investment (*o.i.*) of the cell. × 1000 (after a drawing by Miss Acton).

'central body') which from its position and relationship to the rest of the protoplast is homologous with the nucleus. This body may be truly regarded as an *incipient nucleus*[1], and the disagreements as to the details of its structure are probably due to two causes: first, to morphological misinterpretations; and secondly, to the fact that it does not exhibit a uniformity of structure in the various members of the group. The Blue-green Algæ are undoubtedly very primitive organisms in which the protoplast shows the

[1] It would be preferable to discontinue the use of the term 'central body,' as there is no actual body with definite limitations. It is only a sort of concentration of varying degree of an alveolar protoplasmic network in which certain granules (possibly of one of the chromatin substances) are lodged, and would best be openly recognized as an *incipient nucleus*.

commencement of that differentiation which in higher types has resulted in the complete demarcation between nucleus and cytoplasm. Moreover, on considering the great differences in external morphological features which are exhibited by the various members of such a primitive group, it is not surprising that there should be different grades of incipient nuclear differentiation within the limits of the group.

This *incipient nucleus* consists of an achromatic ground substance occupying the alveoli of a reticulum in which are located minute granules, principally at the angles of the meshes. There is no limiting membrane to this structure, and in the more primitive forms the reticulum is directly continuous with that which occurs in the rest of the protoplast. Concurrently with the absence of a limiting membrane there are in some forms radiating processes of the achromatic ground substance, which have been shown to extend through the coloured portion of the protoplast as far as the cell-wall.

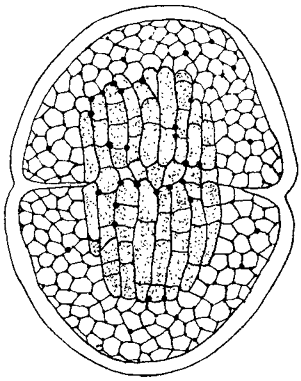

Fig. 6. Cell-division in *Chroococcus turgidus* (Kütz.) Näg. The drawing out in approximately parallel lines of the network of the incipient nucleus is well shown. Stained: iodine-green-fuchsin. ×1000 (after a drawing by Miss Acton).

The granules disposed along the threads of the mesh behave with stains somewhat after the manner of chromatin, but the staining is rather imperfect and less constant. They may be considered as the nucleo-protein substance which, in the course of the evolution of the higher types of protoplast, has become true chromatin with decisive staining properties. It is not at all improbable that these granules were in the first instance merely protein reserves[1], and they are most probably to be identified with Bütschli's 'red granules[2]' and Guillermond's 'corpuscules métachromatiques.'

No structures corresponding with nucleoli exist.

In some of the Blue-green Algæ (*e.g. Chroococcus macrococcus*) there is a clear differentiation of this incipient nucleus (fig. 5), whereas in contrast to this relatively advanced type, the most primitive of all the Myxophycean protoplasts is perhaps that of *Myxobactron* in which a differentiation has not yet been demonstrated (G. S. W., '12). The vacuoles described by certain

[1] The quantity of 'chromatin' described and figured by Gardner ('06) is so surprisingly large that one wonders whether it is really chromatin or merely the accumulation of protein reserves which behave very like chromatin with nuclear stains. Also, is not Gardner's 'chromatin' identical with Hegler's 'anabænin'? It seems probable that both observers were dealing with the same substance notwithstanding the wide difference of interpretation.

[2] These granules must not be confused with 'Bütschli's red corpuscles' in Diatoms.

authors as occurring in the 'central body' are probably due to pathological conditions and occur in cells which are undergoing degeneration.

*Division of the protoplast.* On the division of the cell there is much evidence to prove that the incipient nucleus divides without any mitosis such as is understood in fully differentiated nuclei. There is a constriction of the incipient nucleus, but the only suggestion of mitosis, even in the most highly developed species, is a slight tendency of the net-work to become drawn out in parallel lines, though the meshes are not broken except by the advancing constriction (fig. 6). The presumed chromatin granules do not divide during this amitotic division, but an approximately equal number is found in the two parts after division. There are in the numerous members of the Myxophyceæ various degrees of differentiation of the nuclear structure, which may account for the fact that the division has been interpreted in so many diverse ways. In some cases the constriction of the incipient nucleus takes place before the appearance of any division of the protoplast as a whole, and the view held by Macallum that the 'central body' initiates division is in these cases probably correct. In *Chroococcus macrococcus* there may be a twice-repeated division of the primitive nucleus before there is any sign of the division of the cell itself. In the Chroococcaceæ division of the cell occurs by a gradual constriction, either at the time of division of the primitive nucleus or subsequent to it. There is no septum laid down. On the other hand, in many of the Myxophyceæ with cylindrical filaments a transverse septum is formed on division, and the inward growth of this septum gradually divides both cytoplasm and primitive nucleus into two more or less equal parts.

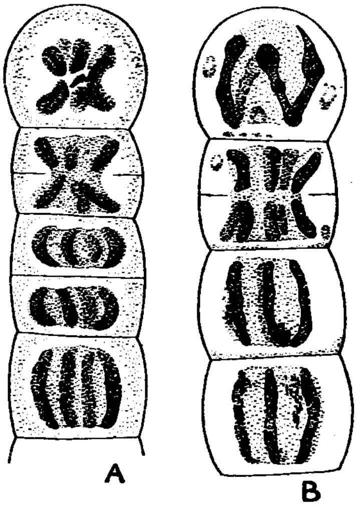


Fig. 7. *A* and *B*, the ends of two trichomes of *Tolypothrix lanata* (Desv.) Wartm., showing successive stages of supposed mitosis. Fixed in sulphurous acid and stained with iron - ammonia - alum hæmatoxylin. × 1160 (after Kohl).

The nuclear mitosis described by Kohl (consult fig. 7), Olive, and Phillips is probably of the nature of an illusion since it is quite easy to imagine the presence of mitotic figures in stained preparations of the dividing cells of many of the Blue-green Algæ. There is, however, such a mass of evidence to the contrary that the mitotic figures of supposed dividing nuclei published by these authors must be considered as the result of unconscious self-deception.

That the central differentiation of the Myxophycean cell can be regarded as an incipient nucleus is fairly clear, but it is not at all clear to what extent the nuclear functions are localized. The mere fact that division of the protoplast may begin by the ingrowth of a ring-shaped septum before there is any indication of division in the primitive nucleus seems to show that that structure has not yet acquired all the physiological attributes of a true cell-nucleus.

THE PIGMENTS AND THE CYTOPLASM. In the majority of the Myxophyceæ the cells are of a rich blue-green colour, the pigments being located in the peripheral zone of the protoplast which surrounds the incipient nucleus. There are three pigments of importance, viz. *phycocyanin*, *chlorophyll*, and *carotin*, of which the first is generally the most abundant and to a great extent masks the chlorophyll. It is the combined effect of the phycocyanin and chlorophyll which gives the characteristic 'blue-green' colouration to the cells. Some forms are reddish-pink in colour and others violet; the former colouration is due to the predominance of carotin, and the latter to the predominance of both phycocyanin and carotin over the

Fig. 8. *Synechocystis aquatilis* Sauvageau, showing various stages of cell-division. Very highly magnified (after Gardner).

chlorophyll. One form of carotin has been named *polycystin* by Zopf; and another form, which is identical with Sorby's *pink phycocyanin*, has been named *myxophycin* by Chodat. All these pigments can be extracted by appropriate methods (consult Lemmermann, '07, p. 9). The phycocyanin is soluble in water, and after rapidly killing the cells, may be easily obtained as a brilliant blue solution from which it can be crystallized.

It has long been known that the Myxophyceæ occurring in deep water are for the most part tinted red, and Gaidukov ('04—'06) has suggested that this is a complementary chromatic adaptation due to the fact that the quality of the light is affected by the depth of the water through which the sun's rays have to pass. He found that a species of *Oscillatoria* changed its colour when grown behind coloured glass or coloured solutions, and that the change was always in the direction of taking on the colour complementary to the light in which it was placed. This complementary colour was only assumed after a series of colour changes, and when once acquired was retained for months after the Alga had been restored to white light.