Algal Taxonomy: Historical Overview

Secondary article

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Article Contents

Taxonomy deals with taxa at all levels from species or below to the highest levels (families, orders, divisions, etc.).

The Beginning

In his famous work *Species Plantarum* (1753), the Swedish botanist Carolus Linnaeus grouped the plants known at the time into 24 classes. Class no. 24 he named the Cryptogams ('Cryptogamia') while all the other 23 classes comprised higher plants. The term Cryptogams indicated that sexual reproduction was unknown (the Greek words *kryptos* and *gamos* meaning hidden wedding) and the cryptogams comprised ferns (Filices), mosses (Musci), algae (Algae) and fungi (Fungi). Linnaeus listed 14 genera of algae but in modern classifications only three of these have been retained: the green algae *Chara* and *Ulva*, and the brown alga *Fucus*. Species now classified as red algae were included in *Fucus* and *Ulva*. Thus *Fucus rubens* is the red alga now known as *Phycodrys rubens*, and *Ulva umbilicalis* is a species of laver, *Porphyra umbilicalis*. The other 11 genera listed by Linnaeus as 'algae' are now classified as lichens or fungi, or the name has been discarded. Linnaeus did not always create the names himself: many of the generic names had been used by previous authors, although sometimes with a somewhat different meaning. Thus *Fucus* is the Roman version of Greek Phycos, seaweed of Theophrastos and Dioscorides. Dalechamps (1587) *Historia Generalis Plantarum* recorded *Chara* as a popular name for an *Equisetum*-like aquatic plant used to clean house utensils by people in Lyon. (***see*** Linnaeus, Carl (Linne).) (***see*** History of plant science.) (***see*** Green algae.) (***see*** Red algae.) (***see*** Brown algae.) (***see*** Lichens.)

Linnaeus gave no circumscription of his genera nor did he assign any taxonomic level to the algae. The latter was done a few years later by his contemporary, the German botanist Joh. Gottlieb Gleditsch, who, in *Systema Plantarum* (1764), grouped the algae as a class of plants, named Algacea (Algaceae). Algacea was one of eight classes into which he grouped the plants. The characteristic features of the algae were given as related to 'fructification' (Fructificatio), which was mentioned as taking place 'in corporibus granulosis, tuberculis, vesiculis aut peltis varie formatis atque dispositis'. Gleditsch listed seven genera of algae, and two of the names are still in use, *Fucus* and *Ulva* (in contrast to Linnaeus, Gleditsch considered *Chara* to be a higher plant). The other genera are liverworts, fungi or organisms of uncertain identity.

The earliest classifications were based solely on species morphology. A new era began in the early 1800s, however, with the publications of Lamouroux in Caen (1813), *Essai sur les Genres de la Famille de Thalassiophytes*, and C. A. Agardh in Lund (1817), *Synopsis Algarum Scandinaviae*. In addition to morphology, Lamouroux and, following him, Agardh also used the colour of the algae in their classifications. Agardh listed no less than 45 genera of algae, which he grouped into five 'sections'. In sections 1–3 the thallus is 'continuous' (frons continua). In section 1, Fucoideae, the colour is olive-brown (olivaceus), or black when exposed to the air, probably meaning dried. The colour is purple or red in section 2, Florideae, and green in section 3, Ulvoideae. Section 4, Confervoideae, contains the genera with tubular and articulate thallus, while the last section, Tremellinae, includes a mixture of algae characterized by their gelatinous thallus (*Tremella* is now known to be a fungus). (***see*** Algal pigments.)

This classification represents a major step forward, but Lamouroux and Agardh were often misled. The first three sections mentioned above, Fucoideae, Florideae and Ulvoideae, roughly correspond to present-day brown algae, red algae and green algae. However, the authors were misled by some red algae not being purple or red: some species of brownish colour were included in the Fucoideae (e.g. *Furcellaria*), while others of a slightly greenish tinge were included in the Ulvoideae (*Zonaria*, *Dictyopteris*), etc. The articulate species comprising section Confervoideae are a mixture of more or less filiform species now known to belong to the red algae, brown algae and green algae. Agardh's last section, Tremellinae, is an interesting botanical garden comprising one genus of brown algae (*Mesogloia*), one genus of green algae (*Chaetophora*), two genera of blue-green algae (*Rivularia* and *Nostoc*), to which is added the bryozoan *Alcyonidium*.

Subsequently, W. H. Harvey in *Flora Hibernica* (Flora of Ireland) (1836) divided the order algae into four divisions: Melanospermeae, Rhodospermeae, Chlorospermeae and Diatomaceae. The first three groups correspond to brown algae, red algae and green algae, but the last group included both diatoms and desmids! These groups had previously caused problems. A few diatoms were described already in 1773 by O. F. Müller in Copenhagen *Vermium Terrestrium et Fluviatilium*. However, since some diatoms are capable of moving, whereas others are nonmotile and form filamentous colonies, the former were included among the animals ('rod animalcules'), the latter among the plants as algae. Müller discussed at length whether *Vibrio paxillifer* (now known as *Bacillaria paxillifer*) is a plant or an animal (he called it the 'stick animal' and compared the movements of the cells within the colony to the strategic movements of an army). The nonmotile diatoms were at first referred to the genus *Conferva* but de Candolle in 1805 in *Flore Francaise* erected the genus *Diatoma* for *Conferva flocculosa*. This name inspired C. A. Agardh to create the order Diatomeae for the group in *Systema Algarum* (1824). In Germany, Kützing in *Synopsis Diatomearum* (1833) divided his family Diatomeen into two main groups (Hauptgruppen), Diatomaceae and Desmidiaceae, i.e. like Harvey he merged diatoms and desmids. It took 10 years before he separated the two groups in *Phycologia Generalis* (1843) and included the desmids as the family Desmidieae into his new group Chamaephyceae (dwarf algae), which also included other one- or few-celled algae. Ehrenberg (1838), also in Germany and a contemporary of Kützing, did not follow these classifications at all but included both diatoms and desmids as families of animals in his 'Infusionsthierchen' (see further below). This treatment apparently did not impress Kützing, who in 1845 in *Phycologia Germanica* went on to move the desmids to their present-day position among the green algae (his Chlorophyceae), without even mentioning Ehrenberg's classification (in the Introduction he thanked Ehrenberg and 36 others for material and literature!). Around 1850 both desmids and diatoms were more or less generally accepted as belonging to the algae. Perhaps accidental but even much later authors, such as Oltmanns (1922) in *Morphologie und Biologie der Algen*, seem to have been impressed by the apparent similarity between desmids and diatoms, two groups that we know now are not phylogenetically related at all. Oltmanns classified the algae into eight groups, of which group 6 is Conjugatae (desmids and related forms), group 7 is diatoms while group 8 is green algae. (***see*** Harvey, William.) (***see*** Diatoms.)

Friedrich Kützing should also be credited as the person who in his monumental book, *Phycologia Generalis* (1843) devoted four pages to the description of the pigments now known as the light-harvesting pigments phycobilins. He gave the name 'phykoerythrin' to the red water-soluble pigment that imparts the red colour to the red algae (he did not mention its presence in other algae). He termed as 'phykokyan' (now phycocyanin) the blue water-soluble pigment in red algae, some 'Vaucherien' (incorrect!) and '*Oscillaria*' (now *Oscillatoria*). (***see*** Algal pigments.)

In these early classifications, blue-green algae and species of present-day Xanthophyceae were usually classified with the green algae because of their greenish colour. Linnaeus included a few of these in the genera *Ulva*, *Byssus* and *Tremella* (e.g. *Ulva pruniformis*, now known as *Nostoc pruniforme*). The blue-green algae were first recognized as a separate taxonomic entity in *Dr Rabenhorst's Algen Sachsens* by Stitzenberger (1860) in Germany, who separated them out as the order Myxophyceae. As distinguishing feature of the new order Stitzenberger mentioned the pigments. The name was subsequently changed to Cyanophyceae by Sachs' *Lehrbuch der Botanik* (1874), owing to the blue pigmentation of many species. This name gained acceptance as being more appropriate. (***see*** Cyanobacteria.)

Recognition of the Xanthophyceae as a separate group came much later. Due to features such as lack of starch in the cells, the yellow-green colour of the chloroplasts, the presence of lipid as reserve material, and the presence of a single flagellum (incorrect!), several genera were separated from other green algae into a separate group Confervales by Borzi (1889, *Boll. Soc. Ital. Microscop.* 1: 60–70; 1895, *Studi Algologici*). They were eventually removed from the green algae by A. Luther (1899, *Bih. K. Svenska Ver.-Akad. Handl.* 24, Afd.3, 13: 1–22), a Finn working in Stockholm, who established the new class Heterokontae for present-day Xanthophyceae and Raphidophyceae. The name Xanthophyceae goes back to Allorge (1930, *Rev. Algol.* 5: 230).

The Flagellates: Flagellata

The taxonomic group Algae initially comprised primitive nonmotile plants whose cells are surrounded by a wall. Flagellates that were capable of swimming, were considered animals, no matter whether they were photosynthetic or not, and O. F. Müller (1773, 1786), who described many species for the first time, called them Animalcula Infusoria. Ehrenberg (1838) in his monumental book, believed that the 'infusoria' were complete but smaller miniatures of more complex animals (metazoa). He gave them the name 'Polygastrica anentera', i.e. the 'gutless stomach animalcules'. This group comprised 12 families, including Astasiaea (now known as the euglenoids), Peridinaea (now the dinoflagellates) and Cryptomonadina (cryptomonads), in all three cases the first recognition of these taxonomic groups, although the Cryptomonadina also included *Prorocentrum* and *Trachelomonas*. The gutless stomach animalcules further comprised the families Dinobryina (*Dinobryon* and *Epipyxis*), Volvocina (which included also *Synura*), Closterina (only the desmid *Closterium*), Bacillaria (diatoms and desmids), etc. Three years later, however, and therefore shortly after the cell theory had appeared Dujardin (1841, *Histoire Naturelle des Zoophytes*) showed that Ehrenberg's Polygastrica were not the perfect miniatures of higher animals that Ehrenberg thought, thus the 'stomach' was a vacuole. In 1853 Cohn proposed the term Flagellata for Ehrenberg's gutless animalcules (*Zeitschr. Wiss. Zool.* 4: 253–281. (*see* Dinoflagellates.) (*see* Cryptomonads.) (*see* Protozoa.) (*see* Dujardin, Felix.) (*see* Phycology.)

Merging of the Algae and the Flagellata into a Common Group

There were problems of distinguishing between the taxonomic groups Flagellata and Algae from very early on. Because they were motile, most flagellates were considered to be small animals (animalcules). Volvocalean flagellates, however, were often considered by botanists to be algae (although they were not initially grouped with the green algae), while zoologists included them in the animal group Flagellata (Linnaeus in *Systema Naturae* (1758) also considered *Volvox* to be an animal). (*see* Cilia and flagella.) (*see* Protozoan sexuality.)

In the late 1800s the increasing number of described species and the generally increasing knowledge led to the conclusion that several groups of organisms included in the Flagellata were in fact related to algae. Thus the filamentous organism known as *Hydrurus foetidus*, and because of its brown colour classified with the brown algae, was found to be related to what was then known as the group Chrysomonadina of the Flagellata (Klebs, 1892, *Zeitschr. Wiss. Zool.* 55: 265–445). Another filamentous alga, *Dinothrix*, also included in the brown algae, reproduced by means of dinoflagellate-like zoospores (Pascher, 1914, *Ber. Deutsch. Bot. Ges.* 32: 36–160). Dinoflagellates further resembled algae by having a cellulose cell wall and by producing starch as storage material and, based on these features, Warming, as early as 1890 in the German translation of his textbook on botany (*Handbuch der Systematischen Botanik*), included the dinoflagellates in the algae. Bohlin in Sweden (1897, *Öfv. K. Svenska Vet.-Akad. Handl.* 1897: 507–529) then described a green amoeboflagellate, *Chloramoeba*, which, in its flagellation (two different flagella), colour (yellow-green) and type of storage material (lipid), resembled both *Vacuolaria* of the flagellate group Chloromonadina Klebs 1892 (now Raphidophyceae) and the algal group Confervales (now Xanthophyceae). Finally, based on many years of detailed studies, Adolf Pascher (1914), working at the German University in Prague, concluded that several algal groups were derived from 'gefärbte Flagellaten', i.e. photosynthethic flagellates. Thus, in a classification reflecting phylogenetic relationships, they should be grouped together, rather than as plants and animals. (*see* Brown algae.) (*see* Dinoflagellates.) (*see* Algal cell walls.) (*see* Algal photosynthesis.) (*see* Protozoan nutrition and metabolism.) (*see* Algal storage products.)

Impact of Electron Microscopy

Electron microscopy was applied to algae from the 1940s onwards and resulted in a much more precise circumscription of the different taxonomic groups of algae, from the highest taxonomic level to species level. The work on marine phytoplankton flagellates in England in the 1950s is now classical and involved Mary Parke at Plymouth Marine Laboratory, who established phytoplankton algae in laboratory culture, and Irene Manton at Leeds University, who was one of the world's foremost electron microscopists. Their joint investigations led the Danish taxonomist Tyge Christensen (1962, *Alger*) to propose three new classes of algae in his Danish textbook on algae, two classes of green algae (Prasinophyceae and Loxophyceae) and one class of golden-brown flagellates (Haptophyceae). All three groups were defined on ultrastructural features, in the case of the Prasinophyceae the presence of organic scales on the cell and the flagella (other green algae were thought to be without scales). (*see* Electron microscopy.) (*see* Phytoplankton.) (*see* Golden algae.)

The Haptophyceae differed from other yellow-brown flagellates (notably the Chrysophyceae) in several features, the most significant being the 'third flagellum' present in some of these organisms, and discovered to be an entirely new type of organelle. It was termed the haptonema and has not so far been found in any other group of protists. Neither Parke nor Manton lived to see the discovery of the function of this organelle as a food-gathering organelle by Kawachi in 1991 (Kawachi *et al.*, *Phycologia* 30: 563–573). Before the time of electron microscopy, haptophytes were believed to be chrysophytes but the presence of two smooth and equal flagella was unusual and so was the presence of the 'third flagellum'. As a consequence they were often grouped together as a separate group within the Chrysophyceae. (*see* Chrysophyceae, Synurophyceae, Tribophyceae and Eustigmatophyceae.) (*see* Algal flagella.)

Of particular interest was the discovery that coccolithophorids belonged to the Haptophyceae. Cells of many haptophyte species are covered on the outside by submicroscopic organic scales that in some species are critical for species identification. Following Manton and her colleagues' work, it became evident that the coccoliths of coccolithophorids are in fact calcified scales. Coccolithophorids had been known to science for a long time, more precisely since 1836, when Ehrenberg saw them in deposits from the Cretaceous (*Ber. Verh. K. Preuss. Akad. Wiss, Berlin* 1836, 84–85). They were believed to be of inorganic origin and Huxley (1858, in J. Dayman: *Deep-Sea Soundings in the North Atlantic Ocean*) saw them in material collected from the sea bottom during the preparations for the laying of the first cable between North America and Europe. Huxley gave them the name coccoliths because of their resemblance to the unicellular alga *Protococcus*. Shortly afterwards, Wallich (1860, *Ann. Mag. Nat. Hist.* Ser. 3, 6: 457–458) found coccoliths attached to spherical bodies, which he termed coccospheres and interpreted as cells. He believed the coccoliths to be part of the cell skeleton and interpreted loose coccoliths as having been released from broken cells. In 1865 (*Trans. Micr. Soc. London* 13: 57–84) Wallich finally saw coccoliths on living cells but another 12 years passed before, in 1877, he described the first genus of coccolithophorids, *Coccosphaera* (*Ann. Mag. Nat. Hist.* Ser. 4, 19: 342–350). The yellow-brown colour of the cells and the presence of chloroplasts were then seen by Murray and Blackman (1898, *Philos. Trans. R. Soc. London* 190 (Ser. B): 427–441) and in more detail by Lohmann (1902, *Arch. Protistenk.* 1: 89–165). Lohmann also saw flagella on the cells for the first time. The yellowish colour of the chloroplasts led Lohmann to classify coccolithophorids as chrysomonads. Schussnig (in *Verh. Zool.-Bot. Ges. Wien*, 1925) proposed that they constitute a subclass within the chrysomonads, a practice that was continued until the advent of electron microscopy. Thus 124 years passed between the first discovery of fossil coccoliths by Ehrenberg in 1836 and the finding by Parke and Adams (1960), that some coccolithophorids possess a haptonema, eventually leading Christensen to classify them in the new class Haptophyceae in 1962. (***see*** Algal calcification and silicification.) (***see*** Algae: phylogeny and evolution.) (***see*** Huxley, Thomas Henry.)

Hibberd and Leedale (1970), based on electron microscopical studies of a large number of species, discovered that the Xanthophyceae, the yellow-green algae, was not a natural class. The new class Eustigmatophyceae was separated from the Xanthophyceae, to contain a number of species superficially similar to xanthophyceans but differing in a several unusual features. Most unusual was a unique type of photoreceptor, associated with the base of the anterior (hair-bearing) flagellum, a feature never seen in any other heterokont algae. Another organism, the green spiderweb-amoeba *Chlorarachnion reptans* described by Geitler in 1930 from samples collected in the Canary Islands, was refound and studied in detail by Hibberd and Norris (1985) half a century after the original finding. Due to its lack of starch, its cell structure and green colour, it was initially included in Luther's group Heterokontae. A detailed study of *Chlorarachnion* showed, however, that it had no obvious affinities to the heterokonts. *Chlorarachnion* combined features of green and brown algae in the most remarkable way, and contained an extra, very small, nucleus in its chloroplasts. The chloroplasts are now known to represent an endosymbiotic green alga, ingested by the host cell and subsequently transformed into a chloroplast. The host is not related to other algae but molecular studies have indicated a phylogenetic relationship to certain protozoa. Several additional species of chlorarachniophytes have now been described. (***see*** Algal chloroplasts.) (***see*** Chlorarachniophytes.)

The 1970s also saw the discovery of the ancestors of the land plants among the green algae by Pickett-Heaps (1975) and others. This discovery was based mainly on ultrastructural studies of cell division and the flagellar apparatus. It was supported by physiologists who discovered that the distribution of two enzymes in the so-called microbody in green algae (an oxidase and a dehydrogenase) agreed with the new ideas of green algal classification based on ultrastructure. The work on green algae marked the beginning of a debate on classification of the green algae that still goes on. While Christensen in 1962 divided the green algae into three classes, a recent textbook (van den Hoek *et al.*, 1995) accepts no less than 11 classes of green algae. Christensen described 11 orders of green algae and many of van den Hoek's classes correspond with Christensen's orders. Thus the orders Cladophorales, Caulerpales, Dasycladales and Charales of Christensen correspond to the classes Cladophorophyceae, Bryopsidophyceae, Dasycladophyceae and Charophyceae. The circumscription of other classes by van den Hoek *et al.* takes into account the new information accumulated between 1962 and 1995, particularly from studies of ultrastructure. Generally speaking, however, the order level of Christensen has been replaced with the class level. Since some of these classes differ from each other in very small details only, the system has not been universally accepted. A generally acceptable classification will probably aim at restoring the class level to its former level by reducing the number of classes. (***see*** Algal reproduction.) (***see*** Algal metabolism.)

One of the most important recent findings with regard to the green algae is undoubtedly that some are related to the ancestors of the land plants. This applies to the morphologically very complex species comprising the order Charales, but also to a number of more simply built green algae such as *Chlorokybus* (unicellular), *Klebsormidium* (unbranched filaments), *Coleochaete* and *Chaetosphaeridium* (branched filaments or more or less modified). As mentioned above, *Chara*, the stonewort, has been known since pre-linnean times but different authors disagreed as to whether it should be considered an alga or a higher plant. The ancestors of the Charophyceae are now thought to be related to flagellates of Christensen's group Prasinophyceae, which is generally accepted as containing the most primitive green plants. (***see*** Embryophyta (land plants).) (***see*** Chlorophyta (green plants).)

Christensen's class Loxophyceae was less well defined and has not been maintained but one of its genera, the very small green flagellate *Pedinomonas*, formed the basis for the new class Pedinophyceae described by Moestrup (1991, *J. Phycol.* 27: 119–133) based on ultrastructural features, in particular details of cell division.

One of the most important recent discoveries involves the green algae serving as the algal partners in lichens. These species have now been shown to comprise a natural group and were united into the class Trebouxiophyceae after *Trebouxia*, one of the main genera (Friedl, 1995). This conclusion is based on ultrastructure, supported by molecular sequence data. (***see*** Lichens.) (***see*** Algal symbioses.)

The trend of splitting large classes into several smaller ones, as mentioned above with regard to green algae, is also currently taking place with regard to other groups. Thus Christensen's Chrysophyceae is being split into several classes, based mainly on ultrastructural features, and sometimes supported by molecular data: Synurophyceae, Dictyochophyceae, Bolidophyceae, Pelagophyceae, etc. It has even been suggested that the diatoms, the class Bacillariophyceae, be divided not into the usual two orders but into three classes and 42 orders (Round *et al*., 1990)! (*see* Chrysophyceae, Synurophyceae, Tribophyceae and Eustigmatophyceae.)

Impact of Molecular Biology

Sequencing of genes is now being done extensively, and the results used at all levels of algal classification. Generally speaking, the data obtained by gene sequencing confirm the conclusions reached by other methods, including ultrastructural studies. One of the most striking exceptions to this rule has been the studies on *Prochloron* and its allies. *Prochloron* is a unicellular, prokaryotic marine alga described in 1975 by Ralph Lewin and Lanna Cheng as a symbiont of tropical ascidians (*Phycologia* 14: 149–152). It was at first thought to be a member of *Synechococcus*, a genus of blue-green algae, but examination of the pigments revealed that both chlorophylls *a* and *b* were present in the cells. Blue-green algae were at the time known to possess only chlorophyll *a*, in contrast to green algae, which contain both chlorophylls *a* and *b*. *Prochloron* was therefore believed to represent an entirely new class of algae, the Prochlorophyceae. It was a matter of debate as to whether it was related to the prokaryote that gave rise to the green algal chloroplast. Subsequently, two more genera of prochlorophytes were discovered, *Prochlorothrix* and *Prochlorococcum*, the former from fresh water and the latter from marine plankton. Gene sequencing of the three genera, using the small subunit of ribosomal deoxyribonucleic acid (rDNA), did not confirm that the three genera were related to each other, however, nor did the sequence data confirm any relatedness to the green algal chloroplast. Instead, the studies indicated that the three genera of prochlorophytes were related to different genera of blue-green algae. Based on this information, the class Prochlorophyceae was abandoned and the three genera were included in the blue-green algae. If this is correct, it may be concluded that chlorophyll *b* has arisen at least four times independently: three times in the 'prochlorophytes' and once in the progenitor of the green algal chloroplast. (*see* Cyanobacteria.) (*see* Chlorophylls.) (*see* Phylogeny based on 16S rRNA/DNA.) (*see* DNA sequencing.) (*see* DNA sequence analysis.) (*see* Algal chloroplasts.)

Conclusions based on molecular methods are not always straightforward because examination of different genes often yields different results. Use of molecular methods in taxonomy is still in its infancy and conclusions have to be made with considerable care. While a phylogenetic tree based on examination of a single gene may give information about the phylogeny of this particular gene, it does not necessarily reflect the phylogeny of the entire cell. Results based on molecular sequencing but not supported by morphological or biochemical methods need to be substantiated further before any far-reaching conclusions are made. One of the greatest impacts of molecular techniques has probably been on concepts of phylogenetic relationships between the different groups of protists. (*see* Algae: phylogeny and evolution.)

Conclusion: Modern Taxonomy

In many ways the taxonomy of the algae is in a flux. Many researchers will accept a classification of the algae into nine divisions (phyla) as follows: (*see* Phycology.)

- Cyanophyta, blue-green algae or cyanobacteria
- Rhodophyta, red algae
- Cryptophyta, cryptomonads
- Dinophyta, dinoflagellates
- Heterokontophyta, heterokonts
- Haptophyta, haptophytes
- Chlorarachniophyta, chlorarachniophytes
- Euglenophyta, euglenoids
- Chlorophyta, green algae.

This classification is based mainly on a combination of ultrastructural and biochemical features. Lamouroux and Agardh's old classification from the early 1800s, based on colour (i.e. pigments in the chloroplasts), is supported by ultrastructure of other components of the cell than the chloroplasts, which are now known to be symbionts. In a future classification, based on phylogenetic relationships, the blue-green algae must be grouped with other prokaryotes, and the remaining divisions with other protists divisions, previously considered as belonging to the animals and the fungi. (*see* Algal symbioses.) (*see* Algal pigments.) (*see* Prokaryotic systematics: a theoretical overview.) (*see* Protist systematics.)

The number of algal classes into which each division is divided is a matter of constant debate and, as mentioned above, some authors raise the old order level to the class level. A similar tendency also takes place at lower taxonomic levels (family, genus, species), undoubtedly as a result of the numerous additional features visible in the electron microscope compared to the light microscope, and therefore available for taxonomic purposes. A good example is the species concept. Since sexual reproduction is unknown and perhaps absent, at least in some algae, the biological species concept is not always applicable and many species are defined solely by morphological features.

As many additional morphological features are visible in the scanning and the transmission electron microscopes, the species now tend to be defined on much finer details, and this has resulted in a much narrower species concept. In many cases this has had the effect that species can no longer be identified by light microscopy only (e.g. scale-bearing flagellates such as *Chrysochromulina*, *Prymnesium*, *Pyramimonas*, etc). An explosion is presently taking place in diatom taxonomy, due mainly to the application of scanning electron microscopy. van den Hoek (1978) mentions about 6000 known species of diatoms but in his revised textbook (van den Hoek *et al.*, 1995) the number is given as 'around 100 000 species'! An explosion in species number may also be expected to take place in the coming years in the blue-green algae (cyanobacteria), when molecular methods have been applied to a larger number of strains. The original species concept in blue-green algae is based on very few morphological characters, and electron microscopy has not added any substantial number of ultrastructural features. Morphology may be insufficient to define the species level in blue-green algae and it will be very interesting to follow the results from gene sequencing in this, the oldest group of algae. (***see*** Species concepts.) (***see*** Algal reproduction.) (***see*** Diatoms.)

Although the species concept presently used in the algae will have to be discussed in the light of future gene sequencing, the results obtained so far have not indicated that any simple answers exist. Relevant questions are presently: how many genes need to be examined before one can conclude that two strains belong to different or the same species? The entire genome? How many nucleotide base differences are required to define a certain taxonomic level? In *Phaeocystis*, Medlin *et al.* (1994) found a difference of 6–10 bases out of approximately 1600 in the 18S rDNA genes between strains collected in the Arctic and those collected in the Antarctic. The arctic strains differed from each other in 0–5 of the approximate 1600 bases of the 18S rDNA gene. (***see*** Species problem - a philosophical analysis.)

Medlin *et al.* concluded that the arctic and the antarctic strains were different species, an argument that is perhaps acceptable because the two entities are geographically separated. If the strains had occurred in the same geographical area, they would probably be considered to belong to a single species.

References

Ehrenberg DCG (1838) *Die Infusionsthierchen als volkommene Organismen*. Leipzig: L. Voss.

Friedl T (1995) Inferring taxonomic positions and testing genus level assignments in coccoid green lichen algae: a phylogenetic analysis of 18S ribosomal sequences from *Dictyochloropsis reticulata* and from members of the genus *Myrmecia* (Chlorophyta, Trebouxiophyceae cl. nov.). *Journal of Phycology* **31**: 632–639.

Hibberd DJ and Leedale GF (1970) Eustigmatophyceae: a new algal class with unique organization of the motile cell. *Nature* **225**: 758–760.

Hibberd DJ and Norris RE (1985) Cytology and ultrastructure of *Chlorarachnion reptans* (Chlorarachniophyta divisio nova, Chlorarachniophyceae classis nova). *Journal of Phycology* **20**: 310–330.

Medlin LK, Lange M and Baumann MEM (1994) Genetic differentiation among three colony-forming species of *Phaeocystis*: further evidence for the phylogeny of the Prymnesiophyta. *Phycologia* **33**: 199–212.

Müller OF (1786) *Animalcula Infusoria Fluviatilia et Marina*. Copenhagen: Möller.

Parke M and Adams I (1960) The motile (*Crystallolithus hyalinus* Gaarder & Markali) and non-motile phases in the life history of *Coccolithus pelagicus* (Wallich) Schiller. *Journal of the Marine Biology Association of the UK* **39**: 263–274.

Pascher A (1914) Über Flagellaten und Algen. *Berichte der Deutschen Botanischen Gessellschaft* **32**: 136–160.

Pickett-Heaps JD (1975) *Green Algae*. Sunderland, MA: Sinauer.

Round FE, Crawford RM and Mann DG (1990) *The Diatoms*. Cambridge: Cambridge University Press.

van den Hoek C (1978) *Algen. Einführung in die Phykologie*. Stuttgart: Thieme.

van den Hoek, Mann DG and Jahns HM (1995) *Algae. An Introduction to Phycology*. Cambridge: Cambridge University Press.

Further Reading

Papenfuss GF (1955) Classification of the Algae. In: *A Century of Progress in the Natural Sciences* 1853–1953. San Francisco: California Academy of Sciences.

Silva PC (1980) *Names of Classes and Families of Living Algae*. The Hague: W Junk.

Smith GM (1951) *Manual of Phycology*. Waltham, MA: Chronica Botanica.

