

A Review of Diversification Trends in Diatom Research with Special Reference to Taxonomy and Environmental Applications Using Examples from Lake Baikal and Elsewhere

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The study of diatoms has diversified strongly since its beginnings in the 18th century. Early work focused upon collecting material for taxonomic analysis but by the mid 19th century a strong global perspective had already developed. In the 20th century, use of diatoms in biostratigraphy, environmental change and ecology and in biogeography proliferated as did work on diatom ultra structures, life cycles, and systematics. Most recently, systematics and molecular genetics have sought to reveal diatom genealogy and to refine taxonomy. Similarly, diatoms are used increasingly as time-space indicators of water quality and there is renewed interest in global diversity patterns. Taxonomy underpins these applications but changing concepts can either diminish or enhance the value of diatoms to the environmental sciences. Some ways in which taxonomic analysis of diatom assemblages can benefit environmental research are discussed with reference to material from Lake Baikal and elsewhere.

Because of their intricate siliceous cell walls and their global distribution in aquatic and terrestrial environments, diatom microalgae have attracted the interest of naturalists and researchers alike since the 18th century. Nevertheless, it was mainly during the 20th century that the value of these organisms in ecological and, due to their resistant skeleton, in palaeo-environmental research became fully recognised. In recent decades, the major role of diatoms in global primary productivity and the carbon cycle has been demonstrated (e.g., Round et al. 1990). At the same time, concern has increased about global biodiversity and the survival of species. Although microorganisms, diatoms are relevant to these issues. They are major contributors to global primary productivity and are abundant in all the earth's major aquatic ecosystems, from the oceans, through wetlands to the alpine lakes. These ecosystems are all perceived as being threatened indirectly or directly by human activities, and time-space changes in the distribution of diatom taxa can provide valuable evidence about the nature and pace of global environmental change.

There are several ways in which diatoms are particularly relevant to global change and biodiversity issues. They are species diverse and, because of their well known ecological tolerances, they can indicate the nature of environmental change (climate, pollution, and habitat loss, for example). Diatom-environment data sets are now widely available whereby diatom assemblages can be used to predict nutrients, pH and salinity in freshwaters (see Stoermer and Smol 1999; Battarbee et al. 2001). However, with renewed interest in the 'ecological quality' of habitats, species monitoring and species comparisons using diatoms (especially in combination with other organismal groups) play an important role in the ecological assessment of water quality types (e.g.,

Coste et al. 1991). Consequently, diatoms are included within the recently introduced Water Framework Directive (WFD, see Foster et al. 2001) for the ecological management of European fresh and transitional waters (e.g., Kelly 2002). Long-term monitoring programmes are particularly useful for detecting trends in inter-annual species change, in relation to acidify for example (Monteith and Evans 2000).

A special characteristic of the diatoms is their ability to form rich sedimentary archives, and this has been exploited in a variety of palaeo-environmental applications from marine biostratigraphy to recent pollution. Sedimentary diatoms are also becoming increasingly useful in conservation policy and management of water quality, particularly those issues focused upon in the WFD, where identification of reference conditions for impacted water bodies is required. Sedimentary diatoms, as well as other sub-fossil organism in dated sediment cores, can provide excellent ecological records of pre-impact conditions and can be used to identify modern reference lakes (Flower et al. 1997). The particular value of palaeolimnological techniques is the provision for providing a variety of reference data where information from long-term monitoring and other sources are absent (Smol 2002).

Application of diatom analysis to environmental issues rests fundamentally on adequate, precise and harmonized taxonomic conventions and techniques. The recognition of morphotaxa in the environment and the unambiguous attribution of ecological optima and tolerances are the essence of diatom-based palaeolimnological reconstruction and of diatom ecology. Even without attribution of these optima, the recognition of taxa remains of fundamental importance to other aspects of diatom research such as biogeography and systematics. Recent developments in diatom taxonomy regarding biogeographical limits for some diatom taxa and the re-definition of many taxa according to new taxon concepts (Mann 1999) have considerable implications for diatom based environmental studies. In the short-term, there is inevitable confusion concerning the new concepts (Stoermer 2001) but, if a more precise, comprehensive and appropriate taxonomic system arises, both diatom diversity appraisal and diatom ecology/palaeoecology will benefit. This paper provides an overview of the diversification of diatom research and examines some issues, applications and implications of recent taxonomic revisions for assessing diatom diversity.

DIVERSIFICATION TRENDS IN DIATOM RESEARCH

Diatoms are readily observable in the light microscope and their occurrence was well known by the late 18th century (see Round et al. 1990), but it was not until the 19th century that awareness of the large diversity of micro-organisms developed as microscopical techniques improved. In the past 150 years or so, diatom research has diversified into several major fields ranging from ecology and micropalaeontology to systematics and molecular genetics. Although these diversification trends are indicated broadly in Figure 1, some of the perhaps less known recent applications are omitted (e.g., toxicology and archaeology, see Stoermer and Smol 1999).

EARLY TAXONOMY.— The pioneering work of Ehrenberg, Greville and others during the early part of the 19th century (see Fig. 1) established diatoms as an important biological group and several classical works followed (e.g., Ehrenberg 1854). These works not only focused on describing species and erecting a taxonomic system for diatoms but the authors also were often very interested in the provenance of diatom taxa. Ehrenberg, for example, corresponded extensively with Charles Darwin seeking diatomaceous material from exotic locations. He was also aware of the significance of the indicator value of marine and freshwater taxa in samples. Darwin sent numerous diverse samples including atmospheric ‘dust’ collected during the voyage of the *Beagle* (Darwin 1839) and the facial paint used by the indigenous people of Tierra del Fuego (see Burkhardt and

Smith 1987). A little later Cleve reported widely on diatoms from disparate global locations (e.g., Cleve 1878, 1894/5). Hence, even at this early stage of diatom research, there was much interest in the geographic distribution of taxa. The early emphasis was mainly on obtaining material for describing new taxa, and it was not until later in the 20th century that diatoms and biogeography began to receive systematic attention (see below). The first diatom catalogues appeared in the late 19th century (Habirshaw 1877; Schuett 1896), and more specific accounts of historical diatom studies are available elsewhere (see Patrick 1982).

BIOSTRATIGRAPHY.— The significance of diatoms in stratigraphic sequences was recognised in the latter part of the 19th century (e.g., Gregory 1854; Kitton 1870). This work developed into diatom micropalaeontology through the studies of Hanna (1927), Calvert (1929), Jouse (1939) and others on terrestrial deposits. In the first part of the 20th century, marine diatom biostratigraphy was mainly restricted to terrestrial deposits, but with the development of deep sea sediment coring technology, palaeoceanography and diatom analysis rapidly expanded, firstly in the Pacific Ocean (Jouse 1960; Burckle 1972; Sancetta 1979; Barron and Baldauf (1995). The international Deep Sea Drilling Project and then the Ocean Drilling Programme opened up the world's oceans to palaeoceanography and diatom biostratigraphic analyses of marine sediment cores. Such analyses have enabled chrono-biostratigraphies to be established and permitted the major taxon groups to be arranged into an evolutionary series according to geological time (e.g., Strelnikova 1990). Freshwater diatom biostratigraphy also expanded and Bradbury (e.g., 1986) began examining continental scale freshwater diatom deposits in exposures and in cores. In the 1990s, deep coring of Lake Baikal (the international Baikal Drilling Programme, BDP) was begun and has recovered an essentially continuous sedimentary diatom record for the past 8 million years (BDP-98 Members 2001).

ECOLOGY.— The 19th century workers (e.g., Gregory 1854; Smith 1856; and Kitton 1870) can also be considered as the progenitors of diatom ecology through their observations and subjective inferences about environmental preferences of diatom taxa. The value of diatoms as ecological indicators of water quality became clearer during the 20th century as the central role of water chemistry in influencing diatom taxa abundances in lakes and rivers was recognised. Firstly, the value of diatom taxa for indicating trophic gradients was established (Kolkwitz and Marson 1908), then for salinity (Kolbe 1928) and pH (Hustedt 1937–39). Environmental applications followed with diatoms being used to monitor river water quality (e.g., Patrick et al. 1954). From the 1970s, multivariate methods were developed to quantify relationships among diatom taxa and environmental variables (e.g., Birks et al. 1990). Temperature was identified in the 1900s as an important descriptor of diatom abundances, but this was later discounted (see Patrick and Reimer 1966). Temperature has attracted renewed interest (e.g., Pienitz et al. 1995), but its value as a common predictor for diatom taxa remains questionable. The tight relationships of diatom taxa with their environment nevertheless makes these organisms highly suitable for 'ecological' monitoring of water quality (e.g., Kelly 2002) and of recovery responses following partial mitigation of water acidification (Monteith and Evans 2000). Irrespective of water quality relationships, diatom floristics alone can contribute to integrated biodiversity assessment of aquatic habitats (Flower 2001).

PALAEOECOLOGY AND PALAEOLIMNOLOGY.— Nipkow (1920), working in Lake Zurich, probably initiated the environmental reconstruction approach using sedimentary diatoms. The work of Deevey (1942) and Pennington (1943) then demonstrated the value of diatoms in sediment cores for palaeolimnology. With the advent of precise sediment dating, diatoms became powerful tools for reconstructing recent limnological change (e.g., Battarbee 1978). However, it was multivariate analysis of contemporary diatom-water quality data sets that made palaeolimnological reconstructions quantitative and numerically sound (e.g., Birks et al. 1990, Battarbee et al. 2001, Smol 2002). Robust models are now available for reconstructing a variety of environmental changes, including

pH (Birks et al. 1990), salinity (Fritz et al. 1991) and nutrients (Bennion 1994). More recent developments include the use of oxygen isotopes in diatom silica to infer lake level changes (Barker et al. 2001) and of diatoms to indicate lake enrichment by fish (Finney et al. 2000). On longer time-scales, changes in freshwater diatom species down long cores have enabled palaeoclimate inferences to be deciphered for several millions of years. For northern California, Bradbury et al. (1991) described climate driven floristic changes over the past 3 million years whereas the diatom record in Lake Baikal sediments now extends palaeoclimate information for more than 5 million years (Khursevich et al. 2001).

LIFE-CYCLES AND EVOLUTION.— Diatom life-cycles interested Victorian naturalists such as GHK Thwaites and W. Smith and, in Germany, L. Rabenhorst; they described several types of reproduction strategies and spore formation (e.g., Smith 1856). Specific interest in life cycles and reproduction was energised by MacDonald (1869) and Pfitzer (1869) following their observations on division and cell size change. Cell division continued to receive much attention in the 20th century, especially from the cytological perspective (e.g., Geitler 1927; von Stosch 1958). Much about morphogenesis of the silica cell wall was understood by the 1980s (Volcani 1978). Towards the end of the 20th century, the significance of life cycle strategies and of resting stages for ecology was being emphasised (e.g., Jewson 1992). Understanding more about the detail of diatom sexuality has enabled the recognition of within species ‘demes’ that are reproductively isolated and sympatric (see Mann 1984, 1999). The significance of the species unit in evolution is currently under debate (*ibid.*).

TAXONOMY AND SYSTEMATICS.— In the first part of the 20th century, taxonomic research increased as Hustedt (1909) began his remarkable half century of diatom publications. Floras specific to more exotic locations also increased and included such regions as South America and Siberia (Frenguelli 1923, Skvortzow 1937). As the number of diatom taxa proliferated and nomenclatural changes ensued, a recording system for diatom names and synonyms became necessary. Comprehensive catalogues, first by Mills (1933–35) and later by VanLandingham (1967–79) and Fourtanier and Kociolek (1999), followed. Major new freshwater diatom floras, which relied mainly on photographs rather than on drawings, began to appear in the 1980s, largely due to the work of Krammer and Lange-Bertalot (e.g., 1986). Interestingly, this period (the last two decades of the 20th century) and the 1840s were the two most prolific for naming new diatom genera (Fourtanier and Kociolek 1999). The advent of electron microscopy (EM) made fine resolution of diatom ultra structures possible (e.g., Helmcke and Krieger 1951, 1953–77) and led the way to the recent taxonomic revisions and the descriptions of new taxa with more structural details. These improvements also enabled ideas about diatom systematics to advance (Simonsen 1971) and, using Hennig’s ideas about cladistic analysis of shared derived characters, taxa were arranged into clades and depicted on cladograms to indicate genealogy (Williams 1985). Advances in molecular biology and in particular the polymerized chain reaction (PCR) for amplifying genetic base sequences, became available by the late 1980s. This permitted the analysis of genetic material, rather than of morphological characters, to be used to infer systematic relationships within the diatoms (Bhattacharya et al. 1992), leading to new ideas about diatom phylogeny.

NEW TAXON CONCEPTS.— With the rapid developments in ultra structure, molecular genetics and reproduction, it is unsurprising that taxon concepts began to change. The diatom species concept can be based on several views (see Theriot 1992, Mann 1999), but, suffice to say here, studies using living and fossil taxa will necessarily always be at least partly based on morphological evidence. Concepts about non-species level taxa also began to change since the 1970s (e.g., Ross and Sims 1973, Lange-Bertalot and Simonsen 1978, Williams 1985, Round et al. 1990). The trend to describe new genera has expanded especially for biraphid taxa. The recent literature contains an

array of these new genera, but it is littered with invalid diagnoses, conflicting designations and idiosyncrasies associated with particular authors. Molecular genetics offers a way of establishing relationships amongst taxa and to some extent validating morphotaxa (Medlin 1997). Gene sequencing work on diatoms has helped in the validation of *Aulacoseira* taxa (*cf.* Edgar and Theriot 2002), but it is unlikely that the technique can be applied to all the controversial morphotaxa in the foreseeable future.

REGIONAL FLORAS AND BIOGEOGRAPHY.— The proliferation of new names, especially in the past decade, has come at a time of renewed interest in diatom biogeography and biodiversity and in diatoms in remote areas and on islands. Whilst providing further evidence for widespread distributions of some taxa, the incidence of discontinuous distributions and endemism is becoming more widely appreciated. However, taxa with regionally restricted distributions were well known in the 19th century (see Cleve 1895/6). Endemism is a special case of restricted geographical distribution, and its high incidence in ancient Lake Baikal was recognised early in the 20th century (Dorogostaisky 1904; Skvortzow and Meyer 1928). Baikalian, Siberian (Palaeartic), relict and other endemic elements were then recognised in Baikal's benthic diatom flora. Also notable for regional endemism are the recent floras of the Patagonian region (Rumrich et al. 2000) and especially of the island of New Caledonia (Moser et al. 1998). As long ago as Smith (1856), the widespread distribution of many diatom taxa as compared with higher plants was recognized, and because many diatom taxa are undoubtedly cosmopolitan, this view has persisted (Lund 2002). However, a minority of diatom taxa do appear to have restricted regional distributions, the significance of which in systematics and biogeography is now being evaluated (Williams 1995; Kociolek and Spaulding 2000).

The diversification of diatom research indicated in Figure 1 suggests that the main lines of development are diverging through time. This impression is only partly justified because current interests in diatom biogeography, biodiversity, ecology and palaeoecology are interrelated. Furthermore, morphotaxonomy provides the essential foundation for these linked lines of research. Hence, there is a necessity to improve ways in which taxonomic convention is achieved and disseminated to all investigators, researching or otherwise. Diatom diversity in time and in space has and will make major contributions to both environmental science and to evolutionary studies. One current challenge is to provide a firm validated taxonomic framework for achieving these aims.

TAXONOMIC OBJECTIVES, PROTOCOLS AND INFORMATION DISSEMINATION

The science of taxonomy is the search for natural order; or is it? According to S.J. Gould, quoted in Håkansson (2002), taxonomy is about genealogy and the search for natural order, but the *International Code of Botanical Nomenclature* (ICBN, Greuter et al. 2001) states that the role of taxonomy is simply to supply a means of referring to a taxon and indicating its rank. The binomial system, developed by Linnaeus and upon which the ICBN is founded, was conceived as an aide memoir for individual taxa and this usage persists, despite other suggested systems (*cf.* Forey 2002). The binomial names and the higher taxonomic levels can usefully indicate something about phylogeny and taxon group affinities, but it is the role of systematics to elucidate biological relationships using homologous characters or genetic markers (Kitching et al. 1998).

In much applied diatom research, the relationships amongst taxa are usually of less importance than the relationships of taxa (usually species level or below) with environmental variables. Nevertheless, typification and the unambiguous designation of diatom taxa remains of fundamental importance in both systematics and environmental applications. Use of diatoms in time-space diversity studies is increasing and requires taxonomic consistency not only for attributional reasons

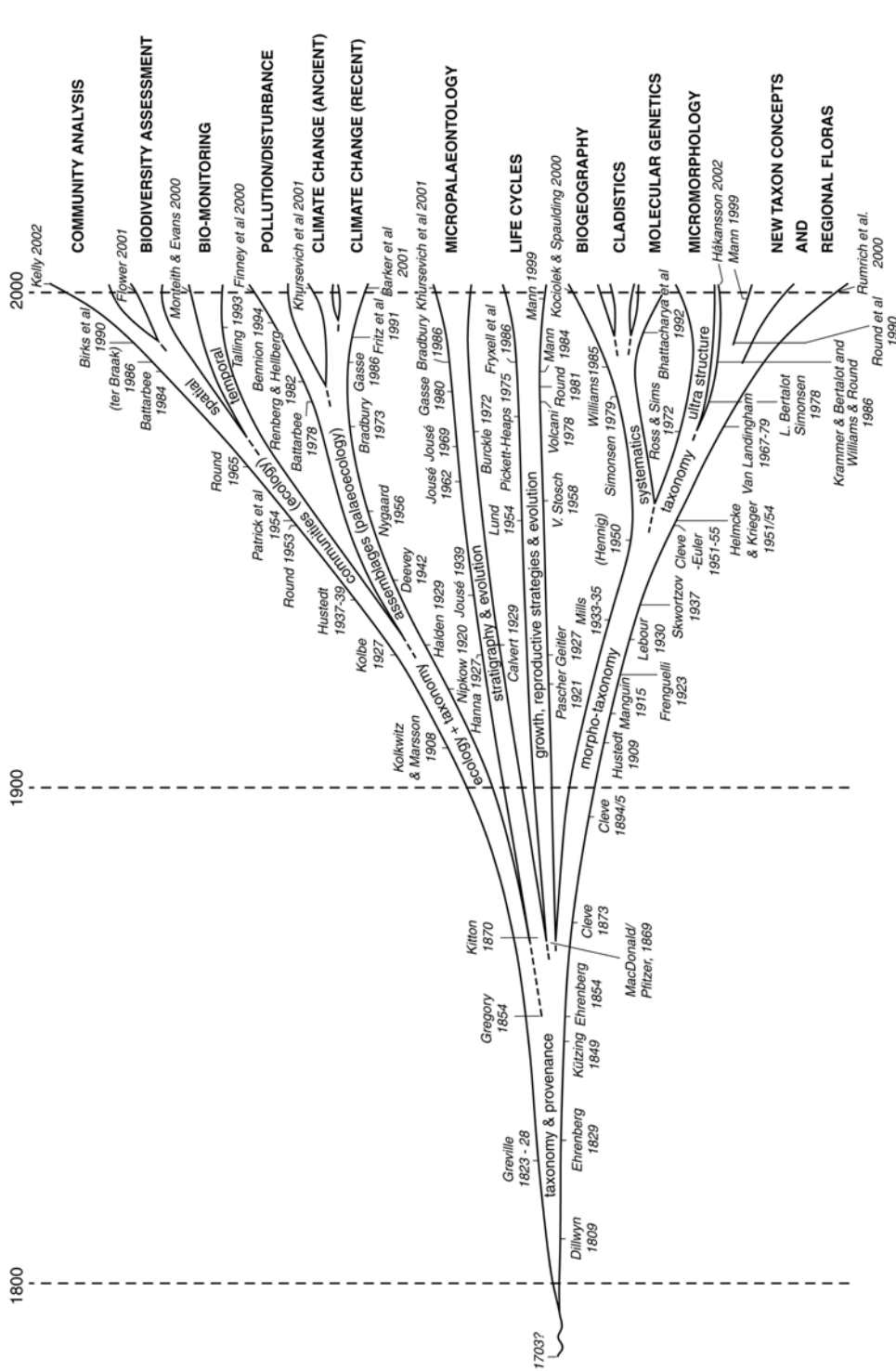


FIGURE 1. A summary diagram indicating trends in the diversification of diatom research during the past two centuries. Note that, i. several important and relevant but non-diatom references are indicated in parenthesis, ii. that the ~2000 AD array of diatom research areas is not exhaustive (see Stoermer and Smol 1999) and that the diagram does not indicate adequately the degree of interactions and facilitation between intra-subject areas.

but also for inter-flora comparisons. It is therefore wise to consider ways in which diatom taxonomy can be made more user-friendly, less 'messy' (Mann 1999) and less ambiguous to promote consistency at both local and international levels.

When a new diatom taxon is described, either at the variety (Flower 1989), species (Skvortzow 1937) or genus (Vyverman et al. 1998) level, typification should be relatively straight forward, assuming the author(s) have carefully checked the literature and relevant type material and obey the conventions (see Greuter et al. 2000). Formal typification is, therefore, regulated. In reality, however, the system is far from straight forward, and difficulties are often amplified when original investigations of particular taxa are translated into identification floras. There is currently a lack of coherence in diatom taxonomy that obstructs consistent and accurate species identifications. This is especially important for routine diatom counting within research consortia where light microscopy is principally used. Taxonomic inconsistencies amongst authors can obfuscate studies of both regional flora comparisons and species distribution patterns. There are several specific ways in which dis-harmonies can arise and these include:

1. The tendency to combine some taxa into rather broad species groups (e.g., Lange-Bertalot and Simonsen 1978) was reversed in the 1980s as many of the traditional species were subdivided into new genera (Williams and Round 1986; Round et al. 1990). This has led to conflicts in the literature (e.g., Kociolek 1998) and creating new genera by re-designation is currently on going (e.g., Round and Maidana 2001). New genera of course have merit where they better reflect different morphological groups but the ICBN definition of taxonomy suggests that some of the genus splitting effort may be questionable because whatever legitimate binomial is used the taxon characteristics are still amenable to systematic analysis.
2. The recognition of sympatric taxa based mainly on sexually incompatible subgroups or demes (*cf.* Mann 1999) raises the issue of describing and typifying many more diatom taxa. The tendency to subdivide conventional species taxa began earlier (e.g., Knudson 1953; Koppen 1975). Steps towards increased taxonomic resolution are generally welcomed by those using diatoms as environmental indicators because it can improve discrimination of environmental change (Flower and Battarbee 1985). However, if a system is adopted whereby reproductively incompatible demes are designated as species (Mann 1999), the great multiplication in names for within groups of (sympatric) taxa, all characteristic of the same environmental conditions, will contribute little more to understanding the role of environmental variables.
3. Increased taxonomic resolution and separating taxa by using details of ultra-structure is an important part of taxonomic research. However, when such details alone are used to discriminate taxa and especially at the generic level then difficulties for routine light microscopy can arise. Defining a taxon using single criteria, for example striae ultra structure (*cf. Kobayasiella micropunctata* [Germain] Lange-Bertalot) or separating two genera (*Cyclostephanos* and *Stephanodiscus*) using ultra structure detail of the external rimoportula (see Guerrero and Echenique 2001) is problematic and such ultra structure requirements led Camburn and Charles (2000) to abandon many taxonomic revisions in their work on the North American softwater diatom flora.
4. There is an increasing trend to use informal and/or (usually) inadequate descriptions of taxa in some floral and palaeoecological studies (e.g., Stevenson et al. 1991). Unverified book-form floras are extremely useful for opening up new areas for investigating diatom diversity (e.g., Rumrich et al. 2000) but they do not provide site-specific species inventories, and can obfuscate identifications by non-specialists. Informal designations can be a useful expedient, but lack of information can make widespread use of inadequately described taxa impossible (examples are many, such as *Frustulia* spec., *Cyclotella kuetzingiana* [agg.] which without accompanying images are of questionable value). Elsewhere, Gould (1989) used the term 'shoe-horning' to describe the tendency to fit potentially new taxa into pre-existing descriptions; undoubtedly this practise has caused difficulties in diatom identification and taxonomic comparisons especially amongst biogeographical regions (Williams 1995).
5. The existence of type specimens for all described taxa together with precisely catalogued synonymies should in a perfect world permit validation of problematic taxa. In practice, type specimen material is often inaccessible, unavailable, poorly conserved or is imprecisely identified. There are many cases where type

material in diatom herbaria is not mounted on glass cover slips (especially the older collections) so making observation difficult. For more modern material, type slides are often lodged in collections without any indication as to which is the type specimen. In mixed material this can make selection of the type subjective or at worst makes the preparation virtually useless for taxonomic validation purposes.

The practical problems of making type material more amenable are now being tackled as techniques to display and characterise individual specimens are ever improving. However, some taxon characteristics will always be questioned and the extents to which current literature conflicts can be rectified is debatable. Taxonomic research cannot, nor should it, be carried out by consensus, but focusing conflicts in the primary research literature would help reduce ambiguity for taxonomy users. Where integration of diatom distributions in time-space is needed, neither molecular nor cytoplasmology is likely to resolve current problems. Neglecting the value of morphotaxa in favour of other taxonomic tools is probably not yet a practicable option in most environmental work. Applied diatom research is growing and there is a pressing need to introduce more consensus into standard taxonomy. For example, European protocols for diatom monitoring of rivers (e.g., Kelly 2002) advocate use of particular identification floras, but this standardisation attempt is subjective. Some steps to reconcile current difficulties could include:

1. Abandon the binominal species name concept and develop a uninominal system (e.g., Ereshefsky 2001), so *inter alia* eliminating confusions caused by generic changes
2. Abandon the binomial naming system and develop an iconographic numerical coding system as is used for chrysophyte cysts (see Duff et al. 1995)
3. Continue with the current system but introduce a consensus platform into taxonomy in a way that reduces ambiguities and makes diatom iconographs and regional floras more accessible to end-users.

The latter step is in many ways preferable and would allow taxonomic research to continue its erratic individualistic course but permit progress towards a *coherent world diatom flora*. This flora, although very incomplete at first, could incorporate many existing works and be updated following decisions made through an authorised consensus forum. In reality, this practice has already been used to harmonise diatom taxonomy within several research consortia projects (Stevenson et al. 1991; Gell 1988; Camburn and Charles 2000). Internet and web site developments are beginning to make such harmonization procedures available on a wider scale. Nevertheless, local concepts and project driven agenda continue to dominate data sets. If AQC (analytical quality control) is to be achieved widely, a permanent over-arching central body or tightly co-ordinated group is needed. This would ideally result in a maintained web site database of images, descriptions and names for all known diatom taxa as well as provenance and environmental information.

Appropriate recording of taxonomic decisions and descriptions should follow ICBN protocols (Greuter et al. 2001) and type specimens must remain the 'gold standard' in diatom taxonomy. Using the virtually limitless capacity of web-based data sets, combined with ease of updating, makes their use attractive and considerable progress has already been achieved. See the following:

<http://www.algaterria.org>, for taxonomic baselines and original type material;
<http://www.calacademy.org/research/diatoms/>, for cataloging diatom names and synonymies;
<http://www.ualg.pt/adiac>, for diatom image identification aids;
<http://www.geog.ucl.ac.uk/ecrc/enclosed/darwin.htm>, for diatom images from Lake Baikal;
<http://www.geog.ucl.ac.uk/ukawmn>, for monitoring diatom taxa and water chemistry;
<http://www.craticula.ncl.ac.uk8000/Eddi>, for images and taxa with ecological optima.

This latter site is particularly useful for applied diatom taxonomy users because it combines taxonomy, ecology and provenance data for application to diatom assemblages in sediment cores so that environmental reconstructions of water quality can be made (Battarbee et al. 2001a).

Diatoms are key organisms for monitoring natural water quality in Europe and elsewhere, but major taxonomic contradictions need to be reconciled. Taxonomy does suffer from a lack of global organisation and planning generally (Alberch 1993), yet taxonomic consistency is a key necessity in diatom research (Kociolek and Stoermer 2001), and it is difficult to envisage how this can be achieved internationally without access to a coherent reference system. If a web-based global image database were developed, this would *inter alia* help harmonise diatom taxonomy (for international monitoring programmes, biogeographic comparisons, etc.). However, any such international system must be (1) comprehensive, (2) have long-term maintenance/up-dating mechanisms, (3) incorporate consensus into taxonomic designations, (4) be of sufficient quality to supersede the use of book-based floras, (5) conservative regarding the verification and incorporation of new taxa from the primary literature, and (6) able to use type specimens where possible. Even if these conditions are met, some problems specific to web sites remain. The e-data are free of peer review (although authentication through consensus management could minimise this criticism), they require permanent specialist staff, and some institutional internet-servers can impart loss of transmitted image quality. Where on-line databases provide environmental data for particular taxa, revisions involving splitting taxa could invalidate any ecological optima. However, updating synonymy dictionaries could help maintain database integrity.

DIATOM DIVERSITY

Diatom diversity is an attempt to describe all the variability present in the group and as such includes an array of factors such as life forms, genetics and morphology. For evaluating time-space diversity aspects in diatom distributional studies, morphotaxon concepts are probably the most useful in the first instance. Despite difficulties in diatom taxonomic harmonisation (above), there are two main ways to consider the diversity of diatom morphotaxa, according to:

1. Spatial scales — these vary from local, through regional to global scales and are modified primarily by water quality, substrata and by biogeographic factors.
2. Temporal scales — these vary from diurnal and seasonal changes through inter-annual and millennial trends to evolution and species replacements over geological time (stratigraphic facies).

The role of temporal and spatial scales on the occurrence and distribution of organisms has a large general literature (e.g., Rosenzweig 1995). Aquatic organisms received rather less attention although environmental change and fish speciation is well researched (Ruber et al. 1998) and Brooks (1950) made a careful global study of endemism in lakes. Both studies demonstrate the importance of morphotaxonomy in comparing systems but the former showed some morphology groups diverged from mDNA phylogeny. Nevertheless, morphotaxonomy remains the initial tool to investigate diversity. Lake Baikal is remarkable for both speciation and endemism (Kozhova and Izmesteva 1998), yet the benthic diatom diversity of Baikal requires thorough re-assessment (see Mann 1999, Flower et al. 2004). This lake can be used as an example for diatom diversity studies from several aspects.

LAKE BAIKAL AND TAXON DISTRIBUTIONS.— Lake Baikal has a large endemic component in its diatom flora. Most of the planktonic diatoms are endemic as are about half of the benthic taxa (according to Skwortzov 1937). This latter estimate will almost certainly need revising upwards (Mann 1999). Initial work on common shallow-water taxa around the lake (Flower et al. 2004) has not demonstrated any major distributional relationships associated with the three main sub-basins. Hence, these diatoms provide no evidence that the Lake Baikal sub-basins were isolated in the past (*cf.* fish populations in Lake Tanganyika [Ruber et al. 1998]). However, distributions of the large

conspicuous endemic taxa (mainly in the deep littoral) remain largely undescribed (Flower et al. 2004). The shallow water taxa appeared to be mainly cosmopolitan forms, but careful examination indicated that some of these too might have restricted distributions. Common *Synedra vaucheriae* (*sensu* Skvortzow) occurs in two characteristic forms in Lake Baikal. Similarly, in Lake Baikal, *Hannaea arcus* (*sensu* Skvortzow) seems to be a new species although it is not restricted to the lake (Bixby 2002).

The more conspicuous deep water benthic endemic taxa in Baikal, e.g., *Didymosphenia dentata* Dorog. are thought to be entirely restricted to the lake (Kociolek et al. 2000). A consideration of the lineage of gomphonemoid taxa suggests that this species evolved in Baikal (*ibid.*) but verification by fossil records is needed. The fossil record can offer definitive evidence about past taxon distributions and immigrations (*cf.* Bradbury 1986). Being able to draw conclusions about the origin of taxa has important bearings on interpreting modern distributions. This is why the Baikal Deep Drilling Project cores and the ~ 5 million years of sediment records are so valuable with many new species and even genera being described (Khursevich et al. 2001). Although this palaeo-work so far indicates *in situ* evolution of endemic planktonic taxa (*ibid.*), benthic diatoms often comprise up to ~10% of the sediment record and their stratigraphic records need evaluating. However, the Baikal record is so extensive that it may be difficult to find comparable sedimentary diatom facies elsewhere for evidencing ideas about speciation. Fossil material from the Vitim Plateau (NE of Lake Baikal) is lodged at the Baikal Museum (see Flower et al. 2004) and casual examination has indicated the presence of several current Baikal endemic taxa (*Aulacoseira baicalensis* and *Cyclotella baicalensis*), indicating wider Siberian distributions of these taxa in Pleistocene lakes. The situation regarding fossil benthic taxa is largely unknown.

LAKE BAIKAL AND DIATOM REGIONALITY.— Some common benthic diatom taxa in Baikal that appear to be rather different from the normal concept of the species form (e.g., *Synedra vaucheriae*) are probably restricted to the Baikal region. *Cymbella stuxbergii* and *Eunotia clevei* also occur in Baikal but have wider though still restricted distributions (Williams et al. 1999; Reid and Williams 2001). Other taxa were recognised by Skvortzow (Skvortzow and Meyer 1928; Skvortzow 1937) as having distributions restricted to Asia. However, many of the satellite lakes around Lake Baikal possess entirely different floras to that in Baikal, but there are important differences in water quality. Also, all the upland satellite lakes have only existed since the last glaciation. In Lake Bolshoie in the Khamar Daban Mountains above Lake Baikal, the surface sediment is dominated by the plankton diatom *Pliocaenicus costatus* v. *sibirica* (see Flower et al. 1998). This diatom genus is mainly known as a fossil, but the taxon is extant in a few sites in Siberia. With only a very few exceptions, the benthic diatom flora of Lake Bolshoie is otherwise very similar to oligotrophic upland lakes in the UK. The unusual distribution of this planktonic taxon seems to be linked more with a limited dispersal and biogeography rather than with special water quality preferences.

Regional issues regarding the relationships of Lake Baikal endemic diatoms with closely related taxa elsewhere can be examined using systematic analysis (*cf.* Williams 1985, 1996). This offers one way of placing Baikal's endemic flora in an evolutionary context by defining lineages. Quantitative comparisons using morphological characters possessed by both the endemics and closely related taxa offers an alternative to using the fossil record. This approach has been applied to *Stephanodiscus* in the USA (Theriot 1992) and to benthic *Tetracyclus* spp. (Williams 1996), but its application to Lake Baikal taxa is perhaps premature. Here the first priority is to provide a thorough inventory of the benthic taxa within the lake, to revise previously described taxa, and to provide an iconograph for the benthic taxa.

LAKE BAIKAL AND MEASURING DIVERSITY.— Assessing diatom diversity in a large lake such

as Baikal presents practical as well as theoretical difficulties. Size can be tackled by systematic sampling (*cf.* Flower et al. 2004), but measuring species diversity offers a variety of challenges. Biodiversity estimation has a considerable literature and an array of methods (Hawksworth 1995; Heywood 1995). Traditionally, a range of ‘biodiversity indices’ have been applied to multi-species sample populations and much information on species:area distributions has been generated (Rosenzweig 1995). Interestingly, however, diatom taxa do not seem to show the expected number and area relationship (Allen et al. 1999) probably for reasons of water quality (Flower 2001). Yet assessing diatom diversity is important and may benefit from an approach other than application of the traditional indices. Refinements for assessing diversity by taxic measures, such as the ratio of genera to species (see Hawksworth 1995), and by phylogenetic methods to reconcile species numbers with genealogical divergence (Williams 1996), are interesting concepts. However, like molecular genetics, using these techniques to address general issues of diatom occurrences and abundances in Lake Baikal and many other poorly described areas must *inter alia* await an adequate base in morphotaxonomy.

No single diversity measure can capture all aspects of ‘diversity’, and at sites such as Baikal, measures that ignore the significance of endemism are incomplete. However, getting taxonomy to the level where Baikal’s endemic taxa can be validated in routine diatom analysis remains a major challenge (Flower et al. 2004). Identifying any within hot spot regions of Baikal for endemic taxa is not yet feasible. Estimates of species richness are, however, relatively easy to make, if consistency in morphotaxon identifications is maintained rigorously (*ibid.*). Partitioning taxa into rare and non-rare categories is an additional measure of ecological quality for a particular site or habitat (see Gaston 1994). Most diatom samples can be characterised by a few common species and a limited number of rare taxa (van Dam 1982), and for Baikal the rare taxon category often captures some of the conspicuous endemics. For shallow water epilithon samples, taxon abundance distributions (examples in Fig. 2) were plotted for 51 stations around Lake Baikal (see Flower et al. 2004). There are considerable variations between abundances of common and less common taxa in each sample. Rather than make assumptions about these distributions (*cf.* Rosenzweig 1995), it is instructive to consider the rare taxa alone. Rare taxa can be defined in various ways (Gaston 1994):

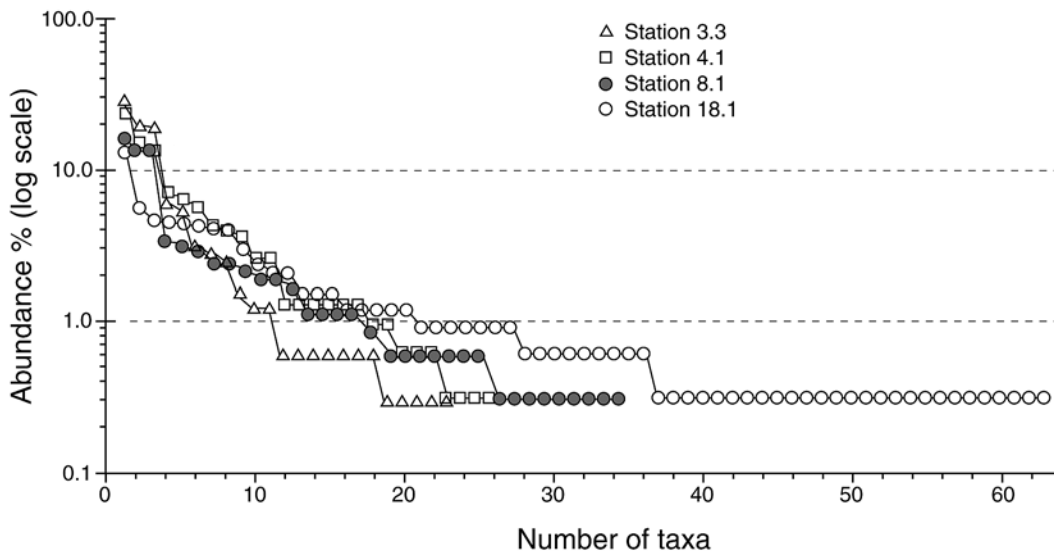


FIGURE 2. Relative abundance rank curves for diatom taxa in several shallow water epilithon samples selected from collections made from 51 sampling stations around Lake Baikal in 1997/98 (see Flower et al. 2004).

they occur at very few sites (either locally or internationally); they are always found at low abundances; or they may be perceived as rare because of identification problems. For these Baikal samples, the 'rare' taxa are those with frequencies of <1% in a fixed count of 300 valves (see Flower et al. 2004).

The rare taxon data can be used to generate a simple index that places an emphasis on the proportion of rare taxa in samples. The relationship between diatom taxa occurrences and abundances is usually log-normal (van Dam 1982), and it is implicit in the log series of species-abundance distributions that the total number of species in a sample is proportional to the number of uncommon or rare species (e.g., Pielou 1974). Nevertheless, the precise relationship between abundant and rare taxa may be of potential value in assessing the relative ecological value of a site, sub-sites or a group of sites. An index of diatom rarity is indicated below. Where n is the number of sub-samples and 1 indicates the population or region of interest, V = the total number of valves counted and z is the number of taxa present at frequency abundances of 1% or less.

A simple diatom rarity index:

$$\text{Diatom rarity index} = 1 - \left(\frac{\sum_{i=1}^n V_i}{\sum_{i=1}^n V_i + \sum_{i=1}^n z_i^2} \right)$$

For sample 1

This index should be <1 assuming rare taxa are always present and the term 'rare' is subject to the count constraints imposed during sample analysis. There is, of course, a substantial number of taxa that are so rare that they will not be captured by this modest count total. In fact, cumulative counting of one Baikal sample (34.1) indicated that only above a count total of 650 valves did the count/taxon curve begin to approach the asymptote. Nevertheless, by carefully fixing the count total, the index can be used to make within lake comparisons amongst communities (Fig.

TABLE 1. Diatom rarity index values (see text) calculated from diatom taxon abundances in shallow water epilithon samples collected from around Lake Baikal (1997/98) and summed to represent each shore zone in each of Baikal's three main basins (WSB=West shore South Basin, WMB = West shore Middle Basin, WNB= West shore North Basin, ENB = East shore North Basin, EMB = East shore Middle Basin and ESB = East shore South Basin).

<i>Shore Zone</i>	<i>WSB</i>	<i>WMB</i>	<i>WNB</i>	<i>ENB</i>	<i>EMB</i>	<i>ESB</i>
	0.25	0.21	0.36	0.46	0.52	0.80
	0.55	0.32	0.40	0.49	0.64	0.60
	0.52	0.18	0.25	0.29	0.66	0.55
	0.14	0.46	0.52	0.49	0.78	0.43
<i>Station scores</i>	0.40	0.49	0.49	0.36	0.60	0.29
	0.55	0.21	0.46	0.40	0.66	0.43
	0.43		0.43	0.43		0.49
	0.32		0.46			0.32
			0.86			0.43
<i>Mean scores</i>	0.39	0.31	0.47	0.43	0.64	0.48

3) and amongst regions (Table 1). Increasing the standard count size will produce more taxa per sub-sample, but when a large number of samples required for comparison, the key factor is to keep the total count size constant.

LAKE BAIKAL AND DIATOM BIOGEOGRAPHY.— The large number of endemic taxa in Lake Baikal is also of interest to ideas about ubiquity and the global distributions of micro-organisms

(cf. Finlay and Clarke 1999). Round (1981) indicated that freshwater algal taxa were more widely distributed geographically than marine taxa but that some freshwater diatoms (*Asterionella*, *Stephano-discus*) were restricted by water quality. Round (1981) also noted that distinctive distributional patterns existed but that studies were very incomplete. Diatom endemism in Baikal offers a major challenge to ideas about ubiquity. The diatom flora of Baikal is demonstrably able to resist invasions and displacement by cosmopolitan species (which generally predominate in small lakes around Baikal). The recent fossil record shows continuous domination by endemic taxa (Flower et al. 1996). Elsewhere and against conservative ideas about diatom distributions, regional diatom endemism is well recognised, in Australasia at both genus and species level (Tyler 1996) and on some oceanic islands (Moser et al. 1999).

There appear to be several types of endemism in Baikal arising from recent *in situ* speciation or preservation of relict taxa (neoendemics and palaeoendemics *sensu* Cronk 1992). Forms of *Navicula lacus-baicali* (Mann 1999) are probably recent whereas some species of *Tetracyclus* (Williams et al. 2002) have a substantial geological record. In the fossil record, *Aulacoseira baicalensis* seems to post date many endemic *Stephanodiscus* and *Cyclotella* taxa (Khursevich et al. 2001). *Eunotia clevei* and *Pliocaenicus costatus* are examples of taxa that are not endemic to Lake Baikal and its environs but nevertheless display distributions that are more restricted today than in the recent geological past. In some continental areas elsewhere, the impact of past glaciations were probably of paramount importance in obliterating centres of endemism and diminishing former wider distributions of ancient taxa. It is notable that much of southern Siberia, like most of Australasia, was not directly affected by major Pleistocene ice sheets. Those lakes that have persisted through major environmental changes are more likely to have retained ancient taxa (see Brooks 1950). Conversely, palaeoendemics seem absent in the post-glacial Great Lakes of North America. The contemporary endemic taxa of Lake Baikal seems largely restricted to the Baikal region and have been unable, possibly through poor dispersal mechanisms or lack of ecological niches, to expand elsewhere.

Making floristic comparisons amongst different regions to delimit the distributions of particu-

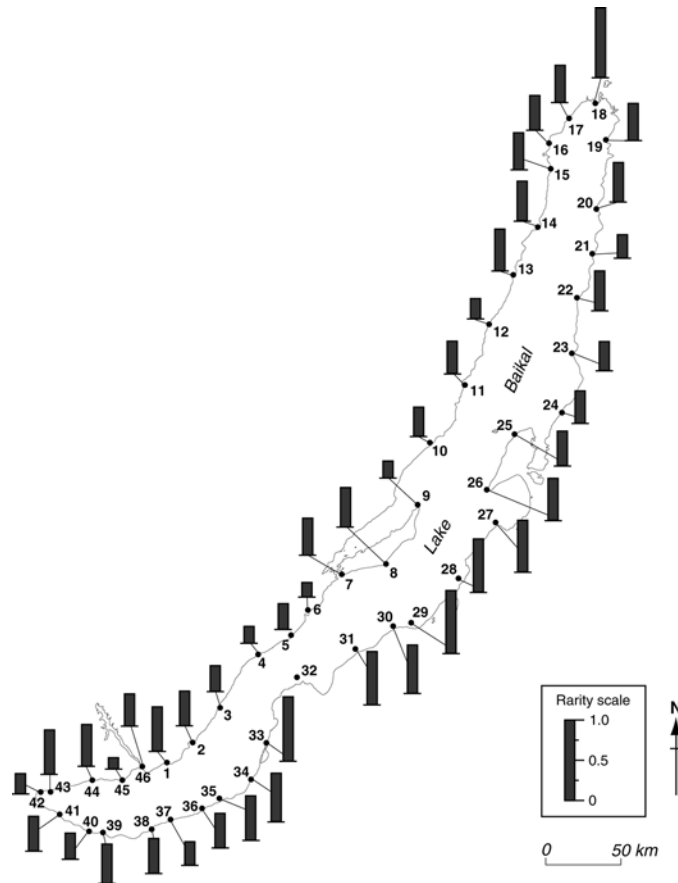


FIGURE 3. Diatom rarity index (see text) values as histograms calculated from shallow water epilithon samples from Lake Baikal (collected in 1997/98) from around the lake (see Flower et al. 2004).

lar taxa can demonstrate clear biogeographic patterns for some taxa (Williams 1995; Kociolek and Spaulding 2000). However, making quantitative comparisons using communities is more difficult, not least because of differing taxonomic concepts and methodologies. Nevertheless, this approach is needed to establish precise taxon based floristic distances between communities or assemblages (see Flower et al. 1997) and to explore the proportional mix of cosmopolitan and endemic or otherwise restricted taxa at a particular site or location. For an extreme and preliminary quantitative comparison of two regional floras, Correspondence Analysis (see Jongman et al. 1987) of combined data was undertaken. These data comprised, (1) 51 samples of shallow water diatom epilithon samples from around Baikal and, (2) 28 samples of epilithon and surface sediment diatoms from the Falkland Islands (R. Flower, unpublished) on the opposite side of the globe (Fig. 4). Sampled substrata were not constant but other sampling and counting variables and taxonomic concepts were consistent because both data sets were enumerated by the same analyst. The most noticeable feature of this initial and crude analysis is that the amount of floristic variation in all the Baikal samples is very much less than that displayed by the 28 individual water body samples on the Falkland Islands. Also, there were only seven taxa common to both data sets and included such cosmopolitan species as *Cocconeis placentula*, *Navicula cryptocephala* and *Staurosira construens*.

The major floristic differences between Baikal and the Falklands samples clearly do not offer an unequivocal test of a biogeographic hypothesis for diatom distributions. Diatom taxa are particularly good indicators of water quality and are used by palaeolimnologists essentially for this reason. We would, therefore, not

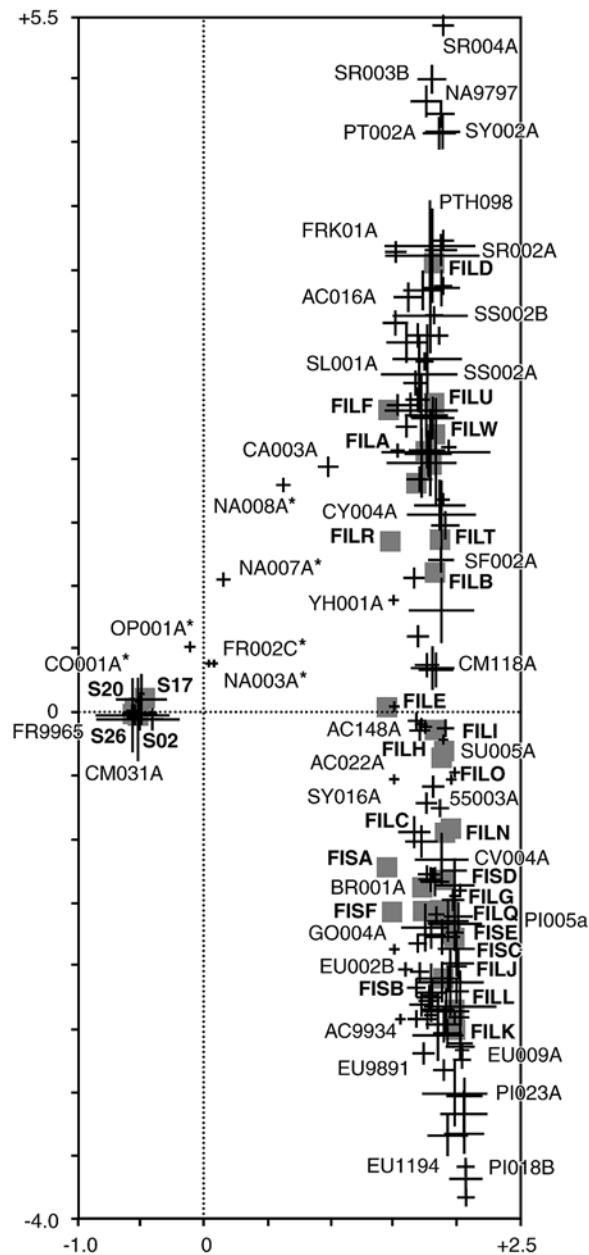


FIGURE 4. Correspondence analysis ordination of a combined data set of diatom taxa (shown as selected alpha-numeric taxon codes and crosses proportional to frequency abundances) and sites (shown as squares and coded with a bold S or FI prefix to indicate Siberian Lake Baikal or Falkland Islands sites). Note, floristic variation is relatively small for the Baikal sites and that few taxa are common to both data sets (see text).

expect ubiquity in species distributions: acidiphilous or alkaliphilous taxa do not commonly occur in calcareous or in siliceous geological regions respectively. Falkland Islands' inland waters were mainly acid. Hence ecological factors could explain most of the taxon differences in the two regions tested and very few, if any, of the Falklands Island diatoms are endemic (as on other glaciated islands, Foged 1964). On the other hand, the extremely basic rocks, unusual water quality and geological time has produced many new species in New Caledonia (Moser et al. 1999). From these few observations it is likely that the incidence of diatom endemism is affected by a variety of factors including, (1) longevity of habitat, (2) extreme environments or environmental instability (palaeoclimate or geological change), (3) proximity to centres of evolution and, perhaps, (4) the nature of the community founder species.

Evidence from numerical comparisons of inter-continental floras is scarce, but higher plant diversity (species number in disjunct genera) is higher in eastern Asia than in North America and seems mainly caused by physiographical heterogeneity in conjunction with climate change (Qian and Ricklefs 2000). Explanations of the spatial differences in diatom distributions must also involve climate, but heterogeneous geochemical conditions are probably more important locally. Causes of large scale differences in diatom distributions can be polarized into two main stand-points. One is based primarily on vicariance biogeography and the existence of regional floras arising from evolutionary events. The other is based on an assumption that taxa have global distributions that are punctuated by ecological conditions. Distributional patterns in the global diatom flora — at least for inland waters — seems to be the result of various combinations of these influences as modified by local ecology and sympatric events. However, a fuller picture of global patterns and trends in diatom diversity cannot be made until consistent floristic comparisons and time and space evaluations are undertaken for more biogeographic regions.

SOME CONCLUSIONS

Ecology, evolution, biogeography, systematics and palaeontology have drifted apart during the 20th century (Ricklefs and Schluter 1993) and a similar trend has occurred within diatom research. Recent major developments in the latter regarding species concepts, speciation, life cycles and molecular biology have all made important contributions but, for the foreseeable future, morpho-species concepts will dominate environmental studies where living and fossil taxa are used. Where concepts about diatom taxonomy and taxon designations have changed markedly, some ambiguities have arisen that give current cause for concern. Reconciling ever-finer resolution of taxa combined with nomenclatural revisions threaten to out-strip the capabilities of end-users (the ecologists, palaeoecologists). Whilst debate is necessary, the current lack of coherence in diatom taxonomy is now hindering some areas of applied diatom research, especially where light microscopy is routine. Introducing more consensus in diatom taxonomy at a level that is accessible to end users is advocated. Developing a more unified approach to accessing diatom type material and nomenclature, regional floras and ecological information through the Internet medium is one promising way of improving taxon designations and identification.

Diatom ecologists generally use the taxonomy available in published floras to identify taxa so that relationships between diatoms and measurable environmental variables can be discriminated. Diatom species distributions are not however always a predictable response to water quality and *inter alia* biogeographical factors can play an important role in the provenance of some taxa. The interplay of biogeographical and water quality factors as an influence on discontinuous distributions of diatom taxa requires the attention of both ecologists and systematic taxonomists. Any 'marriage of necessity' between ecologists and taxonomists (*sensu* Kociolek and Stoermer 2001) that

would help tackle the central issue of explaining diatom species distribution patterns on time-space scales that vary from ancient to modern (e.g., Khursevich et al. 2001) and local to continental (e.g., Fig. 4) is desirable. However, disentangling the causes of these patterns will require consideration of speciation processes, dispersal mechanisms, ecological tolerances, biological interactions and of environmental change. The existing extensive and essentially morphotaxonomic diatom reference system will doubtless endure as the foundation by which research proceeds and unifying and extending this database must facilitate progress.

Despite some of the current difficulties in diatom taxonomy and its relationship with ecology, many endemic or regionally restricted diatom taxa are well defined and offer compelling evidence for the existence of biogeographic factors. They are an important aspect of global aquatic diversity assessment and maintaining global biodiversity has become paramount as anthropogenic changes proceed at unprecedented rates. Sites such as ancient Lake Baikal are hot spots for aquatic diversity and the planktonic and benthic diatom communities are largely endemic or otherwise restricted. Diversity can be measured in a variety of ways and morphotaxa concepts are usually the primary tool to investigate species time-space changes in the environment. However, where taxonomic knowledge is incomplete, concepts about species richness and rare taxa can offer a pragmatic ways of appraising the composition of diatom communities. Such measures cannot substitute for species level inventories or assess the significance of genealogical relationships within communities. Nevertheless, an optimal combination of these measures should help floristic comparisons and define community characteristics. Irrespective of taxonomic discrepancies, diatoms are increasingly important for setting baselines and references conditions and evidencing environmental change through multi-scale studies of their distributions and relationships. These are all essential parts of global biodiversity assessment in aquatic ecosystems.

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