Diatoms

Edward C Theriot, *University of Texas at Austin, Austin, Texas, USA*

Diatoms are single-celled autotrophic organisms with highly ornate siliceous walls. They account for more than 20% of the world's primary production, are responsible for much of the petroleum humans use, and deposits of their shells are mined for numerous uses. The most taxonomically diverse groups of photosynthetic protists, diatoms are of ecological importance in nearly every freshwater and marine habitat. Their closest relatives are a poorly known group of microflagellates, some silicified and some not. Efforts to reconstruct diatom phylogeny are hampered by the fact that their true diversity and that of their closest relatives remains unknown. Genomic studies are creating tremendous new opportunities for study of this important group. Perhaps as much as a third of the diatom nuclear genome is now thought to be recently laterally transferred from bacteria. Diatom adaptation to such a wide range of environments may be a result of the resulting novel gene combinations.

Introduction

Few objects are more beautiful than the minute siliceous cases of the diatomaceae: were these created that they might be examined and admired under the higher powers of the microscope?
Darwin, *The Origin of Species*, Sixth Edition, Chapter 6.
See also: Darwin, Charles Robert

This chapter introduces the single-celled organisms known as diatoms. They are extremely diverse (thousands of species), are unique among all life because of their glass walls, form a crucial part of the food web in the world's oceans, lakes and streams, and are of great ecological importance.

Darwin's statement illustrates the fact that diatoms were once popular viewing objects of the Victorian age amateur microscopist. Amateur diatomists are now few, but there are many professional scientists with an interest in diatoms. We now know that, in addition to admiring them for their beauty, study of diatoms reveals knowledge important to science and to humanity in general.

Diatoms have traditionally been classified as single-celled plants related to the golden-brown (e.g. chrysophytes) and brown algae (e.g. kelps). However, they have an extremely distinct structure and it has been difficult to place them convincingly with one group of algae or another. Increasingly, studies using deoxyribonucleic acid (DNA) sequences (as well as some newer morphological evidence) suggest three things relevant to diatom classification. First, 'algae' are not very closely related to one another but are scattered across the tree of life. Second, the term 'plants' should probably be applied to a much more restricted group of organisms. Third, diatoms belong to a much larger group of organisms, which go by several names, more recently called 'Stramenopiles' (Patterson, 1989). It is also thought that diatoms belong to a group of autotrophic Stramenopiles called 'Heterokonta' (Luther, 1899), a name still in wide use. **See also**: Algal Taxonomy: Historical Overview; Brown Algae

Stramenopiles were first informally named by Patterson (1989), based on cytological evidence. Molecular studies have since corroborated that classification (e.g. Leipe *et al*., 1994). The hairs defining this group have a long hollow shaft giving rise to a small number of fine hairs, and the entire structure inserts into the cell by a basal region. These hairs usually occur on the flagella. Although diatoms do

not have such hairs, molecular studies and morphological studies have corroborated the general grouping, and place diatoms within Stramenopiles. Thus, diatoms are presumed to have lost the hairs during the course of evolution, much as snakes are considered true Tetrapods, but have lost their four limbs during evolution. **See also**: Algae: Phylogeny and Evolution

Diatoms are traditionally thought to be related to Chrysophyceae and Synurophyceae on the basis of morphology and biochemistry (e.g. these taxa have similar pigment composition and use silica in some way to make cell wall coverings, albeit the kinds of coverings differ between diatoms and the other two taxa). However, study of ribosomal DNA (rDNA), the large subunit of the ribulose-bisphosphate carboxylase gene (*rbc*L) and morphological data suggest that a clade of very poorly known microflagellates are sister to diatoms, including algae presently classified as Bolidophyceae and Parmales (Guillou *et al*., 1999; Daugbjerg and Guillou, 2001; Goertzen and Theriot, 2003; Ichinomiya *et al*., 2011).

This article will refer to diatoms as 'protists' as a convenience, as this term will convey to most readers a sense of unicellularity and reproductive mode (mainly vegetative cell division) that diatoms share with other so-called protists. However, readers should be aware that this is meant strictly as a descriptive term and not as a classification. Readers should also be aware that several authors still use the term 'alga' or 'algae' when referring to diatoms, but again only as a descriptive term relaying the notion of a simple, autotrophic organism, typically unicellular and aquatic. Diatoms should be more formally called Stramenopiles or Heterokonta. **See also**: Protist Systematics

Many organisms use silica in some form in their exterior covering, usually only as scales (e.g. the chrysophyte *Mallomonas*). Diatoms, however, make their vegetative cell wall (frustule) out of strongly differentiated large plates (valves) and bands connecting the plates (**Figure 1**). Each half of a frustule is composed of a valve and a set of associated bands. The bands and the valves may each be ornamented, but typically the valves are much more highly ornamented and structured; it is the valve with all its variations that is typically used in diatom identification (**Figure 2**). The valve of the half wall overlapping the other is called the epivalve. The other is called the hypovalve and it is typically slightly smaller than the epivalve. It is these structures that form the basis of diatom classification and lend themselves to a very interesting and unique life history. **See also**: Algal Calcification and Silification; Algal Cell Walls; Silica

Vegetative reproduction is the main mode of reproduction and results from typical mitotic division of the diploid nucleus. Each new cell keeps one half of the frustule (a valve and the girdle band set) from the original cell and forms a new half. Formed inside the new valve, both new valves are hypovalves. Thus, the old hypovalve is now an epivalve and that cell is typically smaller in width and lengthier than the other (however, some diatoms are able to overcome the physical constraints of the parent wall and may either not change in size or may grow longer in one dimension as they become shorter in another). As vegetative division in a cell lineage continues, a variety of cell sizes usually results. Size is regenerated through sexual reproduction, individual cells undergoing meiotic divisions to form haploid gametes. The kinds of gamete formed are important to higher level classification of diatoms. The gametes fuse to create a diploid zygote called an auxospore. The auxospore of a species typically is much more rounded on all surfaces than its vegetative cell, sometimes almost globular. With each mitotic nuclear division of the auxospore, a typical vegetative frustule is formed and the cycle begins anew (**Figure 1**).

Diatom Phylogeny and Classification

Diatoms are traditionally classified into two structurally defined groups, commonly differing in valve symmetry: (1) the centric diatoms with structures are arranged around a central point; and (2) the pennate diatoms with their structure arranged more or less perpendicular to a longitudinal structure called a sternum. Each of these two groups is further subdivided into two groups. The terms 'radial' and '(bi-)multipolar' (or some variant thereof) have recently come into common usage to describe perceived differences in centric diatom general structure. Most diatoms identified as radial centric diatoms have a circular or nearly circular outline, and lack structures such as paired pore fields, which might impose some degree of bilateral symmetry on the markings of the valve. (Bi-)multipolar centric diatoms typically are noncircular (having elongated, triangular, or even star-shaped valves) with two or more structures (e.g. pore fields, setae) arranged toward the edge of the valve, which also impart various symmetries to the cell. We will simply call these polar diatoms. Pennates themselves are often divided into two groups, the raphid pennates (with a pair of slits, typically running through the sternum) and araphid pennates (those without such slits).

Other differences reinforce this distinction and are important characters in the traditional classification (Round *et al*., 1990). Centric diatoms have small discoid chloroplasts. They are oogamous, one vegetative cell becoming an egg and another giving rise to many flagellated gametes or sperm. Araphid pennate diatoms often also have small discoid chloroplasts but are typically isogamous, instead of oogamous (one araphid pennate genus, *Rhabdonema*, is oogamous). Raphid pennate diatoms, however, usually have one or a few plate-like chloroplasts. **See also**: Algal Chloroplasts

This chimeric distribution of morphological characters is broadly consistent with molecular phylogenetic studies (**Figure 3**): radial centrics grade into polar centrics which grade into araphids which grade into raphid pennates. However, support for many nodes along the trunk of the diatom tree is weak, even for multigene studies (Theriot *et al*., 2010, 2011), and any number of rearrangements may occur depending on taxon sampling, choice of phylogenetic inference method and sequence alignment.
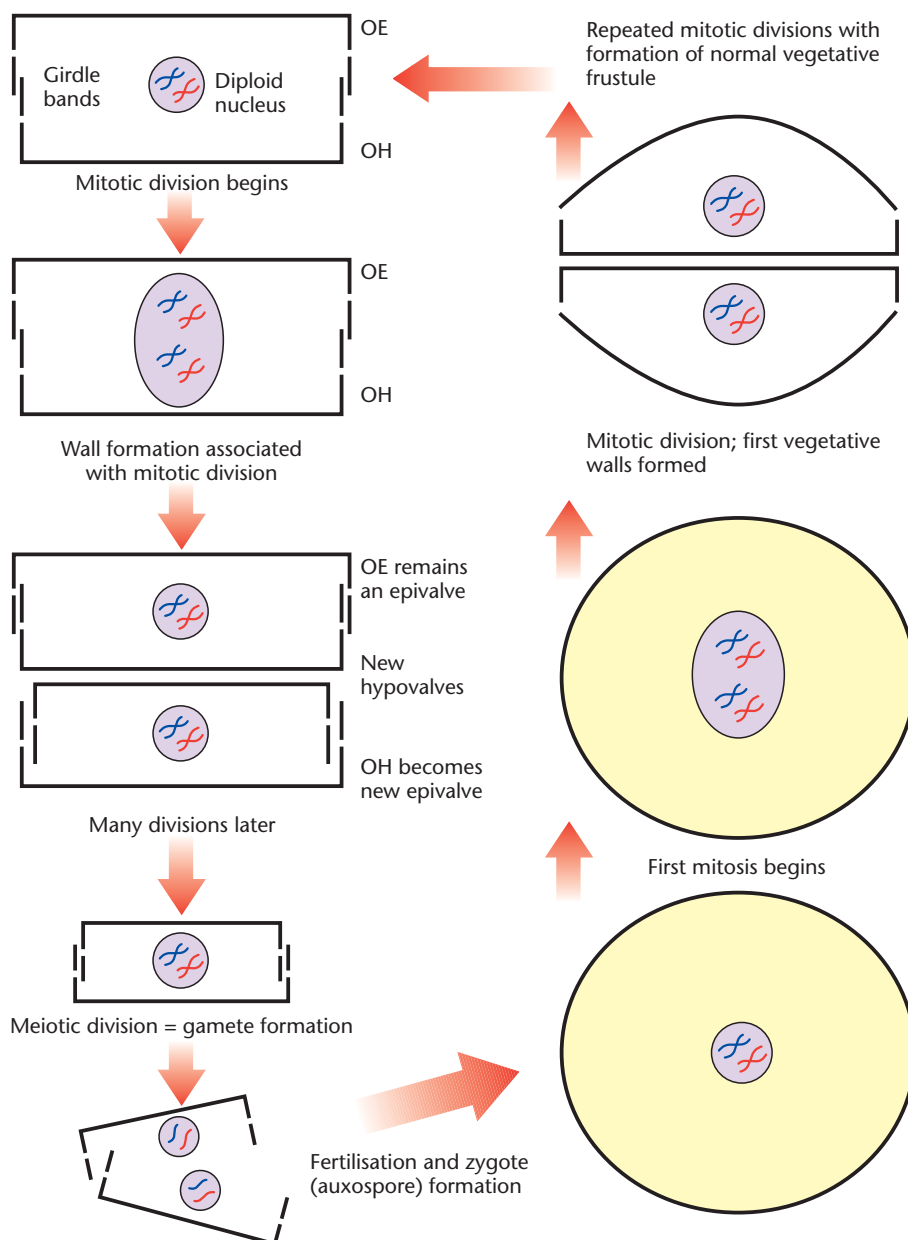
Figure 1 Generalised diatom life history. OE, original epivalve; OH, original hypovalve.

Confounding the uncertainty about the diatom phylogeny is the fact that many prominent diatomists have explicitly eschewed the idea that the diatom classification should be based on the concept of monophyly (e.g. Round *et al.*, 1990; Medlin, 2010). The result has been that the most recent classifications of diatoms are simply substituting one paraphyletic scheme for another (Williams and Kociolek, 2007). The classification currently in vogue places diatoms into one of three classes, with radial centrics (minus Thalassiosirales) being placed in the Coscinodiscophyceae, polar centrics (plus Thalassiosirales) being placed in the Mediophyceae, and all pennates in the Bacillariophyceae. Of these three groups, only the latter is routinely recovered as monophyletic in phylogenetic analyses (Theriot *et al.*, 2010, 2011).

Origin of Diatoms

The difficulty in resolving the diatom phylogeny has not dissuaded speculation about the origin of diatoms, perhaps because they are so unusual and so ecologically important. Historically, diatoms were thought to originate from small coccoidal form, perhaps flagellated, or perhaps a cyst or

Figure 2 Scanning electron micrograph of a plankton diatom assemblage from Lake Michigan, USA. The diatom dominating the centre is a centric diatom (genus *Stephanodiscus*). Numerous araphid pennate diatoms (genus *Asterionella*) are also visible, as is another centric diatom (genus *Aulacoseira*) at the bottom. For the most part, only valves are visible here, as the cell walls were disrupted by acid cleaning, a common preparation technique for better viewing in the scanning electron micrograph. For scale, the *Stephanodiscus* cell is approximately 50 μm in diameter. Species of this genus almost always have radiating ribs ending in a spine, as visible here. In contrast to *Stephanodiscus*, the cells of *Aulacoseira* are typically much taller than they are wide, and so appear as tubes rather than discs. The valves of *Asterionella* are long and thin, but end in a slightly pinched and then expanded tip. All these variations and much more occur in the minute valves of diatoms (see Round *et al.*, 1990).
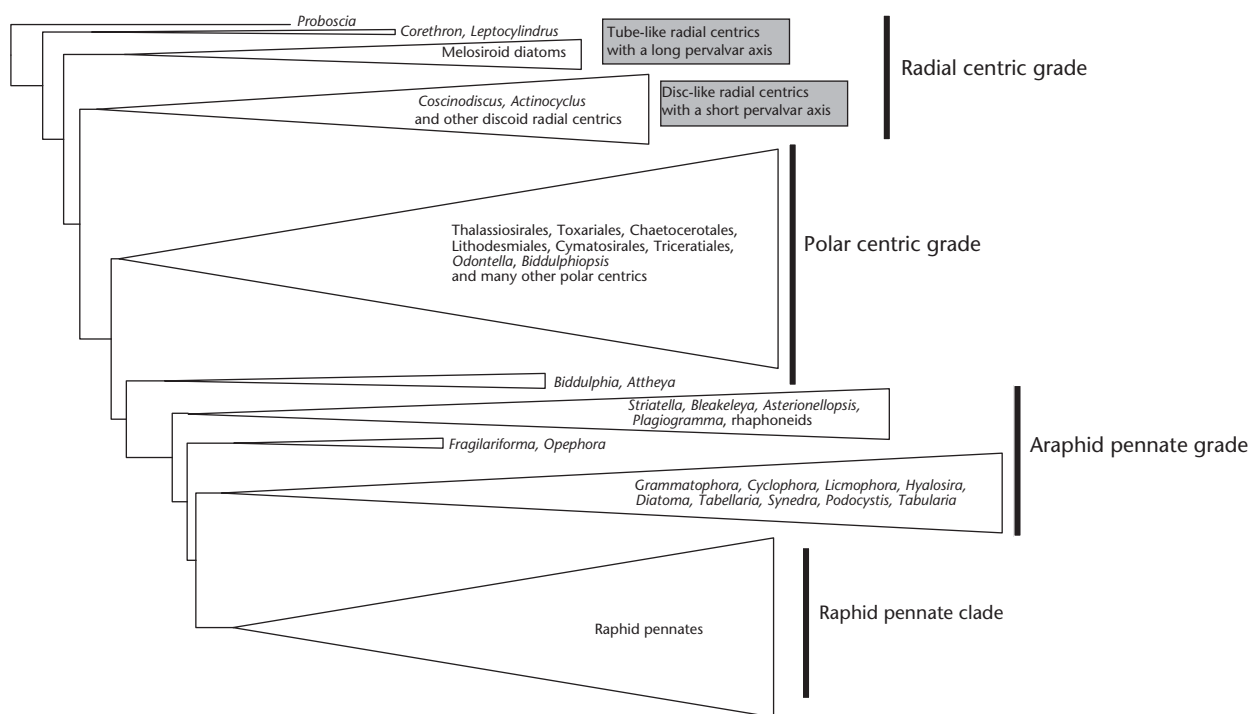
Figure 3 Phylogenetic relationships of large structurally defined groups of diatoms based on maximum likelihood analysis of SSU, *rbc*L and *psb*C genes (see Theriot *et al.*, 2010 for details). Representative taxa of larger clades are indicated by triangles. Long tubular diatoms such as *Aulacoseira* (**Figure 2**) form a grade at the base of the diatom tree. Most discoid radial centrics are found in a single clade. But these are not the only places on the tree where such shapes occur. Polar centrics include diatoms of a wide variety of shapes and forms, from star-shaped cells, to cells with long tubular shape (such as *Stictocyclus*), and cells with a flat discoid shape such as *Stephanodiscus* (**Figure 2**).

cyst-like structure (Round, 1981; Round and Crawford, 1981, 1984; Cavalier-Smith, 1986; Mann and Marchant, 1989). This view has been re-enforced by the finding that Parmales (small siliceous flagellates), Bolidophyceae and diatoms share a close relationship. However, the siliceous Parmales are embedded within the Bolidophyceae (Ichinomiya *et al.*, 2011), suggesting that the siliceous scales of the Parmales and siliceous valves of diatoms are homoplasic and either a result of convergent evolution, or multiple losses of siliceous scales within the Bolidophyceae.

The diatom phylogeny itself suggests that the most recent common ancestor to all diatoms was larger, and perhaps elongate. Many published molecular phylogenies of diatoms have a series of long, tubular radial centrics as a basal grade (e.g. **Figure 3**). What some hold to be oldest diatom in the fossil record, *Pyxidicula* (Rothpletz, 1896, 1900), also has a long pervalvar axis. This is not to say that some small coccoid flagellate was not an earlier ancestor to diatoms, only to underscore again the fact that there are still rather large gaps in our understanding of diatom origin and evolution.

Diversity of Diatoms

There is no widely agreed upon estimate of the number of diatom species. Some experts place the number as fewer than 20 000 (Werner, 1977). If there are 200 000 species as Mann and Droop (1996) conservatively estimated, then nearly 90% of diatoms are yet to be described (Julius and Theriot, 2010). Most descriptions are based on traditional qualitative morphological observations. Detailed statistical studies of morphology and/or genetic studies typically reveal many more phylogenetically independent lineages 'hidden' within these traditionally defined species (Alverson, 2008), suggesting that the number of diatom species could easily exceed 1 000 000. Combining electron microscopy, statistical analysis and molecular genetics will only continue to refine our numbers of diatom species. It is now not uncommon to discover whole new genera. **See also**: Diversity of Life; Electron Microscopy

Ecology of Diatoms

The great diversity of diatoms in turn reflects the great diversity of habitats in the aquatic environment. Diatoms live in all the world's lakes, oceans, rivers and streams. They even live on seeps, on cliff walls, in deserts and in soil. Their silica walls are deposited in lakes and oceans and form a record of environmental change and health. The many species of diatoms are distributed over space in nonrandom patterns, which scientists are actively seeking to explain. **See also**: Algal Ecology
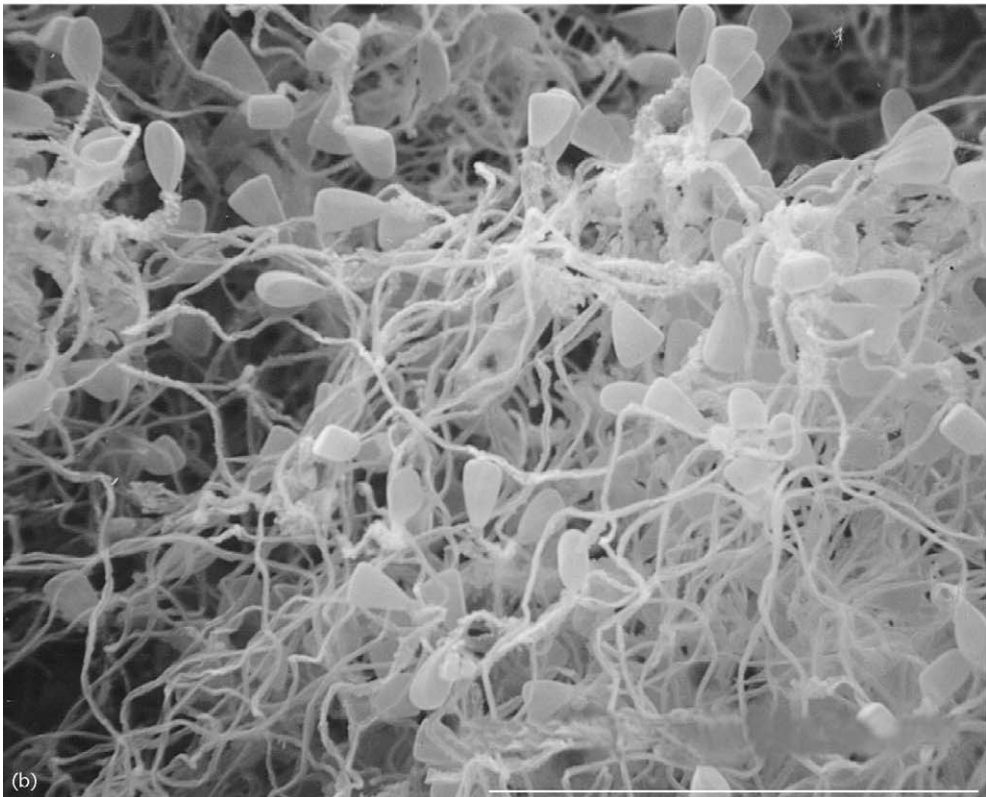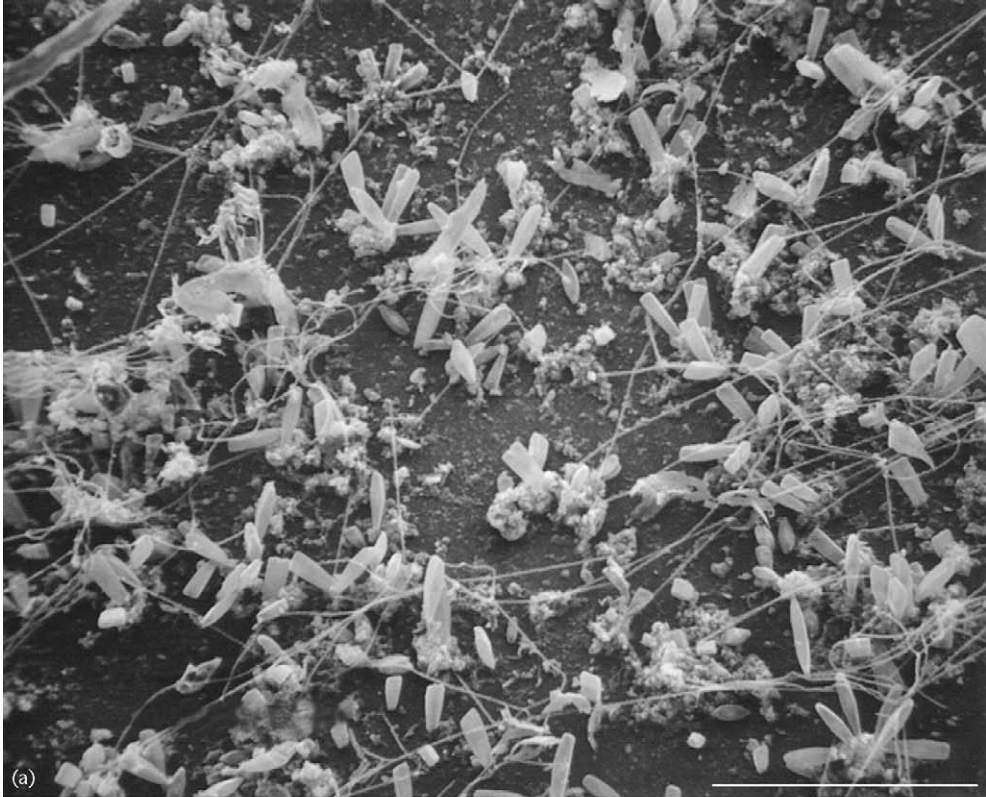
Diatoms exist in nature as single cells or as small colonies of cells. The colonies are typically small filaments of two cells to dozens of cells. Cells may be joined to one another by various kinds of processes of the cell wall or by organic threads extruded from the cells. Cells may also occur in a gelatinous mass. However, there is apparently no significant physiological interaction between cells in colonies. Likewise, morphological differentiation is weak. Some cells in a filament may have different shapes, depending on whether or not they exist at the terminus or the interior of a filament.

Diatoms typically live as free-floating species, making up part of the ecological assemblage known as phytoplankton. Other species grow on various substrates, as part of the ecological assemblage known as periphyton. These periphytic species may just rest on the substrate, be attached directly and closely to the substrate or may be attached by long stalks to the substrate; often these forms colonise and grow on a substrate in sequence (Hoagland *et al.*, 1982). The effect, on a microscopical level, is that of a small forest (**Figure 4** and **Figure 5**). Some species are restricted to attachment to plants, sand grains and edges of rocks. The variety of physical habitats available to the attached diatom explains part of the great diversity of the group. **See also**: Phytoplankton

Diatoms require dissolved inorganic nutrients, including carbon dioxide, nitrogen, phosphorus, silicon and a variety of metals and vitamins, to photosynthesise and reproduce. Different species are more efficient at obtaining certain of these nutrients than are other species; nutrients also vary in time and space. Both factors contribute to the ability of diatoms to exploit a variety of habitats and may help explain the co-existence (Interlandi and Kilham, 2001) of so many species of diatoms. **See also**: Algal Metabolism

Diatoms are also grazed by numerous animals, and top-down control of diatom communities also occurs. As an example of the importance of diatoms in the ecosystem, top-down control of benthic diatom communities can even alter visible patterns in the physical landscape (Weerman *et al.*, 2010).

Diatom shape, form and physiology vary in ways that suggest they have adapted to the different environments in which they occur. For example, silica is typically less available in oceans than in lakes, and marine diatoms have four times less silica per cell than freshwater diatoms, on average (Conley *et al.*, 1989). Frustules of species of the genus *Cocconeis* are curved to fit the walls of algae such as *Cladophora*, to which they are often found attached. Cells in high-energy, high-nutrient environments are typically small with high surface: volume ratios, which are thought to enhance uptake of nutrients and so enable high growth rates.

The great diversity of diatoms and the relationship between diatom species and specific environments have made diatoms a favourite tool of ecologists who are looking for indicators of environmental change and health.

Traditional diatom ecological work consists of comparing floras among lakes, streams and/or oceans over space and time, and correlating species abundance with environmental factors. Repeated observations of a diatom species under particular conditions allow scientists to hypothesise that such conditions represent the factors best for growth of that particular species. Thus, one can look at diatom frustules in sediments of oceans or lakes and understand past environments in great detail, often with the aid of powerful statistical correlation analyses. The best examples are in the study of eutrophication, of acidification of lake systems, and of climate change (Smol and Stoermer, 2010). **See also**: Eutrophication of Lakes and Rivers; Lake Ecosystems

The Laurentian Great Lakes of the midwestern USA and central Canada are a prime example of the use of diatoms in the study of culturally induced eutrophication. Diatom species and diatom abundance in sediments have been used to infer the effect of runoff and phosphorus addition (and subsequent silicate depletion) in those lakes, particularly Lake Michigan (Stoermer *et al.*, 1990). This kind of information ultimately led to reduction in the use of phosphate based detergents. One of the most dramatic examples of the utility of diatoms comes in the use of diatoms to infer the effect of acid rain in lake systems. By correlating diatom species' composition and abundance with the pH in the lakes in which they are found, one may create empirical statistical models to use diatoms in sediments to 'backcast' pH estimates in a lake through time. Where historical data exist, the diatom assemblage can infer pH accurately enough (up to 0.25-pH unit accuracy) to convince environmental managers of the effect of acid rain (Charles *et al.*, 1989). This approach is also being used to correlate diatoms with a number of climatic variables to estimate change in climate (Fritz *et al.*, 1991). Diatoms do not, however, respond directly to air temperature and the amount of rain. The latter case serves as an example. In basins with no drainage away from the lake, the water budget is mainly driven by changes in evaporation versus precipitation, which drives changes in ionic concentrations, which change salinity, nutrient availability, alkalinity and other factors, which then in turn drive changes in diatom abundance. As for the case with pH, diatoms provide a useful (although not as accurate) index of absolute climate change (Smol and Stoermer, 2010). **See also**: Acid Rain

There have been few attempts to mechanistically link changes in diatom assemblages with change in paleoenvironments. For example, resource competition has been used to interpret paleo-lacustrine environments in Yellowstone lacustrine ecosystems, and in saline lakes in the North American high plains (Kilham *et al.*, 1996; Saros and Fritz, 2000). Although this approach is intellectually satisfying in that hypotheses of cause and effect

Figure 4 Stages of periphyton development on glass-slide substrates from Pawnee Reservoir, Nebraska. (a) Typical development after 2 weeks of submersion; diatoms and other microalgae are attached directly to the glass. (b) After 5 weeks, an upper story of diatoms on long stalks has developed, completely overgrowing all lower canopies. Bar, 100 μm. Photographs courtesy of Kyle Hoagland.
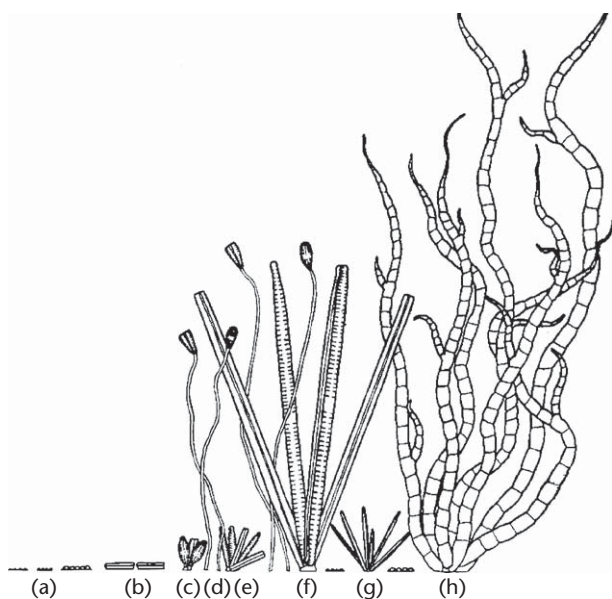
Figure 5 Diagram of succession in a periphyton 'forest'. (a) Attached bacteria; (b) *Navicula menisculus* var. *upsaliensis* – prostrate attachment, mucilage coat; (c) *Gomphonema parvulum* – short stalks; (d) *Gomphonema parvulum* – long stalks; (e) *Fragilaria vaucheriae* – rosette, mucilage pads; (f) *Synedra acus* – large rosette, mucilage pads; (g) *Nitzschia* sp. – rosette, mucilage pads; and (h) *Stigeoclonium* sp. – upright filaments. Reprinted with permission from Hoagland *et al.* (1982). Copyright © 1982 Botanical Society of America.

are employed, it also requires prior experimental study of the diatoms in question, and so is limited in its application, leaving the correlation approach as the most widely used.

The correlation method is most reliable when used within a single system, regardless of the environmental parameter one is trying to estimate. This is because the factors that correlate with diatom growth may not be the limiting or causal ones. In addition, environmental factors may interact differently in different systems. For example, many diatoms have temperature optima in the laboratory at temperatures well above 10°C; however, diatoms commonly are most abundant in the spring in many lakes when nutrients are in high concentration but temperatures are as low as 4°C (Werner, 1977). During this period of growth, they and other phytoplankton typically consume most of a particular nutrient (often silicon) and so do not grow well in summer when water temperatures are higher but the nutrient is in low concentration. In other lakes, however, optimal nutrient conditions may occur later in the year, favouring 'spring' species in the summer. For example, the common diatom *Stephanodiscus niagarae* is most abundant in spring in midwestern lakes, but is most abundant in summer in lakes in the Wyoming Rocky Mountains because nutrient conditions favouring *S. niagarae* occur later in the year (Kilham *et al.*, 1996). Thus, depending on the system, the occurrence of *S. niagarae* in lake sediments may indicate either spring-like or summer-like weather conditions.

It is typically thought that forms of nitrogen, phosphorus and/or silica limit diatom growth, although iron may be limiting in certain ocean environments. The dynamics of these compounds in nature, and of their utilisation by diatoms, is complex. Dissolved forms of nitrogen may come from sources internal to the aquatic system (e.g. the breakdown of organic nitrogen through bacterial action, forming ammonia; nitrate may come from bacterial action on other forms of dissolved nitrogen) or from external sources such as runoff or direct precipitation (lightning creating nitrate from oxygen and nitrogen; nitrate/nitric acid in acid rain). Phosphorus is highly labile and much is regenerated *in situ*. Silica, on the other hand, is very slow to dissolve from dead diatoms and inorganic clays.

Driven in large part by seasonal changes in water temperature, there emerges a basic and common pattern in diatom ecology in lakes and oceans (Werner, 1977). In short, phytoplankton typically occurs in low numbers in the winter. The temperature of the water column is more or less uniform and so is not resistant to mixing. Between the low angle of the sun and the fact that plankton are swept in and out of the surface waters, there is little light for growth. Nutrient-rich deep waters are circulated and well-mixed until spring, when thermal stratification begins. Diatoms and other phytoplankton begin to grow rapidly, with the growth of grazing animals lagging behind (because of initial low concentrations of food). Phytoplankton grows to such abundance and at such a rate that they consume much of the basic nutrient supply. This is particularly true of silicate, which, being relatively insoluble, is transported to the sediments as diatoms die or are eaten (and their shells defecated) by planktivores such as zooplankton. The aquatic or marine system must await autumn turnover (during which nutrient-rich bottom waters are again mixed to the surface) and/or heavy runoff to return nutrients to the well-lit surface waters. In this dynamic system, nutrients are utilised and regenerated at different rates and from different sources.

Consequently, the study of resource physiology of individual diatom species is necessary to understand fully the resource needs and true environmental optima of diatoms. The absolute levels of nutrients and light may not determine diatom species but rather the rate at which nutrients are supplied (through regeneration by dissolution, runoff, precipitation, bacterial degradation, etc.) and the ratios of nutrient concentrations and supply rates. In other words, a system with high nitrogen and high phosphorus may have the same dominant diatom as a lake with low abundance of these nutrients, if the ratios of nutrients are otherwise about the same. This fact is helping to explain the otherwise enigmatic distributions of a number of diatom species.

Diatom Genomics

An entirely new approach to studying diatom ecology has been opened by the advent of new sequencing technologies

and powerful computers. It is now possible to sequence the entire genome of an organism within a reasonable amount of time for a reasonable cost. *Thalassiosira pseudonana* was the first diatom to have its genome entirely sequenced (Armbrust *et al*., 2004). Since then, the genome of *Phaeodactylum tricornutum* has been completed. Comparison of the two suggests that much of the diatom nuclear genome, perhaps as much as a third is relatively recently derived from bacteria (Bowler *et al*., 2008). Armbrust (2009) is an excellent introduction to the potential of genomic approaches to understanding the ecology of diatoms.

Given the phylogenetic and ecological diversity of diatoms, it is critical that a wider variety of diatoms be studied for their genomic properties. Draft sequence is now available for the genomes of the polar species *Fragilariopsis cylindrus* (80 Mb) and the toxic coastal species *Pseudo-nitzschia multiseries* (300 Mb), an araphid and a raphid diatom. However, there are still no radial centrics sampled. In any case, no one exemplar can be said to be representative of a phylogenetic or ecological group. The advent of genomics makes the understanding of diatom classification and natural history more important today than ever, not less important.

Extrapolation from model diatoms to global environmental questions will require that we place genomic data in its proper phylogenetic and natural history context. The first diatom to its genome sequenced is now referred to as 'the model marine diatom', but it may not be. *T. pseudonana* was selected to have its genome sequenced in part because it was thought to be representative of the genus *Thalassiosira*, which is diverse and abundant in the world's oceans. However, the genus *Thalassiosira* has never been proposed as monophyletic in a cladistic sense (no one has ever proposed one or more synapomorphies). This is, in part, due to the fact that many diatomists are content with a phenetic classification, without reference to monophyly. However, recent molecular studies have clearly demonstrated that *Thalassiosira* is polyphyletic and the type species of *Thalassiosira* (*Thalassiosira nordenskioeldii*: a purely marine diatom) is quite distant from *T. pseudonana* (which is common in freshwaters as well as estuaries and the near-shore marine environment). *T. pseudonana* itself is more closely related to the mainly freshwater genus *Cyclotella* than to any other nominal *Thalassiosira* (Alverson *et al*., 2011). This is not to criticise the significance of the many incredible discoveries made about the diatom genome. Rather it is a call for a greater conversation between genomicists and diatom natural historians. It also underscores the need for diatomists to produce a classification based on monophyly so that other disciplines can more effectively interpret results from exemplars.

Contributions of Diatoms to the Food Web

Phytoplankton provides most of the world's free oxygen and form the basis of the food web in most aquatic and marine ecosystems. Diatoms probably contribute more to primary production than any other photoautotrophic group. It is estimated that they account for a minimum of at least 20–25% of the world's photosynthesis (Werner, 1977), and as much as 43% of the global oceanic primary production (Nelson *et al*., 1995). Diatoms are grazed by protozoans, microscopic crustaceans, macroscopic crustaceans, molluscs and even fish, all of which get very high-quality food from diatoms. The low-molecular weight fatty acids that they store as food (in contrast to land plants, which store starch or sugar) are sequestered by animals grazing on them and used in their eggs as an energy-rich food source for their young. One of the most striking illustrations of the importance of diatoms in the food web is the contribution of diatoms to the food web in salt marshes, perhaps the most productive of aquatic ecosystems. Grasses such as *Spartina alterniflora* form the most visible part of the salt marsh; diatoms are orders of magnitude less important in mass. However, stable isotope studies show that diatoms contribute to the food web orders of magnitude more than their biomass would suggest, and sometimes their contribution is equal to that of the macroscopic plants (Sullivan and Moncreiff, 1988). They can do this because of their high growth and replacement rates (diatoms can reproduce once, twice or even four times in a day).

Palaeontology

The fossil record of diatoms, especially the earlier record, has many gaps and uncertainties. For example, several studies accept a minimum age of 175 million years for diatoms based on a report of *Pyxidicula* from early Jurassic sediments (Rothpletz, 1896, 1900). Others, however, point out that this material has been lost and accept much younger records (133.9 million years) as the first occurrence of diatoms in the fossil record (*cf*. Sorhannus, 2007 versus Parfrey *et al*., 2011). Thus, if one accepts the Rothpletz report, there is still a 40 Ma gap between the oldest and next oldest fossil. If one accepts 133.9 million years as the oldest record of diatoms, the next 50 million years or so is still only represented by a small number of geographically and temporally scattered, well preserved and well-studied deposits (many of the deposits known are either yet to be investigated or have very poor preservation). This, in turn, greatly affects molecular clock estimates of the origin and rates of diversification of diatoms.

What is certain is that the fossil record of diatoms contains many puzzles when compared to estimates of the diatom phylogeny based solely on molecular data. Molecular phylogenies place the genus *Lyrella* among the more derived raphid pennate diatoms, yet it is one of the oldest, if not oldest, according to the fossil record (Mann and Evans, 2007). There are numerous extinct diatoms, many of which have no obvious modern analogue. Not surprisingly then, there are long 'ghost lineages' for many groups (Sorhannus, 2007) suggesting that our knowledge of the true diversity and distribution of fossil diatoms is

very incomplete. It is also quite possible (perhaps because of taxon sampling biases caused by extinction) that the reverse is true – that our molecular phylogenetic estimates are also quite incorrect. The reality is that both these things are probably true (Theriot *et al.*, 2010).

As for other organisms, there have been extinctions and originations of diatom species through time. Because of this, and because they are found in most kinds of lake and ocean sediments, diatoms are used by scientists in the field of biostratigraphy (correlating geological strata). In these types of study, for example, geologists may determine that certain kinds of rock may bear economically valuable minerals (commonly petroleum); they then explore other areas for the same kinds of diatom in the hope that, when they find similar rocks, they will again find associated valuable minerals.

Diatoms are important to economic geology not only because they mark deposits with valuable minerals, but also because they produce valuable minerals. In some cases, interests of science and economics intersect. One of the more interesting ways of tracing microscopic organisms in their fossil record is to examine the geochemistry of such sediments. Diatom photosynthetic by-products of fatty acids and oils (or geochemical products derived from diatom fatty acids and oils) contribute to the accumulation of petroleum. Such markers include 24-norcholestanes (Holba *et al.*, 1998) and highly branched isoprenoid alkenes (HBI). A particular form of HBI appears to be restricted to one particular clade of diatoms and can be used as a biogeochemical marker for rhizosolenioid diatoms (Sinninghe-Damste *et al.*, 2004). **See also**: Fossils and Fossilization; History of Palaeontology; Molecular Palaeontology

Motility

Diatoms are relatively immotile single-celled protists. Many other protists have flagella, whip-like organelles that they use to propel themselves through water. As explained in the section 'Introduction', only centric diatoms have flagellated cells in any part of their life history, and these cells are the haploid, reproductive gametes, not the normal vegetative valve. Some centric diatoms are weakly motile in the vegetative stage, capable of slow spinning (Anderson *et al.*, 1986). Raphid pennate diatoms are capable of active gliding, as a result of extrusion of gelatinous materials from the raphe. One species, *Bacillaria paradoxa*, forms a filament of cells face-to-face. They glide against one another rather than against substrate. When fully extended, the filament resembles the folding ruler of carpenters and so has garnered the only common name widely applied to any diatom, 'the carpenter's slide-rule diatom'. **See also**: Algal Flagella

Economic Importance of Diatoms

The economic importance of diatoms is great but mainly indirect: they provide a great abundance of high-quality food to the food web; knowledge of diatoms is important to understanding and managing the environment; and diatoms are used in geological exploration. They are also of direct economic importance. Deposits of diatom shells may be thousands of feet thick and are mined for commercial purposes. A range of examples is provided. Diatomite is highly porous because of the packing of the frustules and the pores in frustules themselves. Moreover, the silicate of the wall adsorbs many ions. Thus, diatomite is both a filter and chemical cleanser and is used in the purification of water. It is also used as an insulator in devices such as autoclaves. (Diatomite is not known to cause the lung disease known as silicosis, in contrast to asbestos, another common siliceous compound used as an insulator.) Diatomite is mixed in polishes and paint as an abrasive and dulling agent, respectively. Again, as an adsorbent agent, it is mixed in animal feeds to increase the availability of nutrients to the animal. Diatom deposits, because of their porous nature, can accumulate petroleum deposits when capped by impervious rocks. As mentioned above, diatoms are also the source of much petroleum, especially apparently that extracted from higher latitudes and deposits laid down since the Cretaceous (Holba *et al.*, 1998).

With the advent of new technologies, diatoms may become even more important to the world's economy by teaching humans new tricks. Diatoms regularly form patterned structures at the nanoscale level, something that is difficult for humans to achieve in today's technology. Thus they are of immense interest to nanotechnologists (Bradbury, 2004; Gordon *et al.*, 2009).

Toxic Diatoms

Most diatoms are benign, which is fortunate, because any time we swim in natural waters we ingest them; however, a few diatoms in the genus *Pseudonitzschia* produce domoic acid, the causative agent of amnesiac shellfish poisoning, which can sometimes cause permanent memory loss or even death. The diatoms themselves occur in abundances too low to affect humans, but shellfish feeding on phytoplankton concentrate the domoic acid and pass it on to humans who eat them. Outbreaks have occurred in north temperate waters in the Atlantic and Pacific Oceans, but species of the genus *Pseudonitzschia* occur in near-shore waters in many areas of the world and it remains unclear as to why they are harmful in some areas and not in others. **See also**: Harmful Algal Blooms; Shellfish Poisoning

Miscellaneous and Unusual Uses of Diatoms

Most people studying diatoms concern themselves with questions related to the above discussion. There are a few interesting sideline uses to which knowledge about diatoms have been and are put. Because diatoms are trapped in the

long bones of the body when a person drowns, diatoms from these bones are used in forensic medicine to establish where a person may have drowned. Diatoms from clothing or shoes have been used to connect criminals with crime scenes. Perhaps the most unusual use of diatoms was to locate the site where the Japanese manufactured balloons used to bomb the USA in World War II. The balloons were released into the strong westerly winds of the jetstream, rising in the day as the sun heated them, and sinking at night. To keep them from sinking out of the jetstream, some ballast bags were released. Some balloons made it to the USA with one or more ballast bags still attached. The diatom species, sand and other geological materials in the ballast bags were used to identify the area from the bags were released. The location was confirmed and the site bombed, helping to end this unusual threat to the United States. Diatoms in pottery in archaeological finds have been used to identify the source of clay used. Because diatom biochemistry is altered as certain nutrients become limiting, diatoms vary in food quality and aquatic biologists manipulate diatom growth to understand the feeding of planktivores and food web dynamics.

Conclusion

The most recent formal summary of the diatoms is that of Round *et al.* (1990), which focuses on the genera of diatoms. An excellent compilation of diatom natural history is that of Werner (1977). In spite of its being over 30 years old, it is still timely and is an excellent compendium of principles and facts. Smol and Stoermer (2010) provide an excellent overview of the application of diatoms in the earth and environmental sciences.

At present, much work remains to be done on diatoms to satisfy both pure and applied science. From what kind of organism did diatoms evolve? What are the basic ecological requirements for species? How do diatoms relate to the whole of the natural environment? The two most fundamental and perhaps traditional questions, however, may remain the most compelling. How many diatoms are there? How can they be arranged in a natural classification?

Diatoms are both writing and being written by earth history. New technologies make the stories recorded in diatoms increasingly significant to humanity. The many open questions and new understanding of the diversity of diatoms and of their role in the world's ecosystem will ensure that the field of diatom biology will remain vital to those interested in the biodiversity of planet Earth and in understanding the health of our environment.

References

Alverson AJ (2008) Molecular systematics and the diatom species. *Protist* **159**: 339–353.

Alverson AJ, Beszteri B, Julius ML and Theriot EC (2011) The model marine diatom *Thalassiosira pseudonana* likely descended from a freshwater ancestor in the genus *Cyclotella*. *BMC Evolutionary Biology* **11**.

Anderson RA, Medlin L and Crawford RM (1986) An investigation of cell wall components of *Actinocyclus subtilis* (Bacillariophyceae). *Journal of Phycology* **22**: 466–484.

Armbrust EV (2009) The life of diatoms in the world's oceans. *Nature* **459**: 185–192.

Armbrust EV, Berges JA, Bowler C *et al.* (2004) The genome of the diatom *Thalassiosira pseudonana*: ecology evolution and metabolism. *Science* **306**: 79–86.

Bowler C, Allen AE, Badger JH *et al.* (2008) The *Phaeodactylum* genome reveals the evolutionary history of diatom genomes. *Nature* **456**: 239–244.

Bradbury J (2004) Nature's nanotechnologists: unveiling the secrets of diatoms. *PLoS Biology* **2**: e306.

Cavalier-Smith T (1986) The Kingdom Chromista: origin and systematics. *Progress in Phycological Research* **4**: 309–347.

Charles DF, Battarbee RW, Renberg I, van Dam H and Smol JP (1989) Paleoecological analysis of lake acidification trends in North America and Europe using diatoms and chrysophytes. In: Norton SA, Lindberg SE and Page A (eds) *Biological Monitoring of Freshwater Ecosystems*, pp. 233–293. Boca Raton, FL: CRC Press.

Conley DJ, Kilham SS and Theriot E (1989) Variation in the silica content of diatoms: differences between marine and freshwater diatoms. *Limnology and Oceanography* **34**: 205–213.

Daugbjerg N and Guillou L (2001) Phylogenetic analyses of Bolidophyceae (Heterokontophyta) using *rbc*L gene sequences support their sister group relationship to diatoms. *Phycologia* **40**: 153–161.

Fritz SC, Juggins S, Battarbee RW and Engstrom DR (1991) Reconstruction of past changes in salinity and climate using a diatom-based transfer function. *Nature* **352**: 52–54.

Goertzen LR and Theriot EC (2003) Effect of taxon sampling, character weighting, and combined data on the interpretation of relationships among the heterokont algae. *Journal of Phycology* **39**: 423–439.

Gordon R, Losic D, Tiffany MA, Nagy SS and Sterrenburg FA (2009) The glass menagerie: diatoms for novel applications in nanotechnology. *Trends in Biotechnology* **27**: 116–127.

Guillou L, Chrétiennot-Dinet M-J, Medlin LK *et al.* (1999) *Bolidomonas*: a new genus with two species belonging to a new algal class, the Bolidophyceae (Heterokonta). *Journal of Phycology* **35**: 368–381.

Hoagland KE, Roemer SC and Rosowski JR (1982) Colonization and community structure of two periphyton assemblages, with emphasis on the diatoms (Bacillariophyceae). *American Journal of Botany* **69**: 188–213.

Holba AG, Dzou LIP, Masterson WD *et al.* (1998) Application of 24-norcholestanes for constraining source age of petroleum. *Organic Geochemistry* **29**: 1269–1283.

Ichinomiya M, Yoshikawa S, Kamiya M *et al.* (2011) Isolation and characterization of Parmales (Heterokonta/Heterokontophyta/Stramenopiles) from the Oyashio Region, Western North Pacific. *Journal of Phycology* **47**: 144–151.

Interlandi SJ and Kilham SS (2001) Limiting resources and the regulation of diversity in phytoplankton communities. *Ecology* **82**: 1270–1282.

Julius ML and Theriot EC (2010) The diatoms: a primer. In: Smol J and Stoermer EF (eds) *The Diatoms: Applications for the*

Environmental and Earth Sciences, pp. 8–22. Cambridge: Cambridge University Press.

Kilham SS, Theriot EC and Fritz SC (1996) Linking planktonic diatoms and climate change using resource theory in the large lakes of the Yellowstone ecosystem. *Limnology and Oceanography* **41**: 1052–1062.

Leipe DD, Wainright PO, Gunderson HJ *et al.* (1994) The stramenopiles from a molecular perspective: 16S-like rRNA sequences from *Labyrinthuloides minuta* and *Cafeteria roenbegensis*. *Phycologia* **33**: 369–377.

Luther A (1899) Über Chlorosaccus eine neue Gattung der Süsswasseralgen. *Bih. Svenska Vet-Akademiens Handlungen 24, Afd. III* **13**: 1–22.

Mann DG and Droop SJM (1996) Biodiversity, biogeography and conservation of diatoms. In: Kristiansen J (ed.) *Biogeography of Freshwater Algae: Proceedings of the Workshop on Biogeography of Freshwater Algae, Developments in Hydrobiology*, pp. 19–32. Dordecht: Kluwer Academic Publishers.

Mann DG and Evans KM (2007) Molecular genetics and the neglected art of diatomics. In: Brodie J and Lewis J (eds) *Unravelling the Algae – the Past, Present and Future of Algal Systematics*, pp. 231–265. Boca Raton, FL: CRC Press.

Mann DG and Marchant HJ (1989) The origins of the diatom and its life cycle. In: Green JC, Leadbeater BSC and Diver WI (eds) *The Chromophyte Algae: Problems and Perspectives*, pp. 307–323. Oxford: Clarendon Press.

Medlin LK (2010) Pursuit of a natural classification of diatoms: an incorrect comparison of published data. *European Journal of Phycology* **45**: 155–166.

Nelson DM, Treguer P, Brzezinski MA, Leynaert A and Queguiner B (1995) Production and dissolution of biogenic silica in the ocean – revised global estimates, comparison with regional data and relationship to biogenic sedimentation. *Global Biogeochemical Cycles* **9**: 359–372.

Parfrey LW, Lahr DJG, Knoll AH and Katz LA (2011) Estimating the timing of early eukaryotic diversification with multigene molecular clocks. *Proceedings of the National Academy of Sciences* **108**: 13624–13629.

Patterson DJ (1989) Stramenopiles: chromophytes from a protistan perspective. In: Green JC, Leadbeater BSC and Diver WI (eds) *The Chromophyte Algae: Problems and Perspectives*. The Systematics Association Special Volume, 38, pp. 357–379. Oxford: Clarendon Press.

Rothpletz A (1896) Über die Flysch-Fucoiden und einige andere fossile Algae, sowie über laisische, Diatomeen führende Hornschwämme. *Zeitschrift der Deutschen Geologischen Gesellschaft* **4**: 854–914.

Rothpletz A (1900) Über einen neuen jurassichen Hornschwämme unddie darin eingeschlossenen Diatomeen. *Zeitschrift der Deutschen Geologischen Gesellschaft* **52**: 154–160.

Round FE (1981) Some aspects of the origin of diatoms and their subsequent evolution. *Biosystems* **14**(3–4): 483–486.

Round FE and Crawford RM (1981) The lines of evolution of the Bacillariophyta. 1. Origin. *Proceedings of the Royal Society of London Series B-Biological Sciences* **211**(1183): 237–260.

Round FE and Crawford RM (1984) The lines of evolution of the Bacillariophyta. 2. The Centric Series. *Proceedings of the Royal Society of London Series B-Biological Sciences* **221**(1223): 169–188.

Round FE, Crawford RM and Mann DG (1990) *The Diatoms, Biology and Morphology of the Genera*. Cambridge: Cambridge University Press.

Saros JE and Fritz SC (2000) Nutrients as a link between ionic concentration/composition and diatom distributions in saline lakes. *Journal of Paleolimnology* **23**: 449–453.

Sinninghe-Damste JS, Muyzer G, Abbas B *et al.* (2004) The rise of the rhizosolenid diatoms. *Science* **304**: 584–587.

Smol JP and Stoermer EF (eds) (2010) *The Diatoms: Applications for the Environmental and Earth Sciences*, 2nd edn. New York: Cambridge University Press.

Sorhannus U (2007) A nuclear-encoded small-subunit ribosomal RNA timescale for diatom evolution. *Marine Micropaleontology* **65**: 1–12.

Stoermer EF, Wolin JA, Schelske CL and Conley DJ (1990) Siliceous microfossil succession in Lake Michigan. *Limnology and Oceanography* **35**: 959–967.

Sullivan MJ and Moncreiff CA (1988) Primary production of edaphic algal communities in a Mississippi salt marsh. *Journal of Phycology* **24**: 49–58.

Theriot EC, Ashworth M, Nakov T, Ruck EC and Jansen RK (2010) A preliminary multigene phylogeny of the diatoms (Bacillariophyta): challenges for future research. *Plant Ecology and Evolution* **143**: 278–296.

Theriot EC, Ruck EC, Ashworth M, Nakov T and Jansen RK (2011) Status of the pursuit of the diatom phylogeny: are traditional views and new molecular paradigms really that different? In: Seckbach J and Kociolek JP (eds) *The Diatom World: 600*. Springer.

Weerman EJ, Herman PMJ and Van De Koppel J (2010) Top-down control inhibits spatial self-organization of a patterned landscape. *Ecology* **92**: 487–495.

Werner D (ed.) (1977) *The Biology of Diatoms*. Botanical Monographs vol. 13. Berkeley: University of California Press.

Williams DM and Kociolek JP (2007) Pursuit of a natural classification of diatoms: history, monophyly and the rejection of paraphyletic taxa. *European Journal of Phycology* **42**: 313–319.

Further Reading

Bowler C, Vardi A and Allen AE (2010) Oceanographic and biogeochemical insights from diatom genomes. *Annual Review of Marine Science* **2**: 333–365.

Seckbach J and Kociolek JP (eds) (2011) *The Diatom World*. Cellular Origin, Life in Extreme Habitats and Astrobiology, vol. 19. Dordrecht: Springer.

Theriot E (1992) Clusters, species concepts and morphological evolution of diatoms. *Systematic Biology* **41**: 141–157.