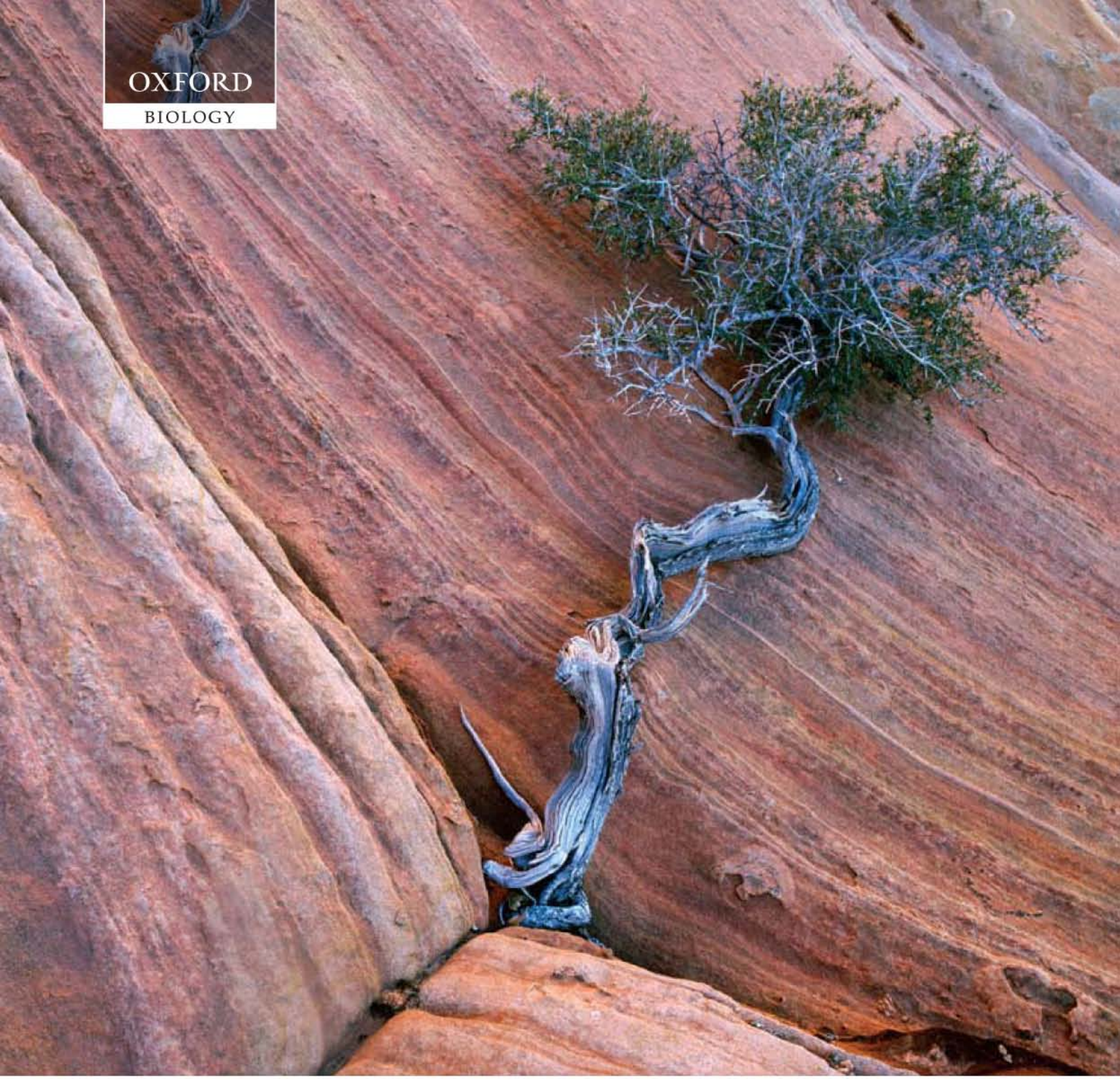

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Diatoms (Bacillariophyta)

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Abstract

The diatoms are one of the best characterized microalgal groups because of the unique features of their silicified cell wall, which is preservable. Modern diatoms constitute three classes, which have an extensive fossil record since the late Cretaceous (100–66 million years ago, Ma). Diatoms from the early Cretaceous (145–100 Ma) are rare and differ in the morphology of their silica wall from modern diatoms. Molecular clocks indicate that the divergences of classes and orders took place in the Triassic (251–200 Ma) and Jurassic (200–145 Ma), following the Permian–Triassic extinctions (251 Ma).

The diatoms are one of the most easily recognizable groups of major eukaryotic algae, because of their unique silicified cell walls (frustules), which consist of two overlapping thecae, each in turn consisting of a valve and a number of hooplike or segmental girdle bands (*1*). Well-preserved frustules are found in the earliest known deposits of fossil diatoms, from the early Albian (~125 Ma) of what is now the Weddell Sea, Antarctica, but these diatoms bear no resemblance to modern diatoms in their morphology (*2*).

Molecular sequence data show that diatoms are heterokont algae. Heterokonts are chlorophyll *a*+*c* containing algae whose motile cells have two heterodynamic flagella, one covered with tripartite hairs and the other smooth (*3*). In diatoms, the flagellar apparatus is reduced or absent; indeed, only the spermatozoids of the oogamous "centric" diatoms are flagellated and these are uniflagellate (*4*), lacking all trace of a smooth posterior flagellum.

Today, the diatoms are found in almost all aquatic and most wet terrestrial habitats. Existing hypotheses of diatom origins tend to agree that the pre-diatom or "Ur-diatom" developed from a scaly ancestor, not in pelagic habitats, but in shallow marine environments and were tychoplanktonic (bottom dwelling). Phylogenetic analyses have documented several invasions and radiations into freshwater (*1*) and have documented that their closest relative is a flagellated picoplankter, the Bolidophyceae.

Most diatomists have long assumed that the diatoms contain two groups: the centrics and the pennates, which can be distinguished by their pattern centers or symmetry, mode of sexual reproduction, and plastid number and structure (*5*). The oogamous centric diatoms, with radially symmetrical ornamentation on their valves and with numerous discoid plastids, are distinct from the isogamous pennate diatoms with bilaterally symmetrical pattern centers and generally fewer, platelike plastids. These groups are known to most aquatic and cell biologists under these terms, and each term conveys a distinct image of a particular type of diatom valve.

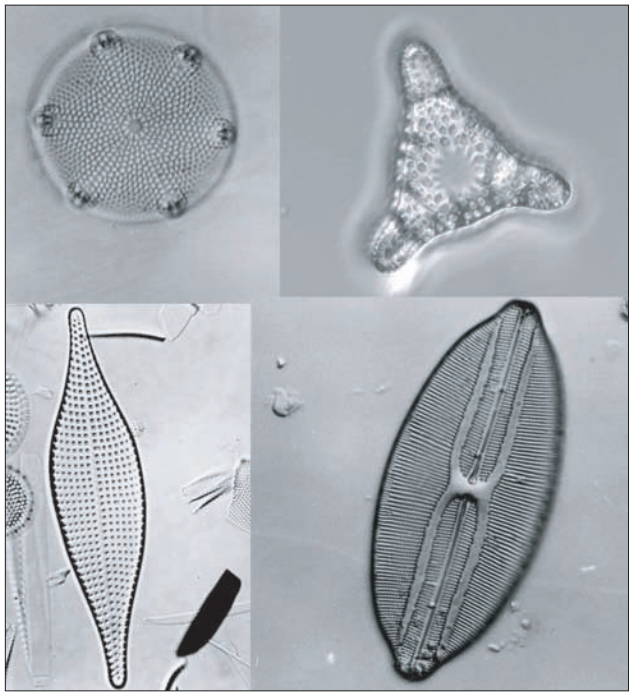

Fig. 1 Diatoms. Typical representatives of a radial centric, Class Coscinodiscophyceae (upper left), bipolar multipolar centric, Class Mediophyceae (upper right), an araphid pennate, Class Bacillariophyceae (lower left) and a raphid pennate, Class Bacillariophyceae (lower right) diatom. Credits: L. K. Medlin.

L. K. Medlin. Diatoms (Bacillariophyta). Pp. 127–130 in *The Timetree of Life*, S. B. Hedges and S. Kumar, Eds. (Oxford University Press, 2009).

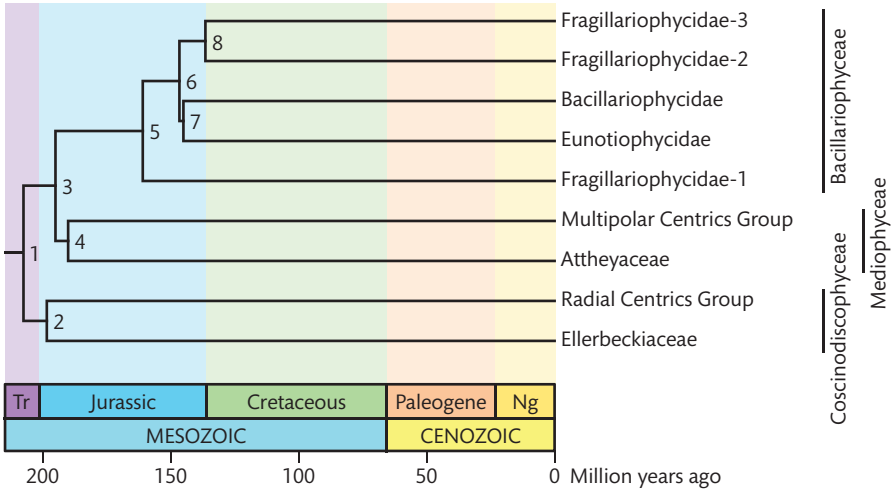

Fig. 2 A timetree of diatoms. Divergence times are from Table 1. Taxa shown are at the subclass and order level. Fragillariophycidae-1 are the basal araphids (*17*), Fragillariophycidae-2 are the core araphids with labiate processes, and Fragillariophycidae-3 are the core araphids wiithout labiate processes. *Abbreviations*: Ng (Neogene) and Tr (Triassic).

Historically, centric and pennate diatoms have been separated as two classes or orders. Round *et al.* (*5*), however, recognized three classes—Coscinodiscophyceae (centric diatoms), Fragilariophyceae (araphid pennate diatoms), and Bacillariophyceae (raphid pennate diatoms)—giving equal ranking to the raphid pennate diatoms (those with a slit opening, raphe, in the cell wall for movement) and the araphid pennate diatoms (those without this slit). Williams (*6*) has traced the historical classification of the diatoms. Recently, Medlin and colleagues (literature summarized by Medlin and Kaczmarska, *7*) have divided the diatoms into two groups on the basis of molecular sequence data. What was initially called "Clade 1" in early molecular work contains those centric diatoms with essentially radial symmetry of valve shape and structure. "Clade 2" consists of two groups, the first of which contains the bi- or multipolar centrics and the radial Thalassiosirales ("Clade 2a"), and the second, the pennates ("Clade 2b") (Fig. 1). Morphological and cytological support for these clades was reviewed in Medlin *et al.* (*8*) and Medlin and Kaczmarska (*7*). Clades 1 and 2 are now recognized at the subdivision level (Fig. 2), as the Coscinodiscophytina and Bacillariophytina, respectively, and Clades 1, 2a, and 2b are now recognized at the class level, as the Coscinodiscophyceae, Mediophyceae, and Bacillariophyceae (*7*) (Fig. 2). The first two classes are not recovered as monophyletic if alignments are not performed using the secondary structure of the rRNA genes as a guide.

There are correlations between the principal molecular clades and certain cytological features. For example, on the whole the Bacillariophytina have a perinuclear arrangement of the Golgi apparatus, whereas in the Coscinodiscophytina, the Golgi stacks are usually in Golgi–endoplasmicreticulum–mitochondrion(G-ER-M) units (*7, 8, 9*). However, there are some exceptions (*8*).

The best independent, nonmolecular support for three classes comes from auxospore structure, the specialized zygote of the diatoms that swells to restore the cells to their original cell size, which has diminished with each vegetative division (*7, 10*). Isodiametric auxospores that can swell in all directions and have only scales are characteristic of Clade 1, anisodiametric auxospores with scales and hoops or bands (a properizonium) to restrict the swelling to bipolar or multipolar directions are found in Clade 2a, and anisodiametric auxospores that form a complex tubular perizonium, usually consisting of transverse hoops and longitudinal bands, are found in Clade 2b.

The rate of evolution in Clade 1 diatoms has been calculated using two different means of calibrating molecular trees: by fossil dates within the entire clade (*11*), and by biomarker compounds for the clade containing

Table 1. Divergence times (Ma) among diatoms.

Timetree		Estimates						
Node	**Time**	**Ref. (*11*)(a) Time**	**Ref. (*11*)(b) Time**	**Ref. (*14*)(a) Time**	**Ref. (*14*)(b) Time**	**Ref. (*15*) Time**	**Ref. (*16*)(a) Time**	**Ref. (*16*)(b) Time**
1	207.5	120	200	380	330	–	180	235
2	198.5	–	–	–	–	–	172	225
3	195.0	86	159	–	–	–	170	220
4	190.0	–	–	–	–	–	165	215
5	161.0	–	–	–	–	–	140	182
6	146.5	84	167	–	–	96.5	127	166
7	145.0	–	–	–	–	–	125	165
8	136.5	–	–	–	–	–	118	155

Note: The node times in the timetree are the average of the minimum (a) and maximum (b) times reported in ref. (*16*). Average (a) and upper limit (b) are reported from ref. (*11*), and results from the analysis of SSU rRNA (a) and large subunit (LSU) rRNA (b) are reported from ref. (*14*).

Rhizosolenia (*12*). Both methods suggest that these diatoms are evolving very quickly (1% per 21.5 and 14 Ma for the rRNA gene, respectively) and this could explain why the morphology of the diatoms changes so rapidly across the Cretaceous, between Lower (146–100 Ma) and Upper (100–66 Ma) Cretaceous floras.

Several people have constructed molecular clocks for the diatoms and most are concerned with dating the origin of the group and the diversification of its major clades, which would be recognized at the class level, when these are recovered as monophyletic groups. Kooistra and Medlin (*11*) made the first molecular clock using a linearized tree where the rate of evolution was averaged across the tree using other pigmented heterokonts as the outgroup. Using the Hillis and Morris model for their clock (*11*), they were able to calculate an average age and an earliest possible age given a 95% confidence interval around any undated node. In this clock, they inferred the origin of the diatoms to be 266–164 Ma (earliest to average). The major clades that constitute the two subdivisions of the diatoms were estimated to have diverged between 200 and 120 Ma (earliest to average). Clade 2 comprising the bipolar centrics and the pennates diverged between 159 and 86 Ma.

The clock prepared by Phillippe *et al.* (*13*) used the ciliates as the closest relative and the origin of the diatoms calculated in that paper corresponded to the origin of the heterokonts, which is the division to which the diatoms belong, probably because too distant an outgroup was used to root the ingroup. This places in doubt the 300-million-year gap in the diatom fossil record concluded in that study. In a second clock paper by Sörhannus from the same group (*14*), the chrysophytes were used as the closest relative to the diatoms, which are likely still too far away from the ingroup, but this gave a more reliable date of 400–330 Ma for the origin of the diatoms based on two genes. The most recent study from Sörhannus (*15*) was based on a single gene, the small subunit (SSU) rRNA gene and used the closest known relative of the diatoms, the Bolidophyceae, as the outgroup. A relaxed molecular clock (PATHd8) was used, which was calibrated from single dating points sequentially. Resulting dates for the origin of the diatoms ranged from 250 to 183 Ma, which is similar to the time estimates Kooistra and Medlin (*11*).

Sato *et al.* (*16*), using four genes and the Bayesian program Multidivtime, with designated maximum and minimum divergence times of 250 and 190 Ma, respectively, found much older divergence times for all of the classes, especially the pennates. Their clock using an ML tree as input suggests that the radial centrics, Class Coscinodiscophyceae emerged 235–180 Ma, the bipolar centrics, Class Mediophyceae split from the Class Bacillariophyceae 220–170 Ma (maximum to minimum). Those results also indicate that the early divergence of the pennates into three major clades, basal araphid, core araphid, and raphid diatoms, took place in a very short period. All major clades (orders or families) of araphid diatoms appeared by the end of the Cretaceous in all analyses. All of the divergences of these lineages took place long before there is a fossil record of diatoms. However, modern diversifications of the genera in these lineages

usually coincide with the first appearances of the modern genera. The reconciliation of molecular diversification with first appearances of selected genera of diatoms is discussed in Sörhannus (*15*), Kooistra and Medlin (*11*), and Sims *et al.* (*1*).

The modern classification of the araphid diatoms will need to be extensively revised because the group is paraphyletic. Among the raphid diatoms, most orders and the families therein have been found to be monophyletic groups, but there are some genera that are not monophyletic and revisions will be needed there as well. It seems that features of the living cell—the zygote morphology and development—define and better support the deeper branches of the tree, whereas the details of the silica cell wall, upon which the classification of the diatoms is based, can best be used to define the tips and younger branches of the tree. Many well-documented genera, such as *Diatoma, Fragilariopsis*, and *Pleurosigma*, arise from within other genera in the trees, making the parent genus paraphyletic. This is problematic for taxonomists and therefore extensive generic redefinitions will be needed unless those paraphyletic definitions are accepted.

In summary, the molecular diversification of the diatoms appears to be much earlier than the first appearance of these taxa in the fossil record at 180 Ma. None of the clocks rooted with appropriate taxa have placed the origin of diatoms earlier than 250 Ma, which likely corresponds to the Permian–Triassic (PT) extinction, 251 Ma. The heterokont algae, of which the diatoms are a member, radiated when the ocean trace metal chemistry changed at the PT boundary and gave the host plants with a red algal plastid an adaptive advantage. Red and green algal plastids differ greatly in their need for certain trace metals. The abundance of Fe after the PT boundary favors the growth of the red algal plastid, which has the Fe-containing cytochrome *c6* in their photosynthetic electron carrier complex instead of the Cu-containing plastocyanin found in the photosystems of other algae (*17*).

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