

Evolutionary Tendencies Among Algae and their Position in the Plant Kingdom

Bohuslav F o t t

Department of Botany, Caroline University of Prague, Benátská 2, Praha 2

Abstract — The algae are an assemblage of phototrophic plants grouped into three or four divisions (phyla), and placed at the beginning of the plant kingdom classificatory system. These divisions, however, contain convergently evolving lines designated as classes and bearing therefore the suffix “-phyceae”. In classes there are various grades of evolutionary advance called orders, containing genera of the same morphological habit. The classes are more or less complete or very fragmentary, containing in the latter case only one level of morphological organisation. Algae from different classes but with the same morphological habit may exhibit very striking convergencies.

Only one class, the *Chlorophyceae*, is directly related to green land plants. For this reason the division *Chlorophyta* should include all green plants. The higher plants, called in modern systems *Telomophyta* or *Trachacophyta*, are in fact further evolutionary steps in the phylogeny of *Chlorophyceae* and their taxonomic units according to the Code should have the relevant suffix “-psida”. I have used in my survey TACHTADŽAN's system for higher plants, as it can be formally adapted without difficulties to fit the system of algae just outlined.

The general objective of all exercises in botanical taxonomy is to group all plants in a natural system. Arrangements should follow the evolutionary progress among plants and the resulting system should demonstrate phylogeny within the plant kingdom. When plant evolution is used as the main classifying principle, plants of different morphological habit, but forming an evolutionary line, are grouped together into taxonomical units. Such lines of plant advance, starting with simple, sometimes one-celled, organisms and ending with differentiated plant bodies, represent the highest taxonomical units, for which the name phylum or, respecting the Code of Botanical Nomenclature, division has been adopted. Viewing the plant kingdom as a whole we can discern, using this principle, many evolutionary lines leading from simple to advanced plant types.

These evolutionary series of plant organisms differ in their biochemical and structural properties rather than in habit, indeed, there are many convergencies and similarities in morphological appearance, especially in those plants which are at the same evolutionary level.

As early as 1813, an excellent French phycologist, LAMOUREUX, classifying the marine Thallassiophytes, discerned green, brown and red algae, using the biochemical property of chromatophore colour. This feature can be used to classify not only the marine algae but also the higher plants. Green plants, division *Chlorophyta*, are characterised by a particular set of assimilatory pigments with predominance of chlorophylls over xanthophylls. The storage product is usually starch, produced within the chloroplasts, and the submicroscopical structure of the chloroplast shows discs arranged in grana. The line

of morphological progression leads from a one celled plant to a differentiated plant body. *Chlorophyta* therefore includes both green algae and higher plants.

The division *Chromophyta* (a term used in a similar sense by the French botanist CHADEFAUD) contains plant organisms, algae only, marked by a predominance of xanthophylls over chlorophyll *a*. Chlorophyll *b* is lacking. Storage products are various, starch being formed exceptionally, but only external to the chromatophores. Submicroscopical structure of chromatophores displays stacks of discs in pairs. In evolutionary lines within the *Chromophyta* the most advanced forms reach the heterotrichous habit and acquired an appearance of a cormus-like thallus. Terrestrial forms equivalent to the green plants are lacking.

The division *Rhodophyta* is distinguished by the presence of phycobilins, phycoerythrin especially, and by the lack of chlorophyll *b*. Storage product is floridean starch. Submicroscopical structure of chromatophores shows solitary discs. Evolutionary line incomplete, involving mostly elaborated algal thalli, unicellular and simple filamentous genera being apparently forms reduced from the more complex ones. *Rhodophyta* halted their morphological progress at the level of elaborated algal thalli and did not evolve to higher land plants.

Besides these main groups of phototrophic plants, defined clearly by the above-mentioned characteristics, there are some groups of flagellates that are not phylogenetically connected with the divisions just outlined. I have called them the residual flagellates.

Euglenophyceae possess a similar set of assimilatory pigments to *Chlorophyceae*, but their storage product is different and quite distinctive. In addition the external and internal morphology of motile cells of the *Chlorophyceae* differ sharply from those of the *Euglenophyceae*. No algal descendants of euglenoid flagellates are known, the class apparently having remained at the level of monadoid organisation. On the other hand many of them are colourless and some have developed phagotrophic nutrition.

The assimilatory pigments of *Cryptophyceae*, another group of residual flagellates, do not differ much from those of the *Dinophyceae*, but their nucleus is quite different from dinophycean type. Some possess phycobilins like the *Rhodophyceae*.

The *Chloromonadophyceae* is a class of coloured flagellates of completely unknown position in the plant kingdom. The assimilatory pigments have not been analysed yet and the structure of flagella is unknown. A distinctive feature of the internal structure of Chloromonads is the supranuclear body, covering the upper part of the nucleus, and the adjacent triangulare space where the contractile vacuoles arise.

Apart from these plants, included in the *Eucaryota*, with a true nucleus and the assimilatory pigments (if any) in membrane-limited plastids, there are the *Prokaryota* (*Cyanophyta* and *Bacteriophyta*) which lack these attributes and exhibit the lowest grades of cell differentiation. The *Myxophyta*, *Phycomyxophyta* and *Mycophyta* represent heterotrophic groups derived from the phototrophic plants in the earliest stages of evolution. They are partly artificial and heterogeneous and due to this, the evolutionary lines that are met with in them are fragmentary and uncertain.

The classifying of phototrophic plants into 3 fundamental divisions, one of which, the *Chlorophyta*, includes the higher plants, clarifies the phylogeny of the plant kingdom and is supported by biochemical and structural evidence.

System of eucaryotic plants

True autotrophic divisions	Classes of algae	Classis of telom plants	Derived heterotrophic groups
<i>Chromophyta</i>	<i>Chrysophyceae</i> <i>Xanthophyceae</i> <i>Bacillariophyceae</i> <i>Phaeophyceae</i> <i>Dinophyceae</i>	0	<i>Myxophyta</i> <i>Phycomycophyta</i> <i>Mycophyta</i>
<i>Rhodophyta</i>	<i>Rhodophyceae</i>	0	
<i>Chlorophyta</i>	<i>Chlorophyceae</i> > → <i>Conjugatophyceae</i> <i>Charophyceae</i>	<i>Bryopsida</i> <i>Psilopsida</i> <i>Lycopsida</i> <i>Tmesopsida</i> <i>Sphenopsida</i> <i>Pteropsida</i>	
Residual Flagellates	<i>Euglenophyceae</i> <i>Cryptophyceae</i> <i>Chloromonadophyceae</i> etc.	0	

In these divisions we can discern lines of morphological progress, each of which constitutes a lower taxonomical unit, the class. This taxon include forms of different habit, ranging from the simplest to the most advanced types and the sequence of stages may be regarded as illustrative of an evolutionary process. In my view, the class concept was derived from algal phylogeny.

The classes of telom plants, used in my synopsis in the sense of TACHTADŽAN (1950), are taken in the latter's *Telomophyta* as phyla. Evidently the telom plants exhibit so high a degree of multiplicity of form that their classification has to start with taxonomic units higher than the rank of class. For example, the higher plants are divided by NOVÁK (1961) into 8 subdivisions, by ZIMMERMANN (1959) into 6 divisions.

The evolutionarily long-ranged line of an algal class is composed of qualitatively different grades of algal habit, beginning with the simplest ones and leading progressively to the complex types of organisation. Using the term "progress" biologically, the question arises as to what the correlations of this process mean. "Lower", "simple", "primitive", are those types from which the other, "higher", "advanced", "derived", plants arose. "Higher" types are on the whole more complex than "lower" ones. But many obviously "low" organisms exhibit remarkable complexities, especially as far as internal structure is concerned. This is due to the fact that they underwent their own evolutionary processes, limited in outer extent of course.

Biological progress, thus defined, occured in time and can be followed only historically. The real historical succession of evolutionary stages can be demonstrated only by fossils. Roughly, plants in Precambrian, Cambrian and Ordovician were algae, succeeded in Silurian and Devonian by Pteridophytes, in Carboniferous, Triassic and Jurassic by Gymnosperms and later on by Angiosperms. Unfortunately, as far as the algae are concerned, there are only a few fossil records of algae that fail to give some idea of their evolution.

In fact, the few types of fossil algae that as yet we know perfectly, exhibit a high level of structural complexity, acquired as early as the "algal" epoch in the Palaeozoic. Fossil remains of blue-green algae prepared from Ordovician and Cambrian schists display the same morphological organisation as recent genera and belong to the more advanced types (CROFT and GEORGE 1959, STARMACH 1963). These discoveries confirm a very important fact, known from the development of higher plants as well, that some plants did not change morphologically at all during long periods of their evolution. The recent types display the same habit and structure as those from the past geological epochs. On the other hand, we can presume that these plants, the fossils of which we can examine now, might have become starting point for further evolutionary processes, leading progressively and gradually to recent advanced plants. Generally speaking, each group of plants at a distinct evolutionary level behaved, under the influence of environment and of other, unknown factors, in a threefold manner: 1) one part did not survive the environmental conditions and became extinct, 2) a second part did survive the new epochs without any obvious morphological changes, and 3) the third portion became adapted to the new conditions by evolving new morphological properties.

Such behaviour of organisms during their evolution is known to occur and brings about the common consequence that both, primitive and derived types live on the earth one beside the other. In some works dealing with evolution (HUXLEY 1942, FELDMANN 1952) this phenomenon was recognised without being designated with a special term. I call it the inequality of the evolutionary process and consider it to be a very important fact in establishing a natural system of plants, or algae. Having no fossil algae tracing the evolutionary steps in biological history, we have to reconstruct the sequence in an algal evolutionary line by grouping the taxa according to the level of their morphological progress. The comparative morphology of algae of the same habit and the existence of links connecting qualitatively differing groups can serve as control for such a systematic arrangement.

As early as 1902, BLACKMANN and TANSLEY outlined an evolutionary line of green algae leading from the green flagellates (*Volvocales*) to the filamentous thalli. The flagellates have been considered (NÄGELI 1849, ROSTAFINSKI 1882, KLEBS 1893) as a primary group of organisms from which not only the algae, but also the heterotrophic plants and animals, have arisen.

Most interesting for our consideration is the evolutionary line of green plants in the division *Chlorophyta*. Starting from monadoid habit, represented by the order *Volvocales*, the distinct steps of algal advance are cells (coccoloid habit) and filaments (trichous habit), with a subsequent, filament-derived, elaborated thallus (cladothalloid habit). Here the algal line is interrupted and the next step is the teloms of higher plants.

This evolutionary series of green plants has been recognised by the majority of botanists. There is no unity, however,⁵ as to where is the starting point of this evolutionary trend. Some presume that solitary cells ("archethallus" of CHADEFAUD 1952) might be the beginning, from which the flagellates have arisen in one direction and the algae in another. There is no objective criterion by which we can solve the problem. Evolution from the primitive ancestors occurred in remote geological epochs and no fossils of the ancestral organisms have been found. We know only the results of evolution, a collection of more and more advanced plants.

The most weighty objection against the theory that flagellates are the ancestral type is that recent flagellates (e.g. *Chlamydomonas*, *Carteria*) exhibit a very complex internal structure as

compared with recent coccoid forms (e.g. *Chlorococcum*, *Chlorella*). That is true, of course, but on the other hand, both groups of organisms, flagellates and coccoid algae, have been subjected to an evolutionary process and have gained (or lost) some features, even if they have retained their original habit. Green cells, in becoming adapted to autotrophic growth, have lost some organelles that are obligate for monadoid existence. It is well known from the theory of biological evolution that progress may be combined with regression, that is to say the loss of some features. Even in this case, the result of the new evolutionary step may be progressive.

In the class *Chlorophyceae*, the most salient feature is the existence of various intermediate stages between the qualitatively different evolutionary grades. Thus between flagellates (*Volvocales*) and coccoid cells (*Chlorococcales*) there exist intermediate types that have gained new taxonomic characteristics (e.g. pseudoflagella) and may therefore be designated as a new taxonomic unit, the *Tetrasporales* (syn. *Tetrasporineae*). The limits between *Tetrasporales* and *Chlorococcales* on the other side, are so vague that some genera can be placed in one or the other order according to the tastes of the observer.

The main difference between *Volvocales* and *Tetrasporales* is the mode of vegetative life, being motile in the former and non-motile in the latter. *Chlorococcales* differ from *Tetrasporales* in the lack of organelles characteristic of flagellates (contractile vacuoles, stigmata, flagella). The common attribute of all these lowest plants is the mode of origin of daughter cells. They are always produced within the mother-cell wall which does not take part in the formation of the new daughter-cell walls. The mother-cell wall, which does not take part in the formation of the new daughter-cell walls. The mother-cell wall in fact, after the formation of daughter cells, becomes a dead structure that disappears by rupture or by dissolution.

The next evolutionary step in the line of algal advances is the development of filaments. This new morphological feature is generally called the t r i c h o u s habit. In the simplest case the filament is a row of uniform cells dividing by producing a transverse wall that separates the new daughter protoplasts. The mother-cell walls persist and are transformed into the daughter-cell walls and this mode of new cells formation is the main distinguishing characteristic between the coccoid (*Chlorococcales*) and the trichous habit (*Ulotrichales*). The development of filaments from coccoid cells is a very important step in plant phylogeny and the difference between these habits is surely greater than the difference between the Pteridophytes and the flowering plants. It took a long period of geological time for this development to be accomplished.

The theory of the origin of filaments from coccoid algae during evolution was put forward by PASCHER (1930) at the V. International Congress in Cambridge. According to this theory, the filament is a uniseriate row of autospores which arise by division of protoplasts into 2 portions. Both portions produce their own cell walls, and remain enclosed by the mother-cell wall which enlarges and grows with the new daughter walls.

The whole process of filament formation from an elongate coccoid alga to a filamentous or elaborated heterotrichous habit came about by small evolutionary changes and we can follow it now in recent examples. The most simple filaments of green algae are in fact rows of autospores. *Radiophyllum conjunctivum* SCHMIDLE and *R. flavescens* G. S. WEST are good examples of single threads formed by rows of autospores. The mother-cell wall only partly covers the newly arisen cell and takes no part in the formation of the new cell wall.

In *Cylindrocapsa*, a primitive but true filament is produced, formed by autospores enclosed in the mother-cell walls. The new walls of the autospores are distinct and can be easily distinguished from the old parent wall.

In elaborated trichous green algae, a septum is formed separating the divided protoplasts. But the lamellated structure of the septum and especially of the longitudinal cell walls indicates that the new cell walls have arisen by the secretory activity of the divided protoplasts (e.g. in *Microspora* etc.).

The development of filaments in algal evolution represents a new morphological feature that has to be designated as a taxonomical unit, the *Ulotrichales*. This taxon includes a great variety of algae of different appearance, the

common characteristic being the trichous habit. The algal body is composed of uninucleate cells arranged either in simple filaments or in elaborated filament-derivatives. The lowest *Ulotrichales* are simple, non-branched threads, the cells of which can easily become detached. A higher degree of organisation is the heterotrichous habit as defined by FRITSCH (1939). The heterotrichous thallus consists of two portions: one prostrate and serving as a means of attachment to the substratum, though usually composed of photosynthetic cells, the other arising from this creeping part and projecting upwards. *Stigeoclonium* and *Trentepohlia* are the best examples of trichous algae producing both prostrate and erect systems of filaments. A more elaborate type of heterotrichous organisation is CHADEFAUD's "cladothallus" consisting of cladoms (CHADEFAUD 1952). The cladom is a system consisting of an axis (or bunch of axes) with unlimited growth; the axis bears ramification called pleuridies, with limited growth. The axis and the pleuridies can exhibit terminal or intercalary growth, like the telomes of higher plants; even the relations between the axis and ramifications of the cladothallus are comparable to those between the caulom and folia.

Among the heterotrichous green algae with a differentiated thallus is *Fritschiella tuberosa*, described by IYENGAR (1932) from moist soil in India. This alga consists of a plant body differentiated into a rhizoidal system, a prostrate system, primary projecting threads and secondary projecting ones. The prostrate portion of the alga has the form of uniseriate or multiseriate filaments, sometimes clearly differentiated into nodal and internodal parts or into irregular parenchymatous clusters. The prostrate filaments ramify extensively in the moist soil and form an irregular network. Reproduction and perennation of the alga is brought about by the prostrate system, the cells of which being densely laden with storage materials are capable of survival throughout the dry period. In addition, the filaments of the prostrate system develop funnel-shaped structures which produce swimmers. These are quadriflagellate and after a short period of swarming develop into new plants. Biflagellate gametes are produced in other plants in a similar manner and form zygotes. These germinate directly to give rise to new plants. Cytological investigations revealed (SINGH 1947) that reduction division takes place during zoospore formation and therefore a regular alternation of two outwardly identical generations exists. *Fritschiella* thus possesses an isomorphic alternation of generations and provides an example of an elaborated green alga that has become adapted to terrestrial life. The haploid prostrate system making parenchymatous clusters and producing gametangia recalls the gametophytes of some Pteridophytes, not only in cytological structure but also in appearance. The erect system of branched filaments grows in a fan-shaped manner, forming a leaf-like structure which projects freely into the air. With *Fritschiella* the line of morphological advance in the recent green algae comes to an end. This alga has left the aquatic environment and become adapted to terrestrial life. It may therefore be considered as the type of alga from which the higher plants have arisen, but the link connecting the two groups of plants, algae and teleomphytes, is missing. The lack of a connecting link does not contradict the theory of the evolutionary origin of teleomphytes from algae. The morphology, cytology and ecology of *Fritschiella* is sufficient support for this view.

The trichous habit of green algae is not the only evolutionary trend in the *Chlorophyceae*. There are two further trends that have developed in parallel and have led to a high degree of differentiation. It seems, however, that their morphological progress was halted and types analogous to higher plants were not produced. The siphonous green algae (*Bryopsidales*) possess a plant body differentiated into delicate bi- or tripinnate fronds in *Bryopsis*; in *Caulerpa* the coenocytic body consists of a branched cylindrical rhizome, bearing numerous well-branched anchoring rhizoids and a number of upright assimilatory shoots, sometimes reaching a length of 80 cm. The coenocytic formation of a simple plant body is met with in the *Tetrasporales* (*Characiosiphon* IYENGAR 1936) and in the *Chlorococcales* (*Protosiphon* KLEBS) and either group can therefore be considered as the place of origin of the *Bryopsidales*.

The siphonocladoid habit (*Siphonocladales*) differs from that of the other orders of green algae in having multinucleate cells, which are arranged either in uniseriate heterotrichous systems or into very complex cladoms. The genera *Microdictyon* and *Anadyomene* form small foliose thalli resulting from abundant branching that occurs essentially in one plane. Even in the siphonocladoid algae there is no progress beyond this morphological status and there are no connections leading to terrestrial and higher plants.

The class *Chlorophyceae* is a good example of an evolutionary line, having all the steps of the process from motile cells to a differentiated algal thallus. Other classes of the green plants (*Chlorophyta*) have only some stages or branches of an evolutionary line. In the *Conjugatophyceae*, the unicellular *Desmidiaceae* reproduce by vegetative division of cells, the mode of reproduction proper to primitive trichous algae. The *Zygnematales* are simple trichous algae, producing no branches. The *Charophyceae*, however, possess a peculiar position in the plant system. Their plant body, a cladothallus, and the morphology of their reproductive organs are quite different from those known among the *Chlorophyta* and because of this they have to be taken as a relic of a special algal class with an unknown evolution.

The theory of lines of algal advance going through the above-mentioned algal habits from the monadoid one to the heterotrichous thallus has great support from the fact that the same sequence of evolutionary grades can be demonstrated in algal classes of the division *Chromophyta*.

Here, in the *Xanthophyceae*, a class with xanthophylls dominating over chlorophyll, the line of algal evolution has the same sequence of habit: monadoid (*Heterochloridales*), intermediate (capsal, *Heterogloales*), coccoid (*Mischococcales*), trichous (*Tribonematales*) and siphonous (*Botrydiales*). The highest morphological form in *Xanthophyceae* is the heterotrichous plant body. The individual evolutionary grades are convergent and morphologically identical with those in *Chlorophyceae*. The only difference is that monadoid and capsal *Xanthophyceae* are naked cells, whereas *Chlorophyceae* of the same grade are walled. The morphological resemblance of convergent coccoid types is so striking that the presence or absence of chlorophyll *b* is the only reliable proof of their taxonomic position (*Nephrodiella-Coccomyxa*).

Further convergent algal lines are the *Chrysophyceae* and the *Dinophyceae*. Even in these classes we can demonstrate the same principal ranges of algal evolution, the monadoid, coccoid and trichous habits. Consequently, algae of the same morphological organisation are ranged in the relevant orders.

The difference of chromophycean algal classes compared with the class *Chlorophyceae* lies in the different degrees of morphological and taxonomic diversity in individual evolutionary grades. In the *Chlorophyceae*, the most advanced order, *Ulotrichales*, exhibits a wealth of morphological types from few-celled filaments to cladoms of heterotrichous habit. Conversely, in *Chrysophyceae* and *Dinophyceae*, the monadoid orders contain many taxonomic units, whereas the advanced orders exhibit a scarcity of forms.

The remaining classes of the *Chromophyta* evolved differently. *Bacillariophyceae* reached only the unicellular status, but within this produced an immense wealth of forms. In the *Phaeophyceae*, the lowest evolutionary series (monadoid, coccoid) are completely lacking and the evolutionary process can be followed only within the heterotrichous habit. On the other hand, the development of heterotrichous status in the *Phaeophyceae* led to many diverse forms.

The elaborate thalli of *Phaeophyceae* are produced either by aggregations of filaments and their branches (multiaxial as in *Leathesia*, uniaxial as in *Spermatochnus*) or by the repeated subdivision of the cells of primary erect filaments, e.g. the parenchymatous types like *Punctaria* and *Scytosiphon*.

Evolutionary lines and convergent grades among algae

Class \ Habit	Monadoid	Intermediate	Coccoid	Trichous			Siphonous	Siphonocla- doid
				intermediate	filamentous	cladothalloid		
<i>Chlorophyceae</i>	<i>Volvocales</i>	<i>Tetrasporales</i>	<i>Chlorococcales</i>	<i>Ulotrichaceae</i>	<i>Ulotrichales</i>	<i>Ulotrichales</i>	<i>Bryopsidales</i>	<i>Siphonocladales</i>
<i>Conjugatophyceae</i>	—	—	—	<i>Mesotaeniales</i> <i>Gonatozygales</i> <i>Desmidiiales</i>	<i>Zygnemales</i>	—	—	—
<i>Charophyceae</i>	—	—	—	—	—	<i>Charales</i>	—	—
<i>Chrysophyceae</i>	<i>Chrysomonadales</i>	<i>Chrysocapsales</i>	<i>Chrysosphaerales</i>	<i>Phaeothamniales</i> p. p.	<i>Phaeothamniales</i>	—	—	—
<i>Bacillariophyceae</i>	—	—	—	<i>Centrales</i> <i>Pennales</i>	—	—	—	—
<i>Xanthophyceae</i>	<i>Heterochloridales</i>	<i>Heteroglocales</i>	<i>Mischococcales</i>	<i>Heterotrichales</i> p. p.	<i>Heterotrichales</i>	—	<i>Botrydiales</i>	—
<i>Dinophyceae</i>	<i>Prorocentrales</i> <i>Peridinales</i>	<i>Gloco-diniales</i>	<i>Dinococcales</i>	<i>Dinotrichales</i> p. p.	<i>Dinotrichales</i>	—	—	—
<i>Phaeophyceae</i>	—	—	—	—	<i>Ectocarpaceae</i>	<i>Isogeneratae</i> <i>Heterogeneratae</i> <i>Cyclospora</i>	—	—
<i>Rhodophyceae</i>	—	—	—	<i>Bangiophycidae</i> p. p.	<i>Bangiophycidae</i>	<i>Florideophycidae</i>	—	—

In the *Phaeophyceae*, the heterotrichous filamentous habit occurs in the most primitive members and shows a marked degree of convergence with that found in *Chaetophorineae* amongst the *Chlorophyceae*. The majority of *Phaeophyceae*, however, are compact multicellular types with a more or less pronounced differentiation of tissues.

In the haplostichous *Ectocarpales* for example, filamentous outgrowths from the axial thread arise superficially and grew intimately apposed to its surface. In this manner a compact superficial cortex arises which may increase by cell division. Such superficial threads usually contain chromatophores and are designated "cortical threads".

In *Laminariales* a bulky parenchymatous thallus develops by progressive septation of an erect filament. Even here, the parenchymatous development is derived from a trichous system. In an adult thallus, the differentiation into rhizoid, stipe and blade is complete and longitudinal growth occurs by means of an intercalary meristematic region. *Fucales* shows considerable anatomical resemblance to the *Laminariales*, but one of the outstanding differences lies in the mode of growth, since the *Fucales* exhibit apical growth effected by a single apical cell. This meristematic cell is three-sided, cutting off segments from its three faces. With the three-sided meristematic cell and with morphological and anatomical differentiation, the *Phaeophyceae* has reached a higher level of organisation than the *Chlorophyceae*. Nevertheless, it is highly probable that evolution of the *Phaeophyceae* followed a similar line to that of the *Chlorophyceae*. The simple types (monadoid, coccoid) probably became extinct and the recent types are all at the heterotrichous level of organisation. But within this level, the *Phaeophyceae* produced a wealth of types, differing in morphology, anatomy, in life cycles, etc. The individual steps of this evolution can be classified as orders.

The third division of phototrophic plants, the *Rhodophyta*, is very sharply defined by its biochemical characteristics and by the distinctive morphology of the sexual organs. As far as the morphology of the plant body is concerned, it is very difficult to discern evolutionary trends running through the only class, the *Rhodophyceae*, containing the two subclasses *Bangiophycidae* and *Florideophycidae*. In fact, there are coccoid types and uniseriate filaments within the class, but these simple types seem to be the result of reduction rather than primitive forms. In addition, no monadoid cells were found in the *Rhodophyceae* and even flagellate reproductive cells are missing.

In some cases the heterotrichous habit is recognisable, especially in juvenile stages. But the majority of thalli exhibit one of a wealth of morphological forms, being invariably pseudoparenchymous and showing varied degrees of compactness. The thalli are composed of dense aggregates of the lateral systems of one or more richly branched filaments which, in the heterotrichous forms, arise from the prostrate system. In this manner, cylindrical thalli usually arise with more or less copious ramification, or a markedly foliose development occurs. The red algae, commonly grouped as one class, the *Rhodophyceae*, exhibit no clear affinities with the other classes of algae and represent therefore a natural group of quite distinct plants which have reached a high degree of complexity in the aquatic environment, but in contrast to the *Chlorophyta* have not evolved to terrestrial existence.

References

- BLACKMAN F. (1900): The primitive Algae and the Flagellata. — Ann. Bot. 14 : 647—688.
BOHLIN K. (1901): Zur Phylogenie der grünen Algen und der Archegoniaten. — Akad. Afhandl., Uppsala, 1—43.
BÖCHER T. W. (1951): Studies on morphological progression and evolution in the vegetable kingdom. — Biol. Meddel. 18 (13) : 1—51.
CHADEFAUD M. (1952): La leçon des Algues. — Ann. biol. 28 : 9—25.
— (1960): Les végétaux non vasculaires (Cryptogamie). — Traité de Botanique systématique 1 : 1—1016.
CHRISTENSEN T. (1954): Some consideration on the phylogeny of the Bryophyta. — Bot. Tidskr. 51 : 53—58.
COPELAND H. F. (1956): The classification of lower organisms. — 302 p., California.
DOMIN K. (1944): Soustava rostlin buněčných. — Acta bot. boh. 15/16 : 1—290.
ENGLER A. (1954): Syllabus der Pflanzenfamilien. — 367 p., Berlin.
FELDMANN J. (1958): Remarques sur la systématique actuelle des Algues. — Uppsala Univ. Ars. skr. 6 : 59—64.

- (1952): Les cycles de reproduction des Algues et leurs rapports avec la phylogénie. — *Rev. cytol. biol. végét.* 13 (1—2) : 1—49
- FOTT B. (1959): *Algenkunde*. — 482 p., Jena.
- (1960): Taxonomische Übertragungen und Namensänderungen unter den Algen. — *Preslia* 32 : 142—154.
- FRI TSCH F. E. (1939): The heterotrichous habit. — *Bot. Not.* 1939 : 125—133.
- (1945): Studies in the comparative morphology of the Algae. IV. Algae and archegoniate plants. — *Ann. Bot.* 9 : 1—29.
- (1949): The lines of algal advance. — *Biol. Reviews* 24 : 94—124.
- GREENWOOD A. D. (1964): The structure of chloroplasts in lower plants. — *Abstracts of papers. Tenth inter. bot. congr. Edinburgh 1954* : 212—213.
- HUXLEY J. (1942): *Evolution, the modern synthesis*. — 646 p., London.
- IYENGAR M. O. P. (1932): *Fritschiella*, a new terrestrial member of the Chaetophoraceae. — *New Phytol.* 31 (5) : 329—335.
- KLEBS G. (1893): Flagellatenstudien I, II. — *Z. wiss. Zool.* 55 : 265—445.
- LANJOUW J. (1956): *International Code of botanical nomenclature*. — 338 p., Utrecht.
- NÄGELI C. (1849): *Gattungen einzelliger Algen*. — 139 p., Zürich.
- NĚMEJC F. (1950): The natural systematic of plants in the light of the present palaeontological documents. — *Acta Mus. nat. Pragae.* 6B, no. 3, *Geol. et Palaeont.* No. 2 : 1—83.
- NOVÁK F. A. (1961): *Vyšší rostliny, Tracheophyta*. — 944 p., Praha.
- PAPENFUSS G. F. (1955): Classification of the Algae. — *A century of progress in the natural sciences*, p. 115—224.
- PASCHER A. (1914): Über Flagellaten und Algen. — *Ber. deutsch. bot. Ges.* 32 : 136—160.
- (1916): Zur Auffassung der farblosen Flagellatenreihen. — *Ibidem*, 34 : 440—447.
- (1918): Von einer allen Algenreihen gemeinsamen Entwicklungsregel. — *Ibidem*, 36 : 390 bis 409.
- (1924): Über die morphologische Entwicklung der Flagellaten zu Algen. — *Ibidem*, 42 : 148 bis 155.
- (1930): Über die morphologische Vergleichbarkeit der Fadenalgen und der fadenförmigen Moos- u. Farnvorkeime. — *Rep. proc. sect. M. 5th inter. bot. Congr. Cambridge* 322—324.
- (1931): Systematische Übersicht über die mit Flagellaten in Zusammenhang stehenden Algenreihen und Versuch einer Einreihung dieser Algenstämme in die Stämme des Pflanzenreiches. — *Beih. bot. Cbl.* 48 : 317—332.
- (1939): Heterokonten. — *Rabenhorst's Kryptogamenflora* 11 : 1—1091.
- ROSTAFINSKI J. (1882): *L'Hydrurus et ses affinités*. — *Ann. Sc. natur.*, VI. ser. *Botan.* T. 14:1—25.
- SINGH R. M. (1941): On some phases in the life history of the terrestrial Alga, *Fritschiella tuberosa* Iyeng., and its autecology. — *New Phytol.* 40 (3) : 170—182.
- (1947): *Fritschiella tuberosa* Iyeng. — *Ann. Bot.* 11 (42) : 159—164.
- STARMACH K. (1963): Blue-green algae from the tremadocian of the holy cross mountains (Poland). — *Acta palaeont. polon.* 8 (4) : 451—463.
- TACHTADŽJAN A. L. (1950): *Fylogenetičeskie osnovy sistemy vyššich rasténij*. — *Botan. Ž.* 35 (2) : 113—139.
- UEDA K. (1961): Structure of chloroplasts in algae. — *Cytologia* 26:344—358.
- VISCHER W. (1953): Über primitivste Landpflanzen. — *Ber. schweiz. bot. Ges.* 63 : 169—193.
- WETTSTEIN R. (1935): *Handbuch der systematischen Botanik*. — 1149 p., Leipzig u. Wien.
- ZIMMERMANN W. (1959): *Phylogenie der Pflanzen*. — 777 p., Stuttgart.