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STUDIES ON MORPHOLOGICAL PROGRESSION AND EVOLUTION IN THE VEGETABLE KINGDOM

BY

TYGE W. BÖCHER

København
i kommission hos Ejnar Munksgaard
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Introduction.

A series of morphological progressions consists of forms which morphologically become more and more complicated. Morphology is here used in the widest sense of the word, thus including anatomy, cytology, and cell-physiological conditions underlying morphological differences. The series of morphological progressions does not require genetic relationship between its steps. It may serve the understanding of the evolution that has taken place, but is not necessarily an evolutionary series. The evolutionary series, on the other hand, requires genetic relationship. It is not always a series of morphological developments, and in respect of the morphological factors may be either progressive or regressive or both, because some organs may develop into a more and more complicated structure, while at the same time others are simplified. To the question of the purpose of distinguishing between morphological progression and evolution this answer may be given: the introduction of the concept of morphological progression means a simplification: the material is considered from one point of view, only, viz. the morphological point of view. At each stage in the series a change takes place which may be defined and mostly demonstrated on recent material. The progression may be briefly expressed through these definitions and these, again, may be used to establish the degree of organisation of a group of plants. By definitionally keeping morphological progression apart from the concept of evolution we obtain a breadth of outlook which is not only of interest in itself, but which may probably be of a certain importance for the theory of evolution as well since the stages of morphological progression have no doubt been traversed by the world of plants during the history of the earth.

At the definitions of the various stages of progression conditions of polarity play a decisive part. Unfortunately the physiological aspect of polarity is not sufficiently known at present. Hence some of the views advanced here will perhaps prove premature or erroneous.

The Main Series of Morphological Progressions.

The main series is used here to denote the series in which there are most stages or steps and in which the final stage comprises plants with the greatest possible morphological differentiation. Besides the main series there are several others, which seem to end at a comparatively low stage of organization.

(0), (1), and (2). From Homopolarity to Heteropolarity.

Certain forms of virus are considered by many research-workers to have a primitive form of life. The complicated, chemically very active substances of which the virus consists have the quality of being able to propagate themselves. The individual molecule forms another molecule of the same type as itself. On the whole the same thing happens when a chromatin apparatus in a cellular organism divides. Every molecule in that apparatus may re-form. The chromatin regulates the processes taking place around it in the rest of the living substance. When by the re-formation of the chromatin apparatus in a cell two similar chromatin masses have developed, there are really two centres, and if these move apart, two poles are formed in the cell in connexion with the two centres. The plant forms in which the polarity in the cell is connected with the process of cell division no doubt represent the most primitive of all types.

Such genera as *Lamprocystis* among the sulphur bacteria or *Microcystis* among the blue-green algae may serve as instances of the most primitive stages that can be established in plants. The cells divide in every direction and are without special organs of locomotion. The *Microcystis* cell is built centrically with an external photosynthetic plasma and an interior in which i. a. the chromatin is found. The photosynthesis conditions a growth of the cell. One might suppose that the cell increased in size during its growth,—that the ball expanded. But this does not happen[1]. It extends in one direction and then divides. We may imagine that certain substances on which the growth depends accumulate in two poles in the cell orientated in opposite directions. These poles are alike. We may term this phenomenon *homopolarity*.

It seems that in the homopolar organization we have found a primitive starting-point; for it is hardly possible to visualize an apolar organism. Geitler (1936 p. 24), it is true, applies the term apolar to homopolar blue-green algae, but adds that this does not mean that these are without predetermined planes of division. Even spherical cells at any rate at times have an axis, i.e. a line between two poles. For that matter apolar organization seems impossible, if only from the following consideration. The form, size, and structure of the undivided spherical cell depend on the genes of the chromatin apparatus. When during the growth of the cell the genes have re-formed so that there are two sets of them, each of these will have properties conditioning the formation of cells of the same size, form, and structure. Therefore the cell does not expand in all directions, but extends and divides into two. Robinow's investigations (1947) of cell divisions in the rod-shaped bacteria are very interesting in this connexion. He has been able to show that the rod-shape was highly the result of an extension of coccoid cells in connexion with rapid successive divisions of chromatinic bodies without a simultaneous division into new cells. In *Escherichia coli* there is a chromosome-like body which splits longitudinally, and the homopolarity of the cell seems completely in accordance with the bipartition of the chromatinic bodies.

The establishment of the fact that homopolarity may change direction is of importance for our understanding of the most primitive homopolar state. The axis connecting the poles may change its situation and e. g. turn through an angle of 90°.

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[1] Heitz (1940, 1942) supposes that the polarity is due to accumulation of growth substance in one part of the cell, thinking of the heteropolarity frequently found in mosses (see below). Starting from this point of view he tried to prevent germination of heteropolar spores of moss by many-sided artificial addition of growth substance. By means of β-indolyl acetic acid he succeeded in making spores develop into larger balls of a volume 40—50 times as large as that of the original spores.

In *Bacterium megathericum* ROBINOW (*loc. cit.* p. 377) by cultivation on 2 per cent. malt agar succeeded in producing sarcina-like clusters by the plane of cell division being turned through 90°. A homopolarity which might be shifted in any direction is probably the most primitive type. Perhaps it corresponds to what was termed radial polarity by SCHUSSNIG (1938). And it may be influenced by external conditions. However, SCHUSSNIG confuses various things since under radial polarity he classes partly the *Chroococcaceae,* partly the *Fucus* zygote. The *Fucus* zygote is not homopolar, but heteropolar. Its polarity appears only at the germination (see INOH 1935) and the division plane of the cell depends on various external conditions, e. g. the direction of incidence of light, *p*H, differences in temperature, influence of certain chemical substances (see ROSENVINGE 1888, LOWRANCE 1937, WHITAKER 1942, WHITAKER and BERG 1944). A similar development is found in *Equisetum* spores (cf. MOSEBACH 1942).

SCHUSSNIG in his work also mentions the existing criteria of polarity in unicellular plants. There are partly morphological, partly physiological criteria, among which he reckons the direction of motion. A flagellate with flagella at one pole here has a distinct front part, thus even if the flagellate is swimming backwards, with its front part behind. In this I agree with him, but when in the same context he mentions a bacterium with flagella at both ends and assumes that only the direction of motion can decide which is the anterior and which is the posterior part, I think he attaches too great importance to the direction of motion. Instead of supposing that the polarity in such a bacterium incessantly changes its direction, I should prefer to consider the bacterium as homopolar, as both ends of it may function as front part, and which end at the moment in question will have the strongest effect, will depend on the stimulation to which the bacterium is exposed. It must be the morphological polarity which is decisive, not a fortuitous state which is made possible by the special structure of the cell.

The transition from a homopolar to a heteropolar state in unicellular plants can no doubt be best studied in bacteria, where the flagella may be placed on all sides (peritrichous), at both ends (amphitrichous), or at one end. Among these the peritrichous type—if existing at all—must be placed first as any polarity as regards flagella is here absent. Next comes the amphitrichous type with homopolar insertion of the flagella, and finally the forms which have one flagellum or a cluster of flagella placed onesidedly. These monotrichous or lophotrichous forms are heteropolar. The transition which can be studied here is not influenced by external conditions. It is a question of different stages of organization.

After these considerations we can more closely define the first stages in the main series of morphological progressions:

(0) Shifting homopolarity.

The plane of division of the cell is not fixed, but can theoretically be in all directions. Polarity closely connected with differences arising in connexion with the mechanism of cell division.

(1) Fixed homopolarity.

The plane of division of the cell is fixed. Morphologically distinct poles are found, which have the same structure. Polarity not always connected with differences arising in connexion with the mechanism of cell division.

(2) Heteropolarity.

Morphologically distinct poles of different structure. The plane of division of the cell is fixed or shifting by the influence of external conditions. Polarity as a rule independent of the mechanism of cell division.

An organism like *Chroococcus turgidus* is at a transitional stage between (0) and (1). Here the plane of cell division is regularly turned through ab. 90°. If the first division is in one direction, the following ones will as a rule take place in a direction transverse to that of the first division. The shifting polarity here is restricted to several definite planes. In *Eucapsis* there are three planes of division at right angles to each other and hence cubical colonies, in *Merismopedia* only two such planes and square-tabular colonies. Finally there is one plane, only, in plants forming catenulate colonies, and here we may therefore use the term of fixed homopolarity.

It is more difficult to find forms showing the transition between homo- and heteropolarity, (1) and (2). We must resort to pluricellular forms, i. e. forms belonging to Stage (3), to

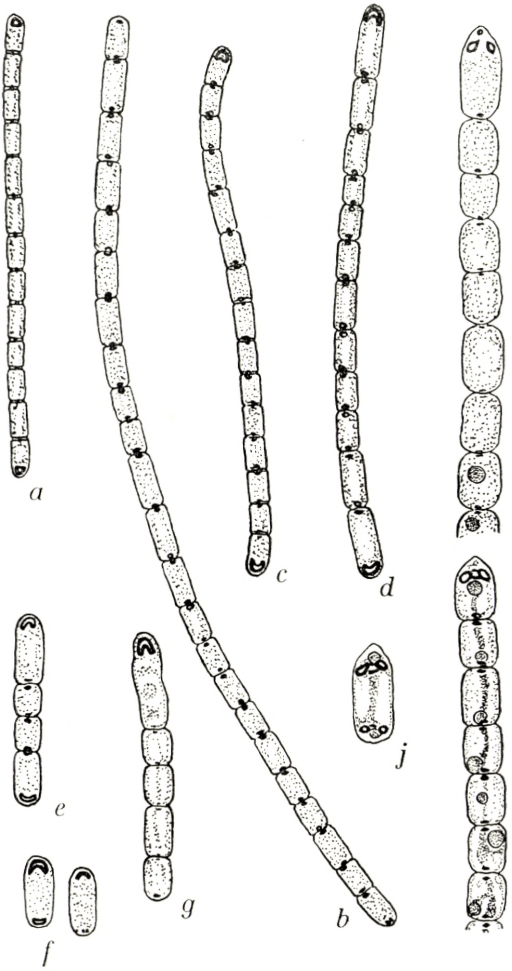


Fig. 1. a—g *Pseudanabaena galeata*, h—j—k *Pseudanabaena biceps*, f and j unicellular "hormogonia" (detached terminal cells). × 1700. After Böcher 1949 a.

illustrate this transition. *Pseudanabaena biceps* and *galeata* are particularly suitable. They are unramified, filiform, with specially equipped terminal cells in which the polarity particularly appears in the terminal placement of the gas vacuoles (Böcher 1949 a). In both species the terminal cells may be detached and grow into new filaments. At the detachment the cell is heteropolar, but soon after it develops in a homopolar direction, small gas vacuoles developing at the end which before the detachment was turned .away from the apex. The cell now gets two similar ends, which are distinct from the middle of the cell. Then it divides and the wall develops in the central part, which no doubt both structurally and chemically differs from the ends. The wall comes to separate two heteropolar cells, the polarity of which is diametrically opposite. Taken as a whole the filament is homopolar, but its various cells are heteropolar. The filament may move in both directions, but as in a train on the suburban railway we cannot speak of a front part and a hinder part. The above-mentioned transformation of the polarity in a detached terminal cell suggests that after the detachment certain chemical changes take place which result in the formation of gas vacuoles in the end just detached. In *Pseudanabaena biceps* this end gradually becomes bright and tapering. The substances most probably existing which give rise to the development of the special structure in the terminal cells may be called terminal substances. As long as the terminal cells are connected with the other cells the terminal substances will have a retarding effect on the pole turning away from the apex. After the detachment the terminal substances will gradually be distributed more and more evenly to the poles until homopolarity has been obtained. To go from a homopolar to a heteropolar state we need only think of a constant retardation of one pole or a constantly unequal distribution of such terminal substances.

In its structure *Pseudanabaena* reminds of a *Streptococcus*, and it was mentioned above that rod-shaped bacteria in certain cases might be regarded as undivided chains of coccoid units. In such forms, too, it may therefore be supposed that there are differences of polarity of the same type as that mentioned. The question now arises whether the heteropolarity arising in such threads can be supposed to be the source or a condition of the heteropolarity occurring in unicellular plants, e. g. in monotrichous bacteria. This can hardly be excluded, but it will mean that heteropolarization follows after trichomatation: trichomatation will be Stage 2 and heteropolarization Stage 3. In this connexion it should be kept in mind that most heteropolar unicellular organisms, e. g. flagellates, have an extremely complicated, greatly differentiated cell structure. However, in numerous cases it is hardly possible to imagine the heteropolarity as having arisen with trichomic forms as intermediate stages, and perhaps this is not necessary, either. When a unicellular heteropolar organism divides, such as e. g. *Ochromonas granularis,* it passes through a homopolar state in the anaphase. The difference between the *Ochromonas* species and a *Pseudanabaena* is that the former after the detachment of the cells does not regenerate a terminal pole in the detached end. Immediately before the detachment of the cells these have opposite polarity, a—b, b—a, and this is maintained. In *Pseudanabaena* we also in a detached terminal cell find the distribution a—b, but here the state then is changed in the direction a—b—a.

(3) Trichomatation.

Already in diplococci or blue-green algae such as *Synechocystis* we find the first beginnings of trichomatation. Trichomatation also takes place in diatoms and desmids, but here the trichomes are considered to be in the nature of colonies or cenobia, while e. g. in the *Oscillatoria* they represent a genuine pluricellularity. The criterion of genuine pluricellularity must be the mutual physiological interdependence of the cells. Visible evidence of a dependency or a collaboration appears in the existence of pores and plasmodesms between the cells. However, it cannot be concluded from the absence of plasmodesms that there is no interdependence of the cells, for it may be assumed partly that there are often submicroscopical plasmodesms present, partly that there may be permeation of substance through the cell wall. Hence it may sometimes be difficult or impossible to decide whether an organism is organized as a filiform colony or as a trichome.

The above-mentioned homopolar trichome found in the *Oscillatoriaceae* will not be mentioned in detail here. It only belongs to the main series provided that it represents a stage which is lower than the heteropolarization. On the other hand the trichome which has a heteropolar structure with a base (attachment cell) and a part growing upwards clearly represents a higher stage in the progressive main series. Such a heteropolar trichome is found already in blue-green algae, such as e. g. *Endonema* (see Pascher 1929) and here has its starting-point in a spherical endospore. In the green algae, on the other hand, the starting-point is a swarm cell of a heteropolar structure which attaches to a substratum and germinates. Schussnig (*loc. cit.* p. 229) mentions that the swarm cell is attached at the front part and that the rear end then grows into a filament. He is of opinion that the polarity in the cell thus obtains an opposite direction. Here it should be noted that the cell is still heteropolar and that we can hardly compare "front" and "rear" in a swarmer with base and apex in a algal trichome. Recent investigations (Kostrun 1944), indeed, have shown that the polarity of the swarmer in green algae mostly is in good accordance with the polarity of the filament. In the cases in which only one swarmer is formed in each mother cell, the longitudinal axis of the swarmer will correspond to the transverse axis of the mother cell. If such a swarmer is attached by the front part, the contents in the part containing the chromatophore are turned through 90°, so that the original polarity of the mother thread is retained. Other swarmers are attached at the flank and grow out without any turning of the contents. Finally there are forms in which the longitudinal axis of the swarmer comes to correspond to the longitudinal axes of the germling without it being possible to see whether there have been any changes in the contents of the cell. Kostrun here supposes that there may be submicroscopical plasmatic changes corresponding to a turning of polarity through 180°. It seems easier to me merely to think of the front part of the swarmer as physiologically corresponding to the basal end of the trichome.

(4) Simple Ramification.

A next important stage is reached when the trichome ramifies. The ramification which takes place in blue-green algae, both the genuine and the false ramification, however, does not belong to the main series, as even the "genuine" ramification here is of another and more primitive character than that found in other Thallophyta. It is characteristic of most of these that the ramification starts from the upper end of the cell (fig. 2). Only

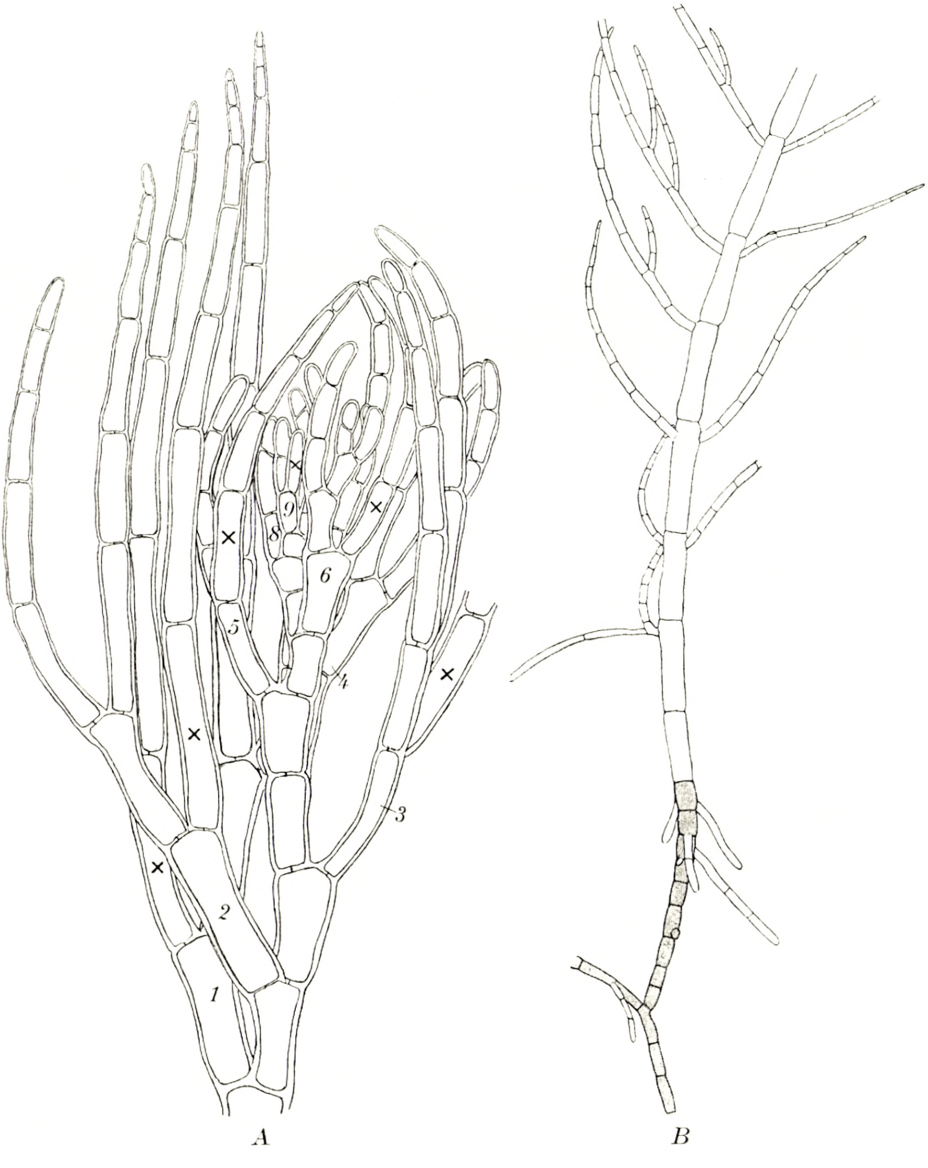


Fig. 2. Examples of simple ramification. A. *Callithamnion tetragonum* var. *fruticulosa*. Upper part of sterile branch. Branches of the first order are numbered. The branches marked with × are of the second order. — B. *Anthithamnion boreale*. Distichous ramification having arisen by the formation of two opposite a_1 poles. Below, rhizoids issued from b poles. A × 200, B × 95. (After Rosenvinge).

in certain much derived forms such as e. g. *Bostrychia*, where the branches form a cortical covering around a central cell filament, the rows of cells corresponding to branches may issue from basal parts of the cells (Falkenberg 1901). In forms of algae in which rhizoids or so-called hyphae develop by ramification, these as a rule are given out from the lower parts of the cells. In both cases the ramification must be supposed to be due to a division of the existing poles into an axial and a lateral pole. When the lateral pole is formed in the upper part of a cell, a lateral branch develops. If it is formed at the base, a rhizoid may develop. No real repolarization has taken place, but there is a division of the existing poles. Now it appears that the branches mostly grow obliquely upwards and grow less intensely than the main filament. Thus, at the division of the poles two similar upper poles and two similar lower ones have not developed, but the lateral ones are slightly different from the axial ones. A difference in polarity has arisen transversely to the longitudinal axis, this difference being maintained together with the longitudinal or axial polarity. In the diagrammatical figures (fig. 4) the axial polarity is termed a—b, the transverse or radial polarity a_1—a_2—a_3, etc.

In a very great number of uniseriate filiform algae with a heteropolar structure the very lowest cells at the ramification are apt to form rhizoids or attached branches only, while the upper cells form obliquely upwards growing lateral branches only (fig. 2 B). This may be supposed to be due to a different concentration of the substances determining the poles. The "a-substances" are in excess in the whole of the upper region, the "b-substances" in the lower cells. According to this theory the a-substances in a homopolar filament will have the intensest concentration at the ends, which undeniably goes very well with the appearance of *Pseudanabaena* (figs. 1 and 7 A). Conditions of ramification in a number of *Chaetophoraceae*, e. g. *Stigeoclonium lubricum*, are interesting in this connexion (see figures in Berthold 1878). At the germination of the zygote a plagiotropic filament creeping in both directions develops, thus a homopolar filament. Provisionally disregarding the upright branches and only looking at those creeping like the mother filament, it may be established that the lateral branches towards the two ends are given out typically from the distal end of the cell, while those in the middle of the mother filament are issued medianly. The midmost cells in such a filament will be more or less homopolar with two comparatively weak poles and a median "pole" which is unimpaired or even strengthened (cf. fig. 7). Therefore it is this median "pole" which here gives rise to the lateral ramification, and the branches morphologically develop like the other distally issuing lateral branches, but the branches from the central cells grow out at right angles to the mother filament. In the diagrammatical figures the poles are marked with α and β in order to show that this is a slightly different type of polarity, which is horizontal, or, better, depends on the plane of the substratum.

(5) Pluripolar Ramification.

In *Stigeoclonium*, however, also upright shoots are given out and it now appears that these, like the branches reduced into hairs, issue from the middle of the cells. This shows that besides the poles α and β a new pole must have developed in these cells, upwards and in the middle of the cell. Here there is no division of an axial pole, but a new-formation.

Before going on, a consideration of the red alga *Trailliella intricata* is of importance, because this alga besides creeping filaments with α—β-polarity has upright main filaments and downwards turned filaments forming haptera (fig. 3). These hapteron shoots like the erect ones issue from the middle of the cells, but diametrically opposite to the former. This clearly

Fig. 3. *Trailliella intricata.* Creeping filament with erect filament and hapter. × 260. After Rosenvinge.

shows that the cells must have four main poles and two crossing axes. They have a horizontal α—β-polarity and a vertical a—b-polarity. As both in the horizontal plane and in an upward and downward direction lateral branches may be given out (often in the form of small gland cells) which are placed regularly near α-, a-, or b-poles, this shows that here we have to do with a very complicated form of polarity. This is the one which is the cause of pluripolar ramification.

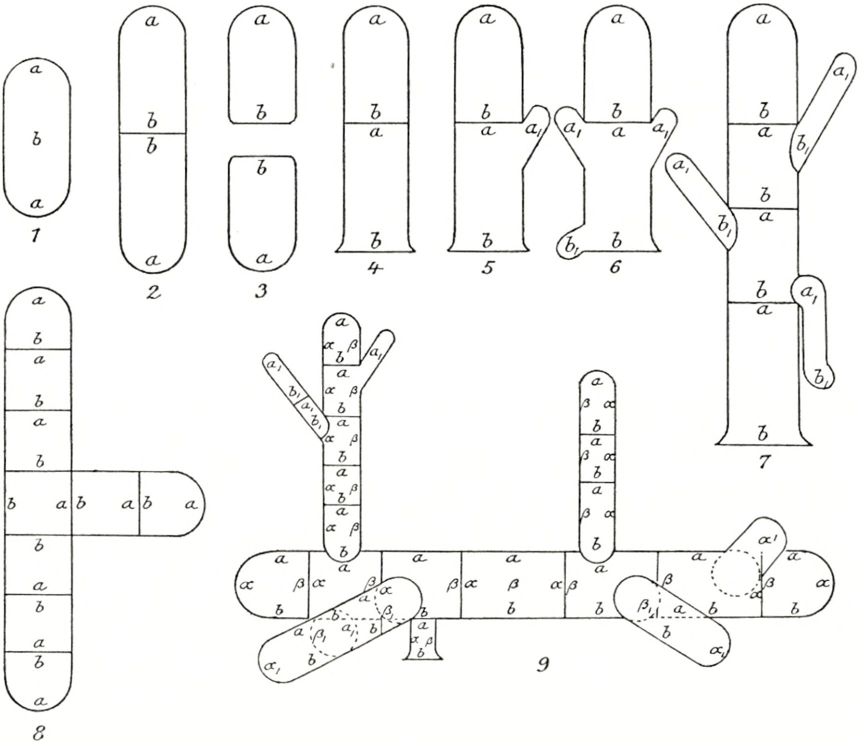


Fig. 4. Diagrammatic figures showing the theoretical conditions of polarity in algae which are unicellular or consist of one row of cells. 1 homopolar unicellular, 2 homopolar bicellular, 3 heteropolar unicellular, 4 heteropolar bicellular, unramified, 5 heteropolar with incipient simple onesided ramification, 6 the same with two-sided simple ramification and rhizoid formation, 7 heteropolar with simple ramification, 8 homopolar with ramification due to turning of polarity (*Stigonema* type), 9 pluripolar ramification (as in *Stigeoclonium lubricum* or *Trailliella intricata*).

The morphological stage of algae of this type is very important as it is possibly a condition of a further progression. It will not be possible to illustrate this until an account has been given of the next stage.

(6) Simple and Pluripolar Syntagmation.

Syntagma is used by SCHUSSNIG to mean "alle jene Thallusbildungen deren anatomischer und organogenetischer Aufbau die Zusammensetzung aus mehreren bis zahllosen, zunächst gleichartigen, später differenzierten Faden oder Schlaucheinheiten erkennen lässt". SCHUSSNIG here is thinking of the thallus as a whole, in the algae, if anything, OLTMANNS' "Springbrunnentypus" and derived forms, and the thallus in lichens and in the fruit body of mushrooms. The peculiarity about the syntagma type is the coalescence of single filaments into larger bodies. Such a feature may also be observed in plants built on other principles. In e.g. *Polysiphonia* and *Delesseria* there are main axes from which lateral axes issue. These, however, do not develop as free cell filaments, but either coalesce into cylindrical bodies or into flat leaf-like bodies. Any form of sideways coalescence of originally similar filaments into firmer bodies may be termed *syntagmation*.

We may now distinguish between a syntagmation of filaments with simple ramification, and syntagmation of filaments with pluripolar ramification. These two types may be termed *simple* and *pluripolar syntagmation*. They cannot be regarded as two independent stages, for it is highly questionable whether the simple syntagmation belongs to the main series. Indeed, it is not necessary to think of simple syntagmation as the basis of the pluripolar one, even if a close connexion between these types is not excluded.

Simple syntagmation is found e.g. already in the cortical zones of a *Ceramium*. Here, however, only primary pores are found between the cells, i. e. the original branches indeed have coalesced, but physiologically they still seem to constitute connected systems of cells. In *Polysiphonia* the syntagmation is more intimate as secondary pores develop between cells which do not belong to the same original system of branches. At the secondary pore formation i. a. *a cell fusion* takes place through which the most intimate contact is obtained. In *Delesseria* as well, which has simple syntagmation, there are plenty of secondary pores (ROSENVINGE 1909—31, p. 466). In the genus of green algae *Coleochaete* there are in the plagiotropic thallus pressed against the substratum all possible transitions between quite free cell filaments and cell discs which have arisen by fusion of plagiotropic filaments (cf. Schussnig, *loc. cit.* pp. 276—277 "Nematoparenchym").

Among the kind of forms which show pluripolar syntagmation there are also degrees of the intimacy of the coalescence. In a "fountain type" like *Furcellaria fastigiata* it is still easy to pursue the individual filaments and their ramifications and there do not seem to be any secondary pores. In other, more derived forms there is a more intimate contact; the cells communicate through numerous prolongations penetrating the very thick walls (e. g. in *Eucheuma speciosum,* fig. 22 in Börgesen 1943). It is no doubt correct to speak about a higher degree of contact, for the filaments in a *Furcellaria* are hardly without contact, the reason being that even though there may not be any secondary plasmodesms between parallel filaments, neither microscopical nor submicroscopical ones, the occurrence of a mutual influence by secretion and absorption from the cells is not excluded. Unfortunately too little is known about this feature.

The germination of the spores and the first stages of growth are of the greatest importance for our understanding of pluripolar syntagmation. In a great number of forms a compact cell disc or hemispherical body closely attached to the substratum develops. Such a basal disc must have developed by divisions partly in a horizontal, partly in a vertical direction, and thus may be regarded as a syntagmation of filaments with both α—β- and a—b-polarity.

Later the erect, pluriaxial main shoots are given out from the basal disc. We may now, no doubt rightly, assume that previously several differences in polarity have arisen between the cells in the basal disc, which grows up to the erect shoots. The probable difference in substances determining the poles in a homopolar, plagiotropic filament was mentioned above. In quite a corresponding way it may be supposed that there are differences in concentration between the central parts of the basal disc and the peripheral parts, which, as said above, correspond to ends of filaments. The appearance of the erect shoot therefore has been determined already in the basal disc. A chemical influence from filament to filament therefore, as assumed above, is hardly the most decisive factor for the morphological development of the plant body. The mutual relation between the filaments—the radial polarity—is determined already before they shoot up. It seems possible to derive this radial polarity from homopolarity during plagiotropic growth by coalescence of plenty of filaments and branches with such growth.

In species with apical or intercalary meristems there is at the development of the meristem a similar radial polarity as in the basal disc, and in these cases it spreads downwards or both up and down, as e. g. in *Nereia filiformis*, which was thoroughly investigated by KUCKUCK (1929).

Forms with large top cells, as found e. g. in *Sphacelariales, Dictyota*, and *Fucus*, might seem greatly deviating from forms with meristems. However, there are a great many features which indicate that growth of a top cell is not a primary, but a secondary phenomenon. As regards *Dictyota* and *Fucus* SCHUSSNIG supposes that the top cells have arisen by sideways "fusion" of several meristem cells. On the other hand, he keeps the *Sphacelariales* outside such a view because in the case of this group he imagines the radial polarity to have arisen in connexion with a suppressed lateral ramification from a main filament (changed central axis type). However, the development of a basal disc in *Sphacelariales* and the transition within this order from the uniseriate *Sphacella* to the pluriseriate *Sphacelaria*, if anything, indicates that the *Sphacelariales* belong to the stage of pluripolar syntagmation. Hence the large top cell may here, too, be interpreted as a "fusion product", which, however, should not be regarded as referring to a real fusion, for what has happened is probably one or more mutations, which have caused plants with genes for a multicellular meristem of pluripolar cells to develop into plants with genes for a single pluripolar top cell. Top-cell growth thus may have developed on the basis of meristem growth, but nothing has happened to justify a reference of forms with top cells to a higher stage in the series of morphological progressions. A *Fucus* or a *Dictyota* with top cell is not at a higher stage than a *Laminariacea* with an intercalary meristem. Besides, it should here be noted that forms with top cells do not belong to the main series.

Already a cross-section of an erect shoot in an alga with a comparatively simple structure like *Furcellaria fastigiata* shows a clear anatomical tripartition of the shoot into a central string of very long, narrow cells, an inner cortex of rather large, short cells, and an outer cortex of small, assimilating cells. The zones are not well-defined and can easily be connected with the above-mentioned radial polarity. In other red algae the differences become more pronounced. As an example may be mentioned

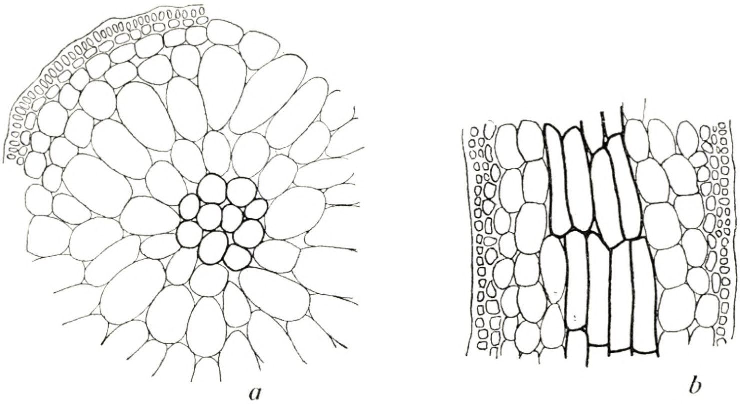


Fig. 5. *Mychodea chamaedoridis* Börgs. a transverse section, b longitudinal section of the thallus. × 60. After Börgesen.

Mychodea chamaedoridis described by Börgesen (1943); see fig. 5. Here there is nearly a tripartition into stele, cortex, and epidermis, and at any rate a close approach to the anatomical differentiation found in stems and roots of primitive archegoniates (cf. p. 21).

(7) Differentiation of idioblasts and formation of cell patterns.

With this stage we are no doubt for the time being at the limit of what on the basis of morphological investigations we dare imagine as regards conditions of polarity. A number of algae both morphologically and anatomically reach a very high degree of differentiation presupposing a further complication of conditions of polarity. We may remind of the sieve-tubes and mucilage canals in *Laminariales* and conceptacles (incl. cryptoblasts) and air bladders in *Fucus*. Also the thalli of macrolichens and the fruit bodies of macromycetes reach very high stages. They represent stages above syntagmation itself, but they do not belong to the main series.

The fundamentally new about these forms in relation to such as only reach syntagmation itself is the development of idioblasts or special systems of tissue which collaborate in such a way that we can begin talking about vegetative organs.

The development of conceptacles in the *Fucaceae* is very instructive. The hair pits are found distributed on the surface of the plants and at more or less regular distances from each other. At certain definite intervals initial cells arise which cause the development of these organs. It very much reminds of the development of lip cells in the epidermis in the cormophytes. Such a differentiation within the same anatomical area in certain definite places (formation of a cell pattern) presupposes a form of polarity on a somewhat higher plane than the above-mentioned forms of polarity. It must be admitted that even in blue-green algae, which otherwise have a very simple structure, there are regularly intercalary cells of a deviating structure (heterocysts). Also hair shoots may occur with great regularity in many algae. However, the conceptacles in *Fucus* and the lip cells with the air-chambers behind them have the character of multicellular organs and may be the result of more complicated cell differentiations.

Cell differentiations or the formation of patterns seem to be connected with growth substances with a retarding effect. Bünning & Sagromsky (1948) in the case of the stomata were able to show that round the individual stoma there is an inhibition zone in which no stomata developed. This was connected with the development of a growth substance which prevented such differential cell divisions as resulted in the formation of new initials for lip cells. On the whole the differentiation of idioblasts in plant tissue (lip cells, root-hair cells, passage cells, or e. g. trichosclereids in air roots (cf. Bloch 1946)) to begin with seems to be inhibited by such substances as may be supposed to be produced by the meristem cells. Only when the concentration of these substances has become sufficiently low, a differentiating, unequal cell division may take place through which an idioblast-initial cell particularly rich in plasma is formed. But this, again, has recovered its embryonal character and now gives off the same kind of substances as inhibit the development of new initial cells in its surroundings.

Such primitive archegoniates as *Rhynia* clearly belong to the same stage as the most highly organized algae. ZIMMERMANN (1930, p. 104) writes about this primeval terrestrial plant that its "Gesamttracht war noch ausgesprochen thallophytisch". What distinguishes it from the algae was tissues or cell types connected with its terrestrial life: the stomata in the epidermis, the tracheids in the simply built protostele, and the water-absorbing cells on its plagiotropic shoots.

According to ZIMMERMANN *Rhynia* was built of telomes, which according to him are uniaxial sections of shoots anatomically consisting of a stele, cortex, and epidermis. *Rhynia* had horizontally creeping and erect shoots which branched by simple bifurcation. As regards ramification it was at a lower stage than e. g. *Polysiphonia*.

(8) Telome-Syntagmation.

ZIMMERMANN regards the telome as a morphological basic element in the cormophytes. According to his theory telomes can form "telome clusters" and the individual telomes in such clusters can coalesce into larger bodies. In a similar way as lateral branches in a *Delesseria* with sideways coalescence form a flat leaf-like organ, so telomes are united into blades, e. g. in *Sphenophyllum* and *Ginkgo*. Basal parts of telomes in telome clusters coalesce into stems with actinostele and still more complicated forms of stele.

In the section on syntagmation the peculiar conditions in the brown algae were mentioned that we should probably consider forms with an apical meristem as most original and forms with a top cell as derived. Hence it is interesting that the same process seems to take place in connexion with the telome syntagmation. In the telome plants with the lowest organization, the *Rhyniaceae*, there was a large number of initial cells at the top of the shoots, while in a great many of the cormophytes with a higher organization there are large top cells. But not in this case either does the top cell represent decisive progress. Indeed, we see that both *Lycopodium*, eusporangiate ferns, and phanerogams have retained the large number of initial cells.

Conditions of polarity of course with the renewed syntagmation have become considerably more complicated and escape any possibility of more detailed investigation from a morphological point of view. On the other hand, it will be possible to make further advances by means of physiological experiments. Many experiments have already been made which show that the a—b-polarity is still present in cormophytes with a higher organization; but this does not mean much. Tissue cultures and influencing these with growth substances are probably the road leading to a profounder understanding.

(9) Axillary Concatenation.

This concept has been taken over from Zimmermann, who points out that any form of ramification from axils is absent in more primitive cormophytes. In phanerogams, on the other hand, axillary concatenation is a typical feature. It is also found in *Equisetum*, ferns, and in the strobili of the *Lycopodiales*. Zimmermann (*loc. cit.* fig. 21) points out three possibilities by which axillary concatenation can arise from ordinary lateral ramification. In all the three cases there must be a suppression of growth in a definite part of the stem.

The question then arises whether this axillary concatenation can be characterized as a new morphological stage of progression. As to this there can hardly be any doubt, for if Zimmermann is right in his interpretation of the origin of the axillary position, the latter must presuppose an inhibition of growth at every single node, which, again, means a further complication of the chemical basis of the morphological differentiation.

(10) Cambial Differentiation.

The secondary growth which is due to cambia and phellogens represents the next stage. It is true that cambia develop from special embryonal cells placed peripherically and formed by the growing-point cells which arising by radial polarity during the development of the growing-point have already obtained a certain lateral determination. Something similar applies to phellogen cells, for even if these are formed secondarily from cells already rather well-developed, it should be kept in mind that the cells which develop into phellogen are placed in the periphery of the plant body in question and thus originate from cells at the growing-point which had obtained a lateral determination by radial polarity. The fundamentally new about the secondary growth—what particularly causes it to represent a new stage—is the fact that cambia and phellogens in all probability are highly active in the processes of morphological differentiation. In plants with secondary growth the morphological development, the differentiation through differences in polarity, besides in shoot- and root-tips is also laid in the lateral meristems.

The lateral differentiation due to cambia is very heterogeneous. Perhaps we ought to distinguish two stages, which might be termed simple and complicated cambial differentiation. In the first case the differentiation mainly consists in different cells developing in a centrifugal and centripetal direction (phloëm and xylem, phellem and phelloderm); in the other case also considerable differences arise between the cells developed on the same side. The numerous elements in the xylem and phloëm of the deciduous trees of our day are the result of such a complicated cambial differentiation. The reason why I have not distinguished these stages more closely is that it is difficult to find a boundary between them.

Cambial differentiation is the highest stage. Possible higher stages are not clearly developed. It is quite interesting to remember that in ligneous lianas there may be a third syntagmation with several trunks growing together. Some deviating specimens of certain trees (e. g. *Fagus silvatica*), too, behave peculiarly and form numerous anastomoses and coalescences of the trunks. However, it is of course impossible to know whether such variants signify the introduction to a new stage of progression.

In what precedes we have nearly exclusively kept to vegetative characters. These are decidedly the easiest to survey, and it seems as if the progression that can be ascertained as regards the structure of sexual organs and organs of reduction division hardly differ on essential points from that which may be ascertained in the vegetative parts. But sexual organs and to a still higher degree organs of reduction division (meiotangia) nearly always represent a higher stage than that reached in the vegetative parts in the same organism. Some examples will illustrate this:

Ectocarpus. Vegetative: Stages 4—5 (plagiotropic filaments are found to have been developed in some species). Sexual organs: with little difference from the vegetative filaments, but a stage above these, as the cells are divided into a great many small cells each of which is changed into a gamete. Organs of reduction division: egg-shaped or spherical organs very different from the vegetative filaments, cell-formation in the organ without simultaneous wall-formation.

Lycopodium. Vegetative: Stage 8. Organs of reduction division (strobili): Stage 9.

Helianthus. Vegetative: Stage 10 (intrafascicular cambium with complicated cambial differentiation). Organs of reduction division: Stage "11". The head is a very complicated formation which presupposes a third syntagmation of inflorescence stems simultaneously with growth retardations in keeping with those described in connexion with Stage 9.

Lateral Series.

The present paper is not intended as a general morphology. Hence, only some examples will be adduced which are of special interest in connexion with the discussion of the stages of the main series. Among lateral series which will not be discussed in detail we may mention the morphological stages of progression that may be ascertained in fungi, lichens, and bryophytes.

(a) Lateral Ramification with Simple Turning of Polarity.

The turning of the plane of cell division through 90° in bacteria and *Chroococcaceae* was mentioned above. In the group which formerly was called *Hormogonales* there are filamentous forms, thus Stage 3 in the main series. But the *Stigonemaceae* take a step further and have "genuine ramification". A close comparison of this ramification with that mentioned in the case of the main series (Stage 4) shows a fundamental difference. The lateral branches in the *Stigonemaceae* are given out from the whole cell, not from its upper or lower part. The uniseriate filament is shaped like a hormogonium and hormogonia have a clearly homopolar structure. A turning of polarity through 90° takes place in connexion with divisions transverse to the longitudinal axis of the filament, a process which presumably corresponds to the turning found in bacteria and *Chroococcaceae*. The ramification may be referred back to the shifting homopolarity and therefore in itself is not something fundamentally new. Hence, the *Stigonemaceae* do not reach Stage 4 and even though the plants may sometimes be heteropolar (*Nostochopsis*, *Doliocatella*) the ramification is not in this case, either, due to the development of any new lateral pole. In *Hapalosiphon* it can be shown that the ramification is initiated in sections of filaments cut off from the end of the filament by a heterocyst. The heterocyst can here be supposed to stop or change the substances conditioning the longitudinal polarity in the filament and thus create a possibility of lateral ramification (Böcher 1950). The heterocysts, however, are not an absolute condition of the lateral ramification. Thus, in the genus of *Doliocatella* there are no heterocysts and in *Stigonema* the lateral ramification is often completely independent of the heterocysts. Here the polarity is turned some little distance behind the apex of the trichome. It may be supposed that the substances of polarity passing in a longitudinal direction are soon weakened behind the apex, while in others it is weakened slowly or only by insertion of heterocysts. Perhaps the chief purpose of the heterocysts is that of regulating, changing, or stopping substances of polarity. A large number of occurrences of heterocysts can be interpreted in this way. For instance the spore formation near heterocysts in *Anabaena* may be due to the heterocysts neutralizing the longitudinal polarity and themselves producing substances conditioning spore formation. But it is difficult to explain the purpose of lateral heterocysts in *Stigonema mamillosum*, *Nostochopsis*, and *Mastigocoleus*. In the last-mentioned genus the heterocysts, however, terminate short lateral branches. In other words, they stop the growth of the lateral branch. Long branches bearing hormogonia or long attenuated branches develop where there is no formation of heterocysts. In *Stigonema mamillosum* the typical place of the heterocysts is outermost in the cell families developing by the transverse growth of the segments. The cell families can be apprehended as contracted systems of branches, and the heterocysts therefore also here "stop" the further growth of certain lateral branches. CANNABAEUS' (1929) studies on the heterocysts show that physiologically these behave differently from ordinary cells. In any case their appearance must be due to a sudden change in the longitudinal polarity, and this fact causes forms with heterosysts to be at a higher stage of morphological progression than forms without heterocysts. The *Oscillatoriaceae* therefore are more primitive than the other groups frequently included among the "*Hormogonales*" (cf. further p. 34).

(b) Lateral Ramification in Connexion with Stoppage of Longitudinal Polarity.

In most forms of "*Hormogonales*" there is a so-called false ramification. This seems to be completely dependent on the occurrence of heterocysts or intercalary dying cells. In a *Rivularia* a heterocyst will interrupt the longitudinal polarity, after which the cell below the heterocyst will behave like a new apex and grow past the heterocyst. In *Scytonemaceae* two sections of filament between two heterocysts separated by a dying cell will be able to grow into two branches. As in the case of hormogonium formation the longitudinal polarity is interrupted. Two homopolar sections of filament will develop and two poles with opposite orientation will be placed opposite to each other at the place of ramification. Intercalary dying cells and separation discs as well as heterocysts must no doubt be due to a change of the longitudinal polarity and hence the false ramification like the lateral ramification in the *Stigonemaceae* mean progression. Biologically the lateral series a and b replace Stage 4 in the main series. None of them seems to lead on to new stages. And still one might feel tempted to apprehend cases of accumulation of trichomes within the same system of sheaths as a kind of syntagmation (see e. g. the very peculiar *Fischerellopsis* described by FRITSCH 1932).

(c) Turning of the Plane off Cell Division without Turning of Polarity in Bipolarly Heteropolar Plants.

It should first be noted that turning of polarity here means a sudden turning by which two adjacent cells get different polarity.

In *Volvox* the zygote is clearly heteropolar, with hyaline plasma in what corresponds to the front part. At the first cell division the zygote is split into two hemispheres each with an equal share in the front part. At the next division the plane of division is turned through 90°, but the four cells still each get their share of the front part of the original cell. At the following divisions, too, the plane of division is turned without the polarity being changed. A cell plate develops which curves and gradually comes to encircle a cavity. At last we get a blastula-like organism of heteropolar cells, which are laterally connected by plasmodesms.

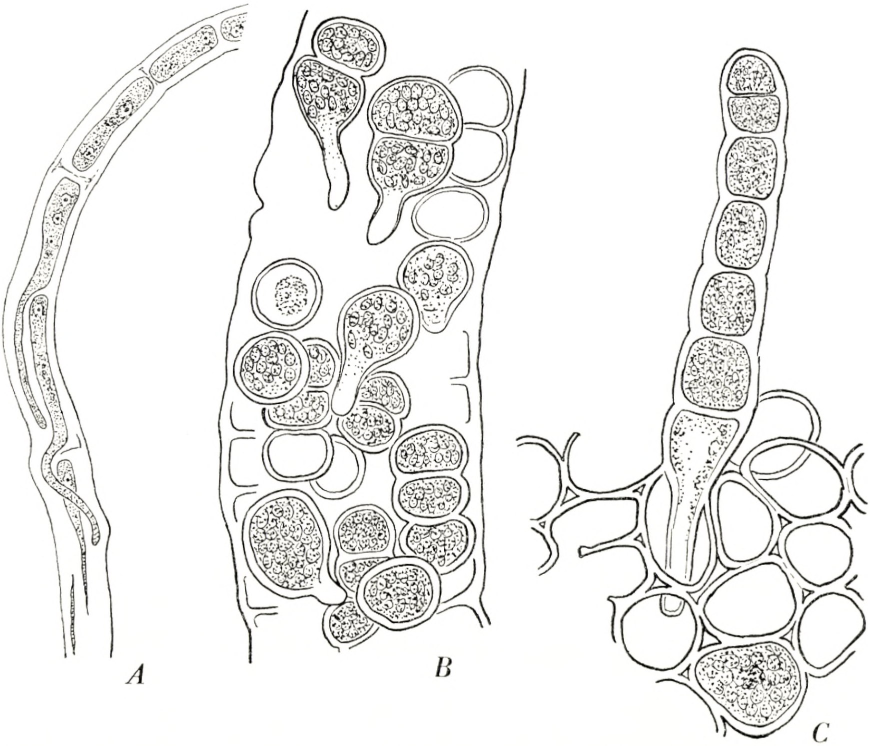


Fig. 6. A, *Chaetomorpha* sp. The basal cell-like sections are heteropolar; the b-poles develop rhizoid-like extensions growing past the section under them. — B—C *Enteromorpha* sp. B, mucilaginescent end of an old filament. Many of the cells have changed into akinetes; some of these have died later and have become empty, others are germinating. C, among many empty rounded cells (akinetes) there are an ungerminated and a germinating akinete growing into a uniseriate heteropolar filament. × 625.

In *Ulva* and *Enteromorpha* the zygote at the germination forms a heteropolar cell filament. A two-layered plate-shaped body or a tubular body with one-layered walls develops by longitudinal divisions in which the plane of division is turned through 90°. The cells in these forms of thallus are all heteropolar and are no doubt unidirectional as regards polarity, as is seen, i. a., when akinetes originating from the ordinary cells germinate (fig. 6 B—C). At the base of the thallus the cells are able to give out descending rhizoids, which contribute to the attachment. These in *Ulva* either grow down between the two layers of cells or externally. They obviously come from the lower pole of the cells, but as there are cells immediately under them, they cannot grow downwards vertically, but have to bend in one direction or the other to get round those under them.

Under the apical cell in a *Sphacelaria*, too, longitudinal walls soon develop which separate cells with the same type of polarity. In this case matters, however, are quite different because the cells are pluripolar (cf. pp. 14—15). *Sphacelaria* is undoubtedly a derived type which does not belong to the main series, but the lateral series of which it is a representative proceeds from a higher stage than the lateral series to which *Volvox* and the *Ulvaceae* belong. These plants are but bipolarly heteropolar and the lateral series in contrast to *Sphacelaria* do not lead to higher stages of morphological progression.

(d) Regular Alternation between Cells with and without Ramification.

In *Sphacelaria* the apical cell gives off segment cells which before longitudinal walls develop are again divided into an upper and a lower segment cell. Now it appears that lateral branches only develop from cells originating from the upper segment cell. This may be explained by means of the theory of differences in concentration of the substances determining the poles mentioned on p. 13. At the formation of a segment cell this as usual will get an upper and a lower pole (a and b). At the division of the segment cell two cells arise, both with a—b-polarity, but with weakened or inhibited polarity around the new wall, so that we have a—(b) in the upper and (a)—b in the lower segment cell. As lateral ramification in simple ramification takes place near the a-pole, only cells originating from the upper segment cell are able to give out branches. Cells originating from the lower segment cell in some species, e. g. *Sphacelaria plumigera,* can give out cortical filaments directed downwards. The peripheral cells of the lower segment here are divided into four storeys of cells, and the filaments directed downwards always issue from the uppermost storey but one, thus from cells with a comparatively high concentration of b-substances. Strangely enough, they are not given out from the lowest storey, where one would expect to find most b-substance. This may be connected with the fact that these cortical filaments on the analogy of other species within the order are not genuine rhizoids, but hold a peculiar intermediate position between rhizoids and lateral branches. In other species the system of cortical filaments becomes very complicated as even a lateral meristem (meristoderm) may develop, which gives rise to secondary growth. Secondary growth in the main series was considered the last stage, which followed after axillary concatenation and telomic syntagmation. In *Sphacelariales,* too, it signifies a higher stage of progression, but there it probably follows after pluripolar trichome syntagmation, only not directly, as previously a stage has developed with alternation of segments with mainly a-polarity and segments with mainly b-polarity. For that matter, the secondary growth is very primitive as compared with that mentioned under Stage 10, the so-called meristoderm giving off cells only centripetally and chiefly giving off only one kind of cells. Thus there is a wide gulf between this form of lateral differentiation and that achieved by cambium in a dicotyledonous ligneous plant. What resembles the secondary growth in *Sphacelariales* most perhaps is the growth which in *Lepidodendron* was due to the phellogen and which chiefly consisted in a development of cells in a centripetal direction. An intermediate stage, however, is clearly missing. Perhaps such a stage was found in *Protolepidodendron* or still older forms. If so, another stage with primitive secondary growth without material differentiation of cells and possibly only with a centripetal development of new cells should be added to the main series.

In connexion with the theory advanced as to the differences in concentration *Cladostephus verticillatus* is particularly interesting. SAUVAGEAU's thorough investigations (1906, 1914) show that at some distance from the apex secondary lateral shoots originate from the upper cells within the originally inferior segments. Other weaker secondary lateral shoots develop from the third storey of cells arising from an originally superior segment and from the third storey arising from an originally inferior segment. The strength of these lateral shoots is excellently explained by the theory of differences of concentration as, with four storeys of cells in each segment, we get three degrees of a-polarity. Denoting the degree of inhibition by 1, 2, or 3 parentheses, we get (cf. fig. 7):

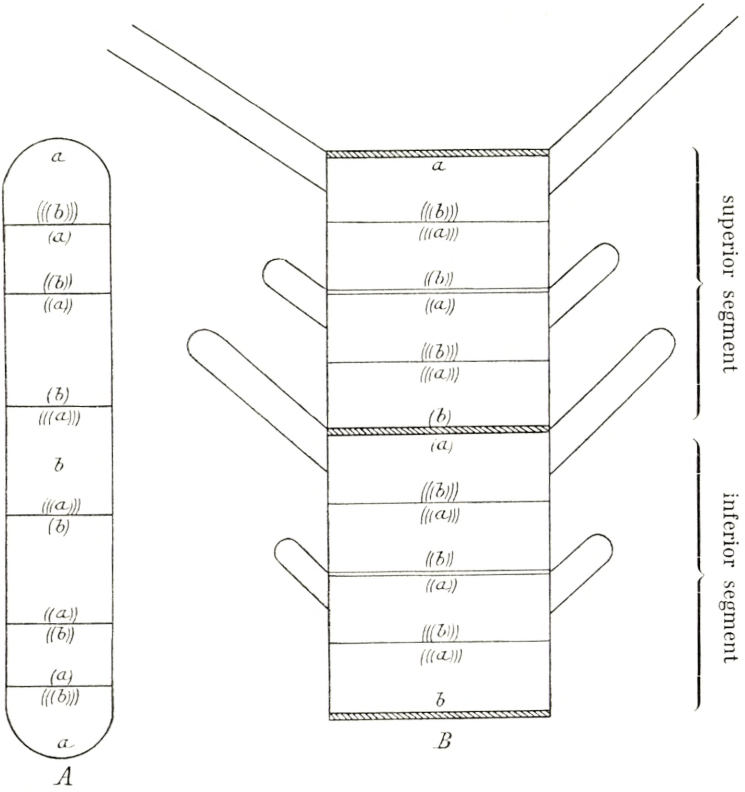


Fig. 7. Diagrammatical figures illustrating the theory on differences in concentration in respect of substances determining the poles. A homopolar filamentous alga with one row of cells (*Pseudanabaena*). The differences are supposed to have arisen by a movement of substance directed from the poles towards the centre and perhaps simultaneously a passage of substance in the opposite direction, towards the poles. B highly organized alga with pluripolar cells (*Cladostephus*), the ramification of which indicates differences in concentration. The boundaries here are not between cells, but between segments and subsegments.

a	pole	forming main lateral branches (primary lateral branches)
(a)	pole	forming large secondary lateral branches
((a))	pole	forming small secondary lateral branches
(((a)))	pole	provisionally forming no lateral branches

The *Charales* morphologically behave in a similar way as the *Sphacelariales.* The nodal cells correspond to the upper segments and the internodal cells to the lower segments. The main difference is that these two types of cells in the *Charales* are not subdivided further, that the nodal cells remain short cells, while the internodal cells stretch very much, and that the branches from the nodal cells are not given out from the upper part of the cell but from the whole cell. As, however, the branches behave like lateral branches from heteropolar plants and grow obliquely upwards, there is hardly any reason to imagine a turning of polarity at every change. It is more probable that a further inhibition or weakening has taken place, perhaps a total disappearance of the pole-determining substances around the wall separating the nodal and internodal cells so that in the upper cell, the nodal one, there are only (or nearly exclusively) a-substances and in the lower cell, the internodal one, only (or nearly exclusively) b-substances. In the nodal cell a formation of some lateral a_1-poles takes place around the axial a-pole, but these lateral poles are not shifted towards the upper part of the cell as there is no pronounced b-pole. In *Cladostephus* secondary lateral shoots could develop from upper cells in lower segments. In the *Charales* such a process does not take place. Here the regular alternation of cells with and without ramification is absolutely firmly established and as there is even a morphological difference between two cells following each other, we may say that the *Charales* represent a further stage in the lateral series introduced with types corresponding to the *Sphacelariales.*

Coenocytic Lateral Series.

Green algae with a coenocytic structure by virtue of their special cytological conditions belong to lateral series. Within the *Cladophorales* there are uniseriate filaments in *Chaetomorpha* in which the basal segments show b-polarity by giving out descending rhizoids issuing from the lower parts of the segments (fig. 6 A). Furthermore there is simple ramification in *Cladophora* with ascending branches and descending rhizoids from respectively upper and lower parts of the coenocytic segments. Within the *Siphonales* there are simple forms such as *Protosiphon*, forms with simple ramification (*Vaucheria*), with ramification according to the central axis principle (*Dasycladaceae*), forms with clear pluripolarity (with repent and erect shoots, e. g. *Caulerpa*), and syntagmatic forms (*Codium*), indeed, even forms with systems of repent and erect syntagmatic thallus segments (*Udotea Desfontainii*). Thus it seems that among the coenocytic algae there are stages of progression corresponding completely to the stages of the main series, a fact that appears very interesting.

Phylogeny and Progression within some Groups of Thallophytes.

A number of phylogenetic and systematic conditions are set in a new light if we study the height of organization of the various forms on the scale of progressive stages. In what follows we shall discuss some examples from the taxonomy of the thallophyta.

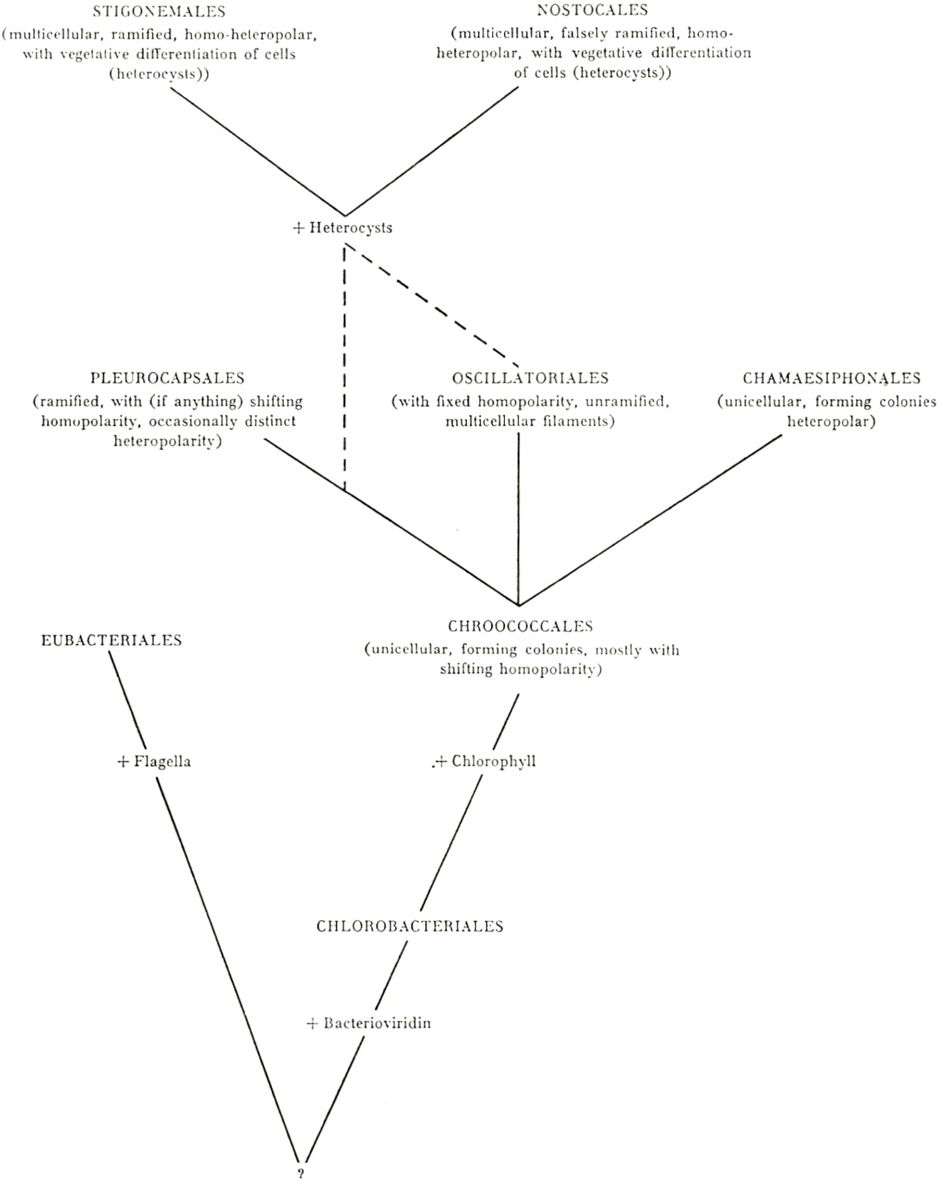
(1) Monera.

Copeland (1938) in accordance with Haeckel (1866) has proposed this name for the group of *Schizomycetae* and *Myxophyta* (*Cyanophyceae*), i. e. the anuclear plants or *Schizophyta*. Later Stanier & Van Niel (1941) have tried to set up a natural system for the kingdom *Monera*. This attempt has aroused general interest and, with the phylogenetic lines to which they have called attention, marks a phase of progress in relation to previous times, more practically arranged bacterial classifications, and one thing is particularly interesting: the greatest importance is attached to morphological criteria, and the groups to a certain degree are arranged progressively morphologically. Stanier & Van Niel's fig. 1 is a survey of the phylogeny of the *Eubacteriales*. The branches of the genealogical tree are based on morphology.

The starting-point is a primitive coccus, thus an immotile organism with shifting homopolarity. From there issue partly a branch of immotile forms, ending with *Sarcina*, partly a branch with polarly flagellated rods, which ends in the morphologically most derived forms, the spirilla. This series is Gram-negative. The third branch is fairly heterogeneous and hardly quite natural. It ends in ramified bacteria and is carried further to the likewise frequently ramified *Actinomycetales*. Finally there is a branch of peritrichous, rod-shaped groups. All these branches end in forms of a higher stage of progression, as flagellate bacteria must have a higher organization than non-flagellate ones. Among the motile bacteria the heteropolar mono- or lophotrichous forms must be at a higher stage than the homopolar (bipolar) mono- or lophotrichous ones. As stated by STANIER & VAN NIEL, it is probable that future work will show the necessity of drastic revisions. The importance of the genealogical table therefore at the present stage is chiefly in the discussion it may bring about. A very important contribution to a greater discussion has recently been made by PRINGSHEIM (1949). Whereas STANIER & VAN NIEL like several other workers point to a close affinity between *Chroococcales* and *Eubacteriales*, PRINGSHEIM arrives at the view (*loc. cit.* p. 87) that "there is no affinity between Bacteria and Myxophyceae". Even though I completely accept PRINGSHEIM's attempt at a circumscription of bacteria and blue-green algae, I do not see that he has produced evidence of anything but the fact that the highly organized bacteria and the highly organized blue-green algae are essentially different. Both groups include several stages of morphological progression and the lowest of these (the immotile coccoid type) is common to both groups. As this lowest stage even cytologically proves to be of a low organization, and this in the same way (absence of a genuine cell nucleus, sap vacuoles, and plastids as well as important accordances with regard to the chromatin apparatus; cf. also NEUGNOT (1950)), it is hardly premature to assume affinity in the form of common origin between bacteria and blue-green algae at the lowest stage of organization. It is evident that the groups besides, during their evolution, have parted. The same applies to the algae, among which forms of low organization within several series indicate a common origin, without our daring otherwise to attempt giving a detailed account of the affinity. A common origin of blue-green algae and bacteria thus is still very probable. On the other hand we are on unsafe ground in attempts at finding out whether blue-green algae or bacteria are the oldest forms. According to STANIER & VAN NIEL the *Chroococcales* may be supposed to have developed from the *Eubacteriales*, as they, with OPARIN (1938), are of opinion that there was a chemical synthesis of organic substance on the earth before the first organisms showed signs of life. These, therefore, might be heterotrophic. This view is inconsistent with experiences from the other parts of the vegetable kingdom, where colourless forms must always be derived from forms containing chlorophyll. VAN NIEL has himself later (1944) in his discussion of the *Pseudomonadales* found it necessary to regard the photosynthetic forms as progenitors of the non-photosynthetic forms. If, therefore, the blue-green algae are to be derived from the bacteria, it must be from such as are morphologically of low standing and which likewise are photosynthetic. Here the group of interest would seem to be the *Chlorobacteriales*, which consist of immotile cocci (*Chlorobium*, cf. NADSON 1912) or rods, which may sometimes assume coccoid forms (BÖCHER 1949a) and which therefore possibly consist of chains of undivided coccoid units (cf. above p. 5).

The genera *Beggiatoa* and *Oscillatoria* have the same structure of cells and the same type of motility. Both STANIER & VAN NIEL and PRINGSHEIM are of opinion that they are related and the *Beggiatoaceae* therefore can be apprehended as apochlorotic colourless blue-green algae. They belong to an order which I propose to term *Oscillatoriales* and which in regard to height of organization (absence of heterocysts) is below the other groups often classed together as "*Hormogonales*". These may suitably be termed *Nostocales* (including all forms bearing heterocysts and with false ramification; cf. p. 26) and *Stigonemales* (mostly forms bearing heterocysts and with ramification by turning of polarity; cf. pp. 24—26).

The *Pleurocapsales* are peculiar by having plagiotropic filaments from which branches may be given out laterally, upwards and downwards (i. e. into the substratum). Conditions may remind of pluripolar ramification and syntagmation, but to all appearance the ramification is of the same type as in the *Stigonemales*



Diagrammatic representation of the phylogeny of the *Cyanophyceae* according to the theory advanced by the present writer.

and is due to a turning of polarity, which in addition seems capable of taking place in any direction, thus a structure greatly reminding of shifting homopolarity. Because of the similarity as regards ramification, the *Stigonemales* may be supposed to have been derived from forms from which the *Pleurocapsales*, too, originated. Only after the two groups had parted, forms with heterocysts arose, and then one branch specialized on false ramification while another retained ramification by turning of polarity. The strange *Fischerellopsis* (Fritsch 1932) has both false ramification and *Stigonemales* ramification.

In my previous paper (1949a) I pointed out the possibility of deriving the *Oscillatoriales* from the *Chroococcales* through the medium of such genera as *Synechococcus, Synechocystis,* and *Pseudanabaena.* Fritsch (1945, p. 859) entertains a similar idea when writing: "from the primitive coccoid type, there may have originated an extinct series of multicellular forms, one branch of which led to the *Oscillatoriaceae*, while another, after the evolution of the heterocyst, gave rise to the other three families of *Nostocales.*" This point of view is the direct opposite of that of Geitler (1925), who is of opinion that the *Oscillatoriaceae* is the most advanced group among the *Hormogonales.* Like Fritsch I go in for the abandonment of the name of *Hormogonales* and instead operate with *Nostocales, Stigonemales* (proposed by Fritsch), and *Oscillatoriales.* On p. 35 there is a survey of my theory of the phylogenetic conditions in the *Cyanophyceae.*

(II) Algae.

A number of instances of the placement of nuclear autotrophic thallophytes in the scale of morphological progression have already been discussed. Some comments on phylogenetic conditions follow.

Great interest attaches to the occurrence of homopolar forms. Whereas in anuclear organisms these were predominant they constitute rather a subordinate element among the nuclear forms. In itself this is not very strange. If unicellular flagellate forms, as supposed by many workers, form a number of primary groups, from which the majority of other groups should be derived, then the starting-point is heteropolar.

Among the great number of different groups there are only two mainly homopolar ones, viz. *Conjugatophyceae* and *Bacillariophyceae* (the diatoms). Furthermore a few red algae have homopolarity and such a form as *Raphidonema nivale,* which belongs to the *Chaetophorales,* is clearly homopolar. The latter species can easily be dispatched, as it is evidently a greatly reduced type. Above, p. 15, plagiotropic homopolar shoots forming the basis of erect shoots were mentioned just as occurring among the *Chaetophorales.* A type like *Raphidonema* can be assumed to have arisen by the loss of such erect shoots. *Pleurococcus vulgaris,* too, is a very primitive type, which can only with difficulty be regarded as heteropolar, but which may remind of plants with shifting homopolarity. However, its divisions on three planes can easily be derived from forms with pluripolar ramification. This, too, is apprehended as a reduced form within the group of *Chaetophorales* (see Fritsch 1935).

Conditions are quite different in diatoms and conjugates. These are two groups rich in species in which the homopolarity is nearly universal. In no place homopolarity is more beautifully demonstrable than in *Closterium,* where the poles have vacuoles with oscillating crystals of gypsum. At the cell division in *Cosmarium* we see something corresponding to the division of a detached cell in *Pseudanabaena* (fig. 1). Between the two a-poles in *Cosmarium* there is a "b-pole", which, however, is not retained, because the cells are separated by the division. The b-pole is at once changed into two new a-poles in the new halves of the two cells detached from each other. But in the *Zygnemaceae* there is a development of filaments composed of cells which mostly are homopolar and not attached. There is, however, an interesting progression to be observed here. The *Zygnema* cell with its two stellate chromatophores is clearly homopolar and accordingly the cell produced by the germination of the zygote is also homopolar (see Kurssanow 1912). *Spirogyra* has spirally placed ribbons of chromatophores running from one end of the cell to the other. The cell here is not clearly homopolar, and at the germination of the zygote it appears (see e. g. Tröndle 1911) that there is a difference between the two ends of the cell, the rear end being colourless and rhizoid-like. In the genus *Spirogyra* we just find attached forms (*S. adnata, S. fluviatilis*) with a basal cell equipped especially for attachment. Here heteropolarity has developed within an otherwise homopolar group.

Apart from conditions of polarity in a cytological respect the *Conjugatophyceae* are more highly organized than the homopolar blue-green algae. And the cells of the *Bacillariophyceae* seem still more complicated. Both conjugates and diatoms, therefore, are highly organized homopolar groups. They are no doubt final stages in two otherwise separate evolutionary series beginning with simple homopolar forms[1]. The *Mesotaeniaceae* are more closely related to these unknown primitive forms than the other groups of *Conjugatophyceae*.

By their homopolar organization together with many other properties both the *Conjugatophyceae* and the *Bacillariophyceae* hold a very isolated position among the nuclear plants. I see but a slight possibility of finding a transition to the heteropolar forms, where the flagellate cell type is completely prevalent. Even if *Spirogyra* reaches heteropolarity, this avails little as it forms no swarmers and has neither flagella nor eye-spots. The facts adduced e. g. by Fritsch (1935 p. 361) in favour of a connexion with the other green algae carry little conviction. He derives a sideways fusion of two immotile or amoeboid, mostly homopolar gamete cells from a fusion of two a-poles in two heteropolar flagellated gametes, which seems rather artificial. He mentions that also in the *Chlorococcales* there is absence of motile reproductive stages, but in this group plants without motile stages obviously are due to reduction of forms with motile stages, and there is no indication of such a process of reduction in the *Conjugatophyceae*. In another modern manual, Smith (1938), it is attempted to derive the *Conjugatophyceae* either from the *Volvocales* or the *Tetrasporales*, thus from pronounced heteropolar forms. This is no doubt done on the basis of the view that "the evolutionary possibilities along the tetrasporine line are infinite. A tendency for the vegetative cells to become non-flagellated but to return directly to the motile condition is found in the tem-

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[1] Having finished this paper I received the very interesting paper on radiation of desmids by Teiling (1950). According to this author it is possible among the desmids to distinguish between several types of radiation (that structural element which is decisive in the shape of the desmids according to their vertical symmetry-planes) and these types seem to form a regressive series. Finally Teiling uses the radiation types or steps as a basis for a phylogenetical survey of the desmids.

porary *Palmella* stages of many unicellular *Volvocales.*" But when an alga enters a *Palmella* stage and loses its motility, it does not at the same time become homopolar.

A possibility of finding a transition between the *Conjugatophyceae* and the other green algae is no doubt to be sought in possible homopolar ancestors of the latter group. But even in *Hormidium,* which in many respects seems primitive as its filaments may come to small pieces which are apparently homopolar, there are biciliate heteropolar zoospores and gametes. Thus there are no forms now living which fulfil the conditions as connecting links between the *Conjugatophyceae* and the *Chlorophyceae,* and hence it is presumably most natural to regard the *Conjugatophyceae* as an independent group. Thus I do not subscribe to the view of all the present-day phycologists which according to SMITH have abandoned the former practice of placing the *Conjugatophyceae* in a special subclass. We shall probably go right back to a homopolar, unicellular, nuclear organism, something like a primitive *Mesotaeniacea,* before obtaining a connexion between the *Conjugatophyceae* and the *Chlorophyceae.*

A similar taxonomic position is held by the diatoms. PASCHER (1921) has advocated the view that the diatoms should belong to a division of "*Chrysophyta*", among which also the *Xanthophyceae* (*Heterocontae*) and *Chrysophyceae* should be classed. The chief correspondences are in the brown colours in the chromatophores and the occurrence of fat oils and not starch as assimilation product. The majority of *Xanthophyceae* and all *Chrysophyceae,* however, are heteropolar, whereas the diatoms are homopolar. A possible connexion between the groups, therefore, must be through the homopolar *Xanthophyceae.* A genus like *Centritractus* set up by LEMMERMANN, the cell wall of which is composed of two similar halves and which has no flagellated stages, might very well be related to the forms from which partly the *Xanthophyceae* and *Chrysophyceae,* partly the *Bacillariophyceae* originated.

Whereas the brown algae probably originate from unknown brown flagellate-like algae, things are quite different as regards the red algae, in which flagella are completely absent. The red algae on the whole are heteropolar, but it is an interesting fact that within the primitive group of the *Bangiales* there are unito bicellular, clearly homopolar forms (*Porphyridium cruentum* and *Chroothece*), a few of which (*Chroothece mobilis*; see Pascher & Petrova 1931) can move by secreting mucilage, particularly at the poles. The apical attachment filaments found both in *Kyliniella*, which belongs to the *Bangiales*, and in floridean forms like *Spermothamnion repens* and *Trailliella intricata* is probably a character pointing to homopolar ancestors.

Particularly Kylin (1930, 1943) has advanced the view that the red algae should be descended from blue-green algae; but this view has been opposed by Geitler (1944) and has not been accepted by Fritsch, either. Reference has especially been made to the more highly organized cell structure of the red algae (cell nucleus, chromatophores). The similarity between the most highly organized blue-green algae and certain primitive red algae, such as e. g. *Goniotrichum* (see Rosenvinge 1909, p. 76), however, is very great. Apart from the cell nucleus and the chromatophores in the latter, they belong to the same stage of progression. As an important addition to the points of resemblance adduced by Kylin between *Cyanophyceae* and *Rhodophyceae* now comes the homopolarity which occurs both in *Stigonemales* and in *Bangiales*, while the fact that the *Cryptophyceae* are markedly heteropolar weakens Geitler's theory of a relationship between these and the red algae. But the finding of missing links in the form of a *Cyanophycea* with cell nucleus or a red alga with a primitive chromatin apparatus or a *Stigonemacea* with incipient division of the chromoplasm into chromatophores will be necessary to form a secure basis of the theory of an evolution from blue-green algae to the red algae. Spearing's cytological investigations (1937) of *Stigonema mamillosum* would seem to indicate that in this species there are certain signs of nucleus formation, as e. g. nucleolus-like bodies and a system of chromatinic filaments reminding of a prophase in a typically nuclear plant have been found there. It will be a very important task for cytology thoroughly to compare the *Cyanophyceae* and the most primitive red algae. A bridge made between the *Monera* and the other plants will open up considerable new vistas, for if typical cell nuclei can have been formed by evolution from the chromatin apparatus in a *Monera* type in one place, this may have happened in other places, too, and the bridge will also give evolution a possibility of following the series of progression in quite another way than may be done when the nuclear or anuclear organisms are considered apart, and this, of course, seems very pleasant, as the assumption of several separate series of living organisms, several "creations" is a hypothesis of little probability. COPELAND (1938, fig. 8), too, assumes the nuclear organisms to have developed from anuclear ones.

If it proves possible to derive the red algae from the blue-green algae, the brown algae will come to hold a comparatively more isolated position, for the most primitive among these are already at Stage 5. The absence of Stages 3 and 4 prevent a contact with the flagellates.

The stoneworts (*Charales*) also hold an isolated position, but here, at any rate as far as morphological conditions are concerned, a connecting link with the other green algae has been found. The genus *Draparnaldiopsis* found by SMITH & KLYVER (1929) and later by BHARADWAJA (1933) and belonging to the *Chaetophorales*, as compared with the other forms of this order signifies a further advance. Here are the long axes composed of alternating long internodal and short nodal cells, and the branches are formed only on the short cells and arise from their median region. The laterals may develop into rhizoid-like filaments, which sometimes form a dense cortical covering around the main axis. Viewed from the stages of progression included in the order, the *Chaetophorales* seem to hold a very important position. It is here the pluripolar structure appears, and furthermore there is in respect of the differentiation of the main axes a progression reminding of that mentioned in connexion with the brown algae (uniseriate, primitive forms—*Sphacelaria*—*Cladostephus*). The *Chaetophorales* show a clear phylogenetic connexion with the *Ulotrichales*, which are at a lower stage of progression, and with *Draparnaldiopsis* as connecting link there is a possibility of a distant relationship with the *Charales*, which include higher stages of progression. Finally, perhaps with a starting-point in *Coleochaete*, there is a possibility of relationship with the forms of green algae which must have existed and which formed the basis of the most primitive archegoniates.

Concluding Remarks.

The concept of morphological progression is here first kept distinct from the concept of evolution, then used for a critical appraisal of certain phylogenetic trends. An unravelment of the relation between morphological progression and evolution seems urgent. In works dealing with evolution, e. g. HUXLEY (1945), the concept of evolutionary progress is mentioned. In the animal world this ends with man, and many biologists, among them HALDANE (1932), call attention to the fact that when speaking of evolutionary progress "we are already leaving the relatively firm ground of scientific objectivity for the shifting morass of human values". No organism is "high" or "low", for they are all results of an evolution and are to an equally high degree adapted to the surrounding nature. HUXLEY opposes this view and is of opinion that evolutionary progress can be defined and studied on an objective basis. To him evolutionary progress consists in "a raising of the upper level of biological efficiency, this being defined as increased control over and independence of the environment, . . . progress is all-round biological improvement". It is very probable that the morphological progression represents a biological improvement. In many cases, however, it is difficult objectively to define the improvement; nor is it easy to find criteria of increased control over the environment. Add to this that the word *improvement* does not exactly tally with the fact that all organisms—including the extinct ones—are or were to an equally high degree adapted to the environments. In the face of these facts morphological progression seems to hold a strong position in respect of objectivity. The concept can be kept clear of the concept of evolution, and the material underlying it can be studied on an exact basis. It must be admitted that my investigations of the stages of progression are but introductory and that future investigations no doubt will modify many details and perhaps result in a subdivision of the stages into more stages; but this does not alter the fact that morphological progression can be studied objectively and used for an appraisal of phylogenetic theories. It seems evident that the world of plants as a whole has passed through the whole series of progression, but that the single trend in some respects may have developed progressively, in others regressively. The species of *Rafflesia* have a very highly organized flower, but their vegetative, myceloid body by regressive development has dropped far down in the progressive series of stages.

A progressive development accordingly becomes a rise in respect of morphological complication continued through the history of the world. As behind greater complication of the external forms there is a corresponding greater complication of conditions of polarity (the morphological differentiation as a physiological process), it is evident that our eye must be directed towards the results to be obtained from growth-substance research as regards morphological differentiation. Furthermore it will naturally be directed towards such mutations as are capable of surviving (ecologically possible) and at the same time result in a greater complication of the structure of the plants. Behind each stage in the progressive scale there are one or more mutations, which change the cells and plants as a whole so that the structure gets more complicated; but even if perhaps some mutations have been necessary for the development of each of the ten stages mentioned in the main series, it seems that the progression in itself is due to comparatively few, but then very important, mutations. Only an infinitesimal number of the mutations taking place result in types capable of surviving and, particularly, of competition, and an even smaller number of the mutations result in morphological progression. The nearly countless number of variations displayed by the species in the world of plants put together, therefore are presumably in the first place due to non-progressive mutations. It seems as if the progression drags along, whereas the formation of species and the ecological specialization is fast.

The progression in respect of the structure of the reproductive organs seems closely connected with the vegetative progression, these organs, however, as a rule being somewhat more complicated than the vegetative ones in the same organism. We should here speak of reproductive organs, not of sexual organs, since the latter, as in the cormophytes, may undergo a considerable regressive development. It is the aggregate reproduction apparatus of the plants which is developed progressively. Within the group of cormophytes we see how the organs of reduction division develop slowly, but progressively, gradually taking over the function of the sexual organs. Exactly because reproductive organs follow the slow progression, they seem conservative and homogeneous as compared with the vegetative organs. They are rigid, whereas the vegetative organs are plastic, and hence they are the fixed data to which taxonomists and phylogeneticists must cling in the rough sea of vegetative variation.

This can also be illustrated through the fairly numerous available studies of race biology. Such a species as *Prunella vulgaris* e. g. in respect of vegetative development can be extremely heterogeneous. It consists of races which are cushion plants, repent, erect, annual, biennial, perennial, etc.; but in floral characters it varies little (cf. Böcher 1949b). An annual and a perennial race belong to two different life forms. We see that the ecological race, the ecotype, as it has been termed by Turesson, is a forerunner of the life form. Widely different groups of plants in respect of vegetative characters are plastic, and by convergent development produce a number of life forms corresponding to certain external conditions; but this development does not affect the floral characters. Such a group as the *Leguminosae* has developed trees, shrubs, dwarf shrubs, and annual and perennial herbs. This development is a fast-going, ecologically stamped evolution, whereas the development by which the *Leguminosae* arose from *Rosales*-like ancestors is a slow progressive or phylogenetic trend.

Out of consideration to the clearness of the discussion, we shall finally for a moment distinguish between the mutations producing new progressive stages from these which mainly takes place within the same stages and result in ecotypes, species, and life forms. The latter appear in great numbers of small hereditary changes which in some cases do not result in a subdivision into races, but in the appearance of nearly continuous character-gradients or clines. The former, the progressive mutations are very little known. If they are of the same order of magnitude as the others, they will easily escape observation as the appearance of the progressive stage to which they were to contribute probably extends over a considerable period. The chance of coming across them therefore is small, and as they represent small deviations from the norm, only, they will be difficult to discover. However, it is not certain at all that they are always small. The undoubtedly rare mutants capable of living and competing which include several genes, perhaps are of the greatest importance exactly for the progressive evolution[1]. Within the animal kingdom there has been a development from an earth-bound existence to a flying life in insects, reptiles, and mammals. Here already the first mutation must have resulted in a type which was capable of using its transformed limbs for something which perhaps was not exactly flying, but e. g. keeping hovering for a short time, thus being able to escape a pursuer. But such a mutation is very comprehensive. As an instance of great deviation (probably a mutation) of a progressive type I may mention a strange *Myosotis* plant which some years ago I found among hundreds of normal plants in a garden (fig. 8). Unfortunately it was not fertile, but it was very interesting by showing vegetative as well as floral progression. The flowers were 8—10-merous and in the vegetative parts an umbelliform inflorescence with formation of involucres, i. e. a development indicating a *local* process of growth inhibition similar to that mentioned in the chapter on axillary concatenation (p. 22) and in the brief section on the inflorescence in *Compositae* (p. 24).

But even though there may be quantitative differences in respect of the mutations which give rise to the two forms of evolution, the adaptive and the progressive evolution, it is evident that this is not a case of quite different things. Conditions in the algae seem particularly suitable to illustrate this. Fritsch (1935, pp. 26—27) has some interesting surveys of parallelism in evo-

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[1] Recently Goldschmidt (1948) has advanced views which on some points are in agreement with mine. He does not think that small mutations, selection, and isolation result in anything but ecotypes, whereas macromutations are needed to produce species. Goldschmidt writes: "Major systematic differences and adaptions can only originate in single major steps which establish at once the main features of the new organizational and physiological pattern."

lution in the algae. His types of construction (e. g. "heterotrichous filament", "crust or cushions", "multiaxial compact type") are a kind of life forms. We have heterotrichous filaments e. g. in *Stigeoclonium, Ectocarpus,* and *Chantransia,* crusts or cushions in e.g. *Pleurocapsa, Pseudopringsheimia, Ralfsia,* and *Hildenbrandia,* the "central axial type" is realized in *Batrachospermum* and *Draparnaldiopsis,* etc. The crust-cushion type is no doubt a good life-form as it is specialized for epiphytic or epilithic life, and we see that the most different groups of algae convergently have reached this life form. However, this type is also of a very high progressive significance as a prostrate growth is a condition of radial polarity (p. 13) and of the formation of a larger attachment disc which enables growth of larger algal bodies (p. 18). The "fountain type", too, is a kind of life form which is found realized both in red and brown algae, and which is approximately reached by the *Rivulariaceae.* Coenocytic green algae like *Codium* as well belong to this type, and furthermore we must assume that cellular unknown green algae have reached this life form; but only in the last-mentioned case the fountain type became of fundamental importance for evolution as the algae in question became the first stages of the scale of progression which was later continued in the cormophytes. These instances show that progressive development in many cases—perhaps always—coincides with adaptive development, and indeed it is evident that the progressive mutations must also be ecologically important. For reasons of selection it cannot be otherwise. If they were not ecologically well-equipped, they would perish.

As a main result it may be stated that the majority of mutations capable of surviving are not progressive; they do not result in new stages. As for the vegetative parts the non-progressive evolution results in the formation of a great number of ecotypes and species and—in the long run—life forms, which give the species and groups of plants a possibility of living in different environments. Few of the vegetative, ecologically important mutations are *also* progressive, resulting in new stages or parts of them. As for the reproductive organs, e. g. the flowers, great numbers of varieties with different colours and sizes of the flowers, properties of fragrance, etc., corresponding to the ecotypes will develop in the non-progressive evolution and give the species a possibility

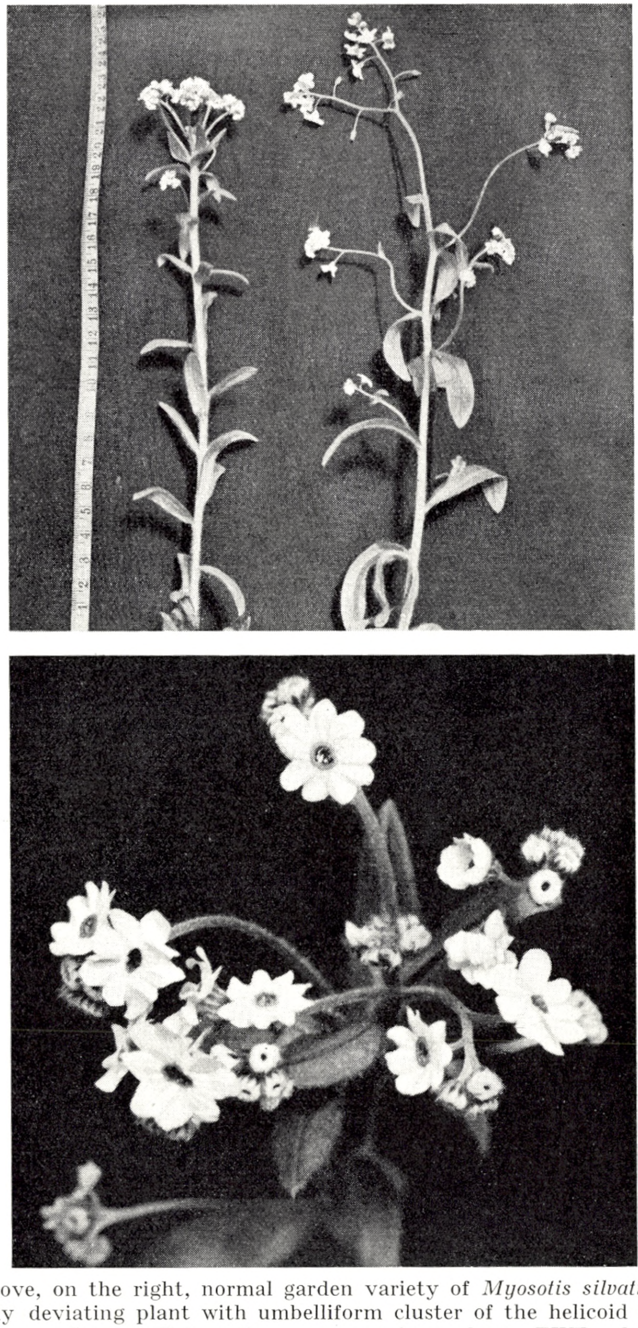

Fig. 8. Above, on the right, normal garden variety of *Myosotis silvatica*, on the left greatly deviating plant with umbelliform cluster of the helicoid cymes and 8—10-merous flowers. Below, the same seen from above. TWB. phot. 1934.

of managing i. a. under different conditions of pollination. But very few mutations are *also* progressive, leading to reproductive organs of a more complicated structure. As these mutations are also important from the point of view of floral biology (ecologically), the result will be that at each stage of progression an advantage is obtained from the point of view of floral biology. Therefore we find simultaneously with the morphological progression in the reproductive organs of the plants an increasing degree of care for the embryos culminating in epigynous forms in the angiosperms.

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Biologiske Meddelelser

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