Algae: Phylogeny and Evolution

Introductory article

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Article Contents

Ideas on the phylogeny and evolution of the algae are presently based on a combination of ultrastructural and molecular data. Following the discovery that the chloroplasts of eukaryotic algae arose after one or more symbiotic events, the term algae is now used as a colloquial term for primitive plants, including both prokaryotic and eukaryotic species.

Definition of Algae

Algae is a general term for primitive plants, i.e. organisms using the green pigment chlorophyll *a* in their photosynthesis but lacking the features of more advanced organisms (e.g. flowering plants) such as a vascular system for internal transport of water and nutrients. Algae were until recently believed to constitute a natural group of organisms, i.e. a group of related species. Prokaryotic forms were classified as the division blue-green algae, while eukaryotic forms were classified in several divisions. However, the single feature uniting the algae, the chlorophyll-*a* based photosynthesis, is located in the chloroplasts of eukaryotic algae and chloroplasts have now been shown unequivocally to be symbionts.

The ancestors of the eukaryotic algae are presently believed to be phagotrophic amoebae and flagellates, i.e. organisms feeding on and digesting other organisms in food vacuoles in the cell ('protozoa'). It was originally thought that the chloroplast of the eukaryotic algae originated after ingestion and transformation of a blue-green alga. This idea is still believed to be correct for some algae. Instead of digesting the prey, the prey is retained more or less intact in the food vacuole of the host and photosynthesis is able to proceed. Products from photosynthesis such as carbohydrates are then transferred to the host through the food vacuole membrane and utilized in the metabolism of the host. This symbiosis is so successful that in many cases the host has given up phagotrophy altogether and become an obligate phototroph. The blue-green alga remains in the cell of the host, separated from the cytoplasm by two membranes. The innermost membrane is the cell membrane of the blue-green alga, the outer membrane is the food vacuole membrane. Most of the DNA from the blue-green algal genome has been transferred to the host nucleus.

Ultrastructural evidence accumulating from 1960s onwards has shown that in many groups of algae this idea is far too simple. In these groups the chloroplasts are separated from the cytoplasm by more than two membranes, whose origin was initially hard to explain. However, the finding of a second nucleus associated with the chloroplast of cryptophyte flagellates by Dennis Greenwood at Imperial College, London in 1974 served as an eye-opener. It was realized that the chloroplast of cryptophytes is not a blue-green alga but an entire eukaryotic alga. This alga itself, however, was the result of a symbiosis between a protozoan host and a blue-green alga. In other words the chloroplast of cryptomonads arose as a result of two successive symbioses. Additional studies made it clear that the chloroplasts of other eukaroytic algae arose as a result of as many as three symbioses, and F. J. R. Taylor in 1974 coined the phrase 'the serial endosymbiosis theory'. In some cases chloroplasts were subsequently lost during evolution of the algae, complicating matters even more.

Studies of DNA base sequences have confirmed that chloroplasts arose by one or more serial symbioses. It has also given information on the identity of the organisms that were taken up by the secondary and tertiary symbioses. The organisms formerly classified as protozoa, algae and primitive fungi are now grouped together as protists and the following account discusses the evolutionary origin of the algal groups of protists, based on ultrastructural, biochemical and molecular data. The term protist (kingdom Protista) goes back to the famous German zoologist Ernst Haeckel (1866, a contemporary of Charles Darwin), and Haeckel included under this term a number of the smaller algae, in addition to foraminifera, myxomycetes and various other groups of heterotrophic organisms. Protoctista was introduced by H. F. Copeland (1956) to include also larger algae such as brown algae and red algae. This term is now generally considered superfluous, however, and Haeckel's term protist is used for all primitive eukaryotes previously known as algae, primitive fungi or protozoa.

Prokaryotic Algae

Most prokaryotic algae possess a single type of chlorophyll, chlorophyll *a*, while phycobilins and carotenoids serve as accessory pigments. Such algae are classified as blue-green algae (or cyanobacteria, see below) and they form one of the oldest groups of organisms on earth, dating back to the earliest days of organic evolution 3.5–4 thousand million years ago. Oxygen of the present-day atmosphere is thought to have evolved as a result of the photosynthetic activity of blue-green algae. In the 1970s a prokaryote containing both chlorophylls *a* and *b* was discovered as a symbiont of some marine ascidians in the tropics (*Prochloron*). Subsequently two free-living genera of what became known as prochlorophytes were discovered, one in marine and the other in freshwater plankton. The three genera were for a while considered to represent a second group of photosynthetic prokaryotes. However, gene studies have indicated that the three genera are only distantly related to each other and that they are related to different species of blue-green algae. This has resulted in the idea that chlorophyll *b* developed from chlorophyll *a* several times: three times in the three 'prochlorophyte' genera, once in the chlorarachniophytes (see below) and once in the progenitor of the green algal chloroplasts. The class Prochlorophyta has now been abandoned and the three genera classified among the blue-green algae. Phylogenetically speaking, the blue-green algae are related to Eubacteria and this has resulted in the term Cyanobacteria. Both the terms cyanobacteria and cyanophyta (blue-green algae) are valid, the former stressing the phylogenetic relationship to heterotrophic bacteria of the group Eubacteria, the latter the algal nature of the group (i.e. utilizing chlorophyll *a* for photosynthesis).

Some Comments on the Evolution of Eukaryotes

There are indications from DNA sequencing that many of the major groups of organisms arose more or less at the same time during the geological history of the earth, the so-called crown groups of organisms (**Figure 1**). This origin probably dates back to at least one thousand million years ago, perhaps longer. A few groups arose before the crown groups, perhaps some of those whose cells lack chloroplasts, mitochondria or even the Golgi apparatus and microbodies. One algal group, the euglenoid flagellates, and their protozoan relatives, the bodonid and trypanosomatid flagellates, also branch off early in the trees generated by examination of the 18S rRNA tree. However, studies of other genes do not agree with this finding, showing instead that these three groups arose together with the crown groups. The three groups contain a full complement of cell organelles, thus agreeing with the latter interpretation.

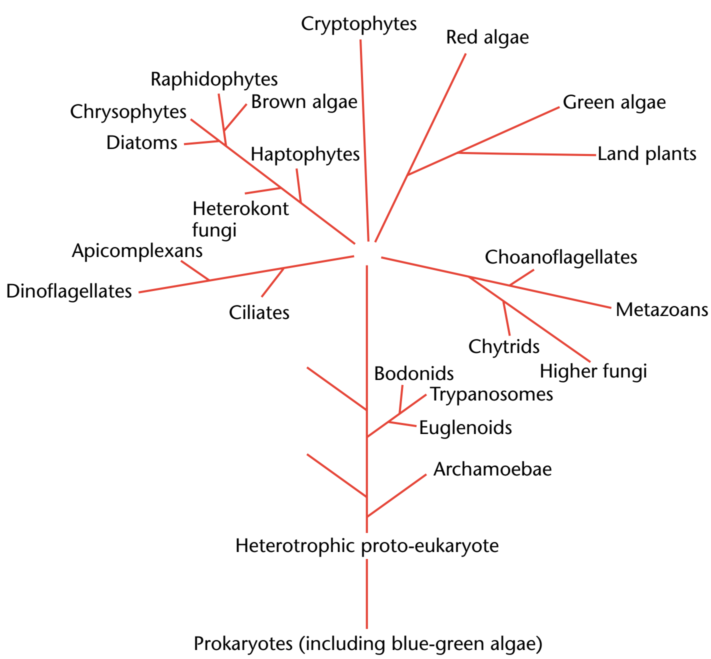

Figure 1 Phylogenetic tree, illustrating present ideas on the relationships between algal and other groups of protists. Five main branches have been drawn to radiate from approximately the same point, indicating that these branches (the so-called crown groups) may have appeared at approximately the same time during the history of the earth.

Algae Whose Chloroplasts Arose After a Single Symbiotic Event

The chloroplasts in two of the main groups of algae, the red algae and the green algae, are separated from the cytoplasm by only two membranes, indicating that they arose by transformation of a prokaryote. In the phylogenetic trees the red and green algae sometimes form sister groups, indicating that they have a common origin. The ancestor of the chloroplast is probably to be found among the blue-green algae. An intermediate group may be the class Glaucophyta (Glaucocystophyta), whose few members (less than 10 species) contain so-called cyanelles in the cells. The cyanelles are undoubtedly blue-green algae, each located in a vacuole and sometimes retaining a thin cell wall. The ultrastructure of the flagellar apparatus also indicates a phylogenetic relationship between glaucophytes and green algae (red algae lack flagella altogether). The green algae, red algae and glaucophytes may form one of the crown groups.

Algae Whose Chloroplasts Arose by Secondary Endosymbiosis

This is the majority of algae, here grouped under six headings: cryptophytes, chlorarachniophytes, dinoflagellates and other alveolates, heterokonts, haptophytes and euglenoids.

Cryptophytes

The cryptophytes stand out from all other algae particularly in the structure of the flagellar apparatus, and they are not known with any degree of certainty to be related to any other protist group. Cryptophyte flagella carry flagellar hairs somewhat resembling the hairs lining the anterior flagellum of heterokonts but details are different. Also, mitochondria of cryptophytes contain flat cristae like red algae and green algae, rather than the tubular cristae of heterokonts, dinoflagellates, haptophytes and numerous other protists. Sequence data indicate that the chloroplast of cryptophytes is a transformed red alga, which lost all organelles upon ingestion, except the nucleus (now known as the nucleomorph) and the chloroplast. An additional chlorophyll (of the chlorophyll *c* group) developed within the chloroplast, probably from chlorophyll *a*. Phycobilins changed from forming distinct phycobilisomes on the thylakoid surface as in red algae and blue-green algae into less well-defined contents in the thylakoid lumen of cryptophytes. Most of the nuclear DNA was transferred to the host nucleus, leaving only three small chromosomes behind.

Chlorarachniophytes

The chlorarachniophytes resemble cryptomonads in possessing a nucleomorph-containing chloroplast, but they are otherwise very different. The few species known are green, containing both chlorophylls *a* and *b*, and they almost certainly obtained the chloroplast from transformation of a green alga. Ultrastructurally they are very unlike any other group of algae. Their relationship to other protist groups remains unresolved.

Dinoflagellates

Dinoflagellates constitute a relatively well-defined group, now known to be related to ciliates and apicomplexan protozoa (the latter group also known as sporozoa). They differ from other algae particularly in the structure of the nucleus, mitosis and details of the flagellar apparatus. The cell wall, if present, is composed of plates deposited in flat cisternae beneath the plasma membrane. Similar cisternae are present in ciliates and apicomplexans, and nucleotide sequencing has confirmed that the three groups are interrelated. They are now known as the 'Alveolata' and form one of the crown groups. A small group of parasites known as the perkinsids appears to form a phylogenetic link between dinoflagellates and apicomplexans. Only half of the known dinoflagellates are photosynthetic. Many of the others are now being found to be phagotrophic, some ingesting their prey (other algae, even weakened cells of their own kind) by sucking out the contents of the prey through the so-called peduncle. This probably accounts for the chloroplast diversity found in dinoflagellates. It indicates that endosymbiosis took place independently several times. The cytoplasm of the endosymbiont was retained in food vacuoles while the prey cell membrane was usually left behind. Some dinoflagellates even obtained their photosynthetic apparatus by tertiary symbiosis (see below).

Heterokonts and other stramenopiles

The heterokonts are a large group of organisms previously classified as algae, fungi and protozoa. That these are all related and form a natural group was shown early on by electron microscopy and it has been confirmed by DNA studies. The algal heterokonts comprise the chrysophytes, diatoms, raphidophytes, xanthophytes, eustigmatophytes and phaeophytes. Several smaller groups are sometimes classified as separate classes (synurophytes, pelagophytes, dictyochophytes, etc.). The heterokonts are readily identified by the structure of the motile stage, which is typically biflagellate. The anterior flagellum carries two opposite rows of tripartite hairs, while the second, often posteriorly directed flagellum, is smooth. The chloroplast, if present, is surrounded by four membranes, indicating that a eukaryotic prey was engulfed and transformed into a chloroplast. During this transformation all organelles were lost except the chloroplast and a few cisternae. The combination of pigments, which includes chlorophyll *a* and various types of chlorophyll *c*, in addition to the carotenoid fucoxanthin, is shared with some haptophytes. The ancestor of the chloroplast in these groups is, however, not known, but DNA studies have confirmed that the heterotrophic heterokonts arose before the phototrophic ones. The heterokonts form one of the crown groups (**Figure 1**). The term stramenopiles (straminopiles) is sometimes used as a common term for heterokonts (i.e. species with one hairy flagellum carrying tripartite flagellar hairs and one smooth flagellum) and related organisms such as opalinids, proteromonads, etc., whose flagella are different.

Haptophytes

The haptophytes differ from other algae particularly in the structure of the flagellar apparatus and in the possession of a haptonema, an organelle not known in any other group of protists. The chloroplast is very similar to that of many heterokonts, but in some species the pigments are modified types of fucoxanthin. Haptophytes were formerly thought to be related to chrysophytes but neither ultrastructural investigations nor DNA studies have confirmed this view. In DNA studies, the haptophytes often appear as a sister group to the heterokonts.

Euglenoids

The euglenoid flagellates form a well-defined group of phototrophic and heterotrophic organisms. They differ from other algae in the ultrastructure of almost all cell organelles and they are related to none of these. They are, however, related to two groups of heterotrophic flagellates, the bodonid and trypanosome protozoa, forming a sister group to these two groups. The chloroplast of euglenoids almost certainly originated after ingestion of a green alga by a phagotrophic host. Pigments of the two groups are similar while formation of starch in the chloroplast was replaced after establishment of symbiosis with formation of another carbohydrate, paramylon, in the cytoplasm. It has been suggested that the chloroplast of euglenoids arose after uptake of green algal chloroplasts rather than whole cells of green algae. This is not likely, however, since chloroplasts do not contain all the genetic material necessary for their ongoing function, and additional genes reside in the nucleus. The bodonids, trypanosomes and euglenoids form a natural group, believed from 18S rRNA studies to have arisen very early. Other studies indicate, however, that they originated with the crown groups.

Algae Whose Chloroplasts Arose by Tertiary Endosymbiosis

A few dinoflagellates group together under this heading. They are not otherwise related, indicating that secondary endosymbiosis took place independently in the three groups mentioned below.

Cells of *Peridinium balticum* contain an entire eukaryotic cell with its chloroplast, and there are indications from gene sequencing that the endosymbiont is a transformed diatom that lacks the siliceous frustule. The diatom cytoplasm is separated from the dinoflagellate cytoplasm by a single membrane, probably a food vacuole formed by the dinoflagellate, which may have obtained the endosymbiont by sucking out the contents of a diatom into a food vacuole.

A few dinoflagellates are blue in colour and contain either a little transformed blue cryptophyte or a more normal looking chloroplast surrounded by three membranes. In all cases the endosymbionts apparently represent cryptophytes. In the latter cases they have been strongly modified, losing most organelles and membranes.

A few brown or yellow-brown dinoflagellates, well known as fish killers in the sea, contain aberrant pigments in their three-membraned chloroplasts (*Gymnodinium breve*, *G. mikimotoi*). The chloroplasts almost certainly have their origin in the haptophytes, whose chloroplasts may contain very similar pigments.

Conclusions

It is clear from the data above that the algae do not form a natural group of phylogenetically related organisms. One group is more related to certain bacteria, others to different groups of protozoa, others again to higher plants. The term algae is still a useful one, but it should now be regarded as a term on par with ‘trees’, ‘xerophytes’, etc. There are similar problems with delineation of ‘bacteria’, ‘animals’, ‘protozoa’, ‘plants’ and ‘fungi’. Numerous cases have been found where algae possessing a fully functional photosynthetic apparatus are also capable of phagotrophy, the food uptake process associated with animal cells. This so-called mixotrophy applies to many chrysophycean heterokonts in particular, and to dinoflagellates and haptophytes. It gives the cells the capability to switch between phototrophy and phagotrophy, depending on external conditions such as light, prey availability, etc. It seems likely that the organisms in question were previously phagotrophs but retained the capability of phagotrophy after establishing one of the prey cells as a photosynthetic symbiont.

Further Reading

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