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MINI REVIEW: The evolution of the diatoms and a report on the current status of their classification

Abstract

This mini review describes the newest classification of diatoms based on their evolution, which was obtained from molecular data. Because centric forms were found earlier in the geological record it is assumed that the pennate diatoms evolved from the centric forms and 3 classes were described: the centric diatoms, the araphid pennate and the raphid pennate diatoms. However, molecular data showed that the centric diatoms are most likely paraphyletic and the diatoms are now divided into two groups: Clade 1 contains the radial centric diatoms and Clade 2 contains two sub-Clades: the first sub-Clade contains the bipolar centrics and the Thalassiosirales and the second sub-Clade contains the pennate diatoms to which many of the microphytobenthos species belong. These Clades and additional morphological support for this new taxonomy is discussed in this mini review.

The diatoms are one of the most easily recognisable groups of major eukaryotic algae, because of their unique silicified cell wall, which consists of two overlapping thecae, each in turn consisting of a valve plus a number of hoop-like or segmented girdle bands. Such structures are present in all living diatoms (except following secondary loss, e.g., in the case of the endosymbiotic diatoms living in foraminifera), and also in early, well-preserved fossil diatoms from the early Albian (Lower Cretaceous) of what is now the Weddell Sea, Antarctica (Gersonde and Harwood, 1990). Molecular sequence data have consistently shown that diatoms belong to the heterokont algae. These chlorophyll $a+c$–containing algae typically have motile cells with two heterodynamic flagella, one covered with tripartite mastigonemes and the other smooth. In diatoms, the flagellar apparatus is reduced or absent; in fact, only the spermatozoids of the oogamous 'centric' diatoms are flagellated (Manton and von Stosch, 1966) and these are uniflagellate, lacking all trace of a smooth posterior flagellum or basal body. Nevertheless, the characteristic heterokont mastigonemes are present on the single flagellum and diatoms also possess similar plastid ultrastructure (with four bounding membranes, lamellae of three thylakoids, and usually a peripheral ring nucleoid) and pigment composition to e.g., the brown algae.

Diatom origin has been speculated upon by several workers. Diatoms may be derived from a spherical uniformly scaled monad (Round, 1981; Round and Crawford, 1981, 1984) with an anterior flagellum (Cavalier-Smith, 1986), or be derived from a cyst-like form like the extant Parmales in the chrysophyte algae (Mann and Marchant, 1989). A scaly ancestor likely existed at some point in their phylogeny because of the presence of scales on reproductive cells of diatoms and scales on the reproductive stage of the Labyrinthuloides, an earlier divergence in the heterokont lineage (Medlin *et al*. 1997a). Recent phylogenies constructed from nuclear-encoded small-subunit ribosomal RNAs place the diatoms within the pigmented heterokont algal lineages (Bhattacharya *et al.*, 1992; Leipe *et al.*, 1994, Medlin *et al.*, 1997b), most closely related to the new algal class, the Bolidophyceae, which are picoplanktonic algae with a simplified cellular organization (Guillou *et al.* 1999). Both diatoms and bolidomonads commonly possess similar pigments and two transverse plates at the base of each flagellum. A molecular clock constructed from 4 genes has placed the average age of the diatoms ca. 135 Ma ago with their earliest possible age being no earlier than 240 Ma ago (Medlin *et al*. 1997a, 2000).

Most diatomists have long assumed that the diatoms contain two groups: the centrics and the pennates, which can be distinguished by their type of sexual reproduction, pattern centers or symmetry, and plastid number and structure (Figure 1A, Round *et al.* 1990). The oogamous centric diatoms with radially valve symmetrical ornamentation and with numerous discoid plastids are distinct from the isogamous pennate diatoms with bilaterally symmetrical pattern centres and with fewer plate-like plastids. Both groups are known to most aquatic and cell biologists under these terms. Historically, the centric and pennate diatoms have been classified into two distinct classes based on these characters. Pennate diatoms undoubtedly evolved from the centric forms because they first appear later in the geological record. Coscinodiscophyceae (centric diatoms), Fragilariophyceae (araphid pennate diatoms), and Bacillariophyceae (raphid pennate diatoms) are the three classes presently recognized in Round *et al.* (1990) (Figure 1A) because the raphid pennate diatoms (those with a slit opening [raphe] in the cell wall for movement) were given equal taxonomic ranking with the araphid pennate diatoms (those without this slit). An alternative classification based on molecular data supported by different cellular features has been presented by Medlin and Kaczmarska (2004) and in Figure 1B.

The first molecular evidence that clearly demonstrated that the centric diatoms were paraphyletic was presented by Medlin *et al.* (1993). In the same study, araphid pennate diatoms were also shown to be paraphyletic. Among the taxa studied in this first paper, the centric diatom, *Skeletonema costatum* was most closely related to the pennate diatoms, with high bootstrap support in molecular analyses. Additionally, Sörhannus *et al.* (1995) showed that centric and araphid taxa were paraphyletic using an analysis of partial sequences from the 28S large-subunit (LSU) rRNA coding region from eight diatoms. These initial data suggested that presently used higher level diatom systematics do not reflect their evolutionary history. All subsequent analyses from three more genes have supported this finding (Medlin *et al*. 1996, Medlin *et al.*, 2000, Ehara *et al*. 2000), and the diatoms have been consistently divided into 2 groups: Clade 1 contains the radial centrics and Clade 2 can be subdivided into two sub-Clades; the first of which contains the bipolar centrics and the radial Thalassiosirales (Clade 2a), and the
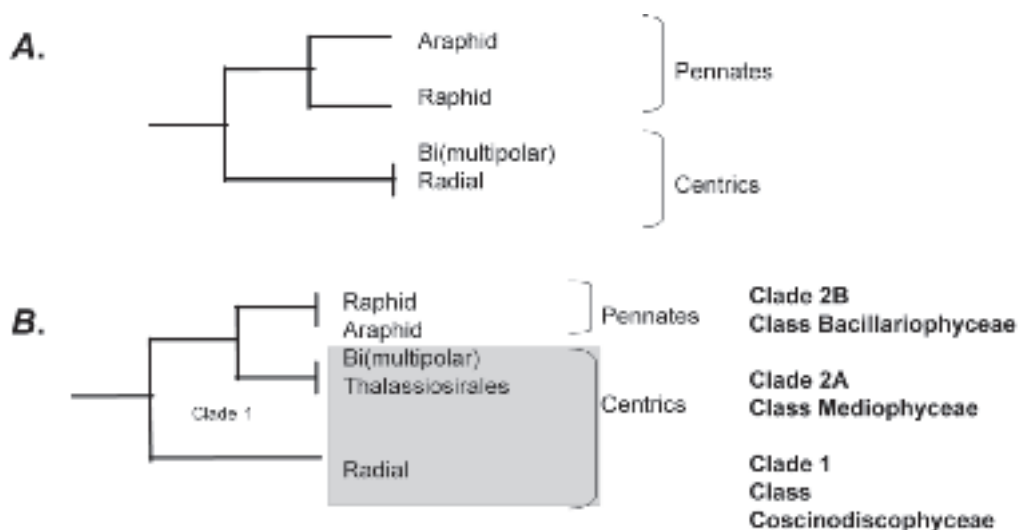
Figure 1. Stylised tree depicting current classification of the diatoms (A) based on morphological data and that proposed by Medlin and Kazcmarska 2004 based on molecular data (B).

second, the pennates (Clade 2b). Morphological and cytological support for the two Clades was reviewed in Medlin *et al.* (2000) and Medlin and Kaczmarska (2004).

Clade 1 and Clade 2, are recognised now at the subdivision level, as the Coscino-phytina and Bacillariophytina, respectively, and Clades 1, 2a and 2b are recognised now at the class level: Class Coscinodiscophyceae, Mediophyceae and Bacillario-phyceae (Medlin and Kaczmarska (2004). Primary support for two subdivisions comes from the Golgi arrangement, which is in Clade 1 primarily the G–ER–M unit and in Clade 2, a perinuclear arrangement. Weaker support for the two subdivisions comes from the sperm/chloroplast arrangement, which is in Clade 1 primarily merog-enous and in Clade 2 primarily hologenous.

The primary support for the three classes comes from the auxospore structure. Isodiametric auxospores with scales are characters of Clade 1, anisodiametric aux-ospores with scales and hoops or bands (a properizonium) are noted in Clade 2a, and anisodiametric auxospores that form a complex tubular perizonium, usually consist-ing of transverse hoops and longitudinal bands, are only in Clade 2b. Weaker support for the three classes comes from the pyrenoid structure, which has a single thylakoid crossing the pyrenoid that is not connected to the plastid thylakoids in Clade 1, is usually without a crossing thylakoid in Clade 2a (or if present, is similar to Clade 1 or just lies along the periphery of the pyrenoid centre), or has a single thylakoid crossing the pyrenoid that is connected to the plastid thylakoids in Clade 2b. Fossil support from the earliest best preserved fossil deposit (Gersonde and Harwood (199)) suggests that diatoms lacking any structure in the valve centre and having complex linking structure were the likely ancestors of Clade 1 diatom, whereas those with a central tube structure in the valve and less complicated linking structures likely gave rise to Clade 2 diatoms.

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