

Diatoms
Taxonomy and Ecology:
A Marriage of Necessity

Proceedings of a Workshop
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Edited by

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**Participants in the Workshop
Taxonomy and Ecology: A Marriage of Necessity
held 23–27 October 2002 in Kulice, Poland**

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Preface

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The workshop, “Diatom Ecology and Taxonomy: A Marriage of Necessity,” was convened by J.P. Kociolek and A. Witkowski, from 23–27 October 2002 at the University of Szczecin’s Conference Center in Kulice, Poland. The workshop was sponsored by the California Academy of Sciences (San Francisco), University of Szczecin (Poland), Alexander von Humboldt Foundation (Germany) and Carl von Ossietzky University (Oldenburg, Germany). A total of 48 participants from Albania, Belgium, Belarus, Croatia, Denmark, Germany, Hungary, Ireland, Macedonia, Poland, Russia, Spain, Sweden, Ukraine, United Kingdom and USA were in attendance.

A number of invited speakers raised issues related to the workshop’s title, with regard to fossil and recent diatoms, and freshwater, estuarine and marine habitats. Viewpoints of those focused primarily on taxonomy and ecology were presented. The plenary presentations provided the springboard for lengthy facilitated discussions. The areas of overlap and separation were discussed, and topics that might promote synergy for the two disciplines explored. The papers comprising this volume represent most of the invited speakers at the workshop. The workshop could serve as a model for future discussions by diatomists across scientific disciplines.

The organization of and ongoing support for the Workshop by faculty, staff, and students of the University of Szczecin was above reproach. Their efforts assured our workshop’s ultimate success, and the attendees were both aware of and greatly appreciated the hard work that went into dealing with the workshop’s many practical and impractical elements.

Taxonomy and Ecology: Further Considerations

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In this overview, points of the initial publication by Kociolek and Stoermer are reviewed and expanded upon, noting the gulf between the disciplines of taxonomy and ecology and the modest ways the two areas currently intersect. Some research areas for synergy are suggested. Previously published data on diatom community structure are assessed in terms of decreasing taxonomic resolution. The varying levels of taxonomic refinement are compared to the original data, and argue for the finest degree of taxonomic resolution. The final session of the workshop is summarized related to the desirability and implementation of on-line taxonomic resources, especially floras.

The publication of our paper on the need for a marriage of diatom taxonomy and ecology (Kociolek and Stoermer 2001) prompted a wide range of comments and responses directed to us, some constructive, some not, and was one of the most requested either of us have ever published. It also prompted the gathering/workshop, which generated the series of papers included herein. The workshop was developed to foster dialogue on the general topic of describing and promoting ways for taxonomists and ecologists to collaborate. Despite some initial cultural hurdles, by the end of the workshop participation by the entire group was open, honest and constructive.

The present report has three objectives: First, it reviews, amplifies and (hopefully) clarifies some of the points made in the earlier paper related to integrating taxonomic and ecological studies. Second, an example is based on previously published data showing the relationship (and dependency) on ecology and relative to fine- and coarse-grained taxonomy. Lastly, one of the areas of extensive discussion that coalesced the opinions of many in the final workshop session is summarized and discussed; namely the potential and desirability of flexible, on-line taxonomic products, particularly floras.

TAXONOMY AND ECOLOGY—MORE DIFFERENCES THAN SIMILARITIES

Tradition is one of the greatest barriers separating the disciplines of Ecology and Taxonomy. The number of strictly taxonomic (versus morphological/ultrastructural) papers in the diatom literature is relatively modest, compared to the number of papers with ecology as a focal point. And the breadth of places for publications of ecological papers far exceeds the relatively smaller number of publication venues for taxonomic works. Taxonomic works rarely contain any specific ecological data—cursory summaries are usually the most offered. When included, ecological data have rarely been used to substantially forward our knowledge about the taxonomy of specific entities. Many ecological studies use taxonomy as a means to an end, but the species lists (usually containing many errors in names and authorities) usually suggest a continuation of previous approaches (and errors) rather than any serious analysis of taxonomic results (though many more diatoms are being seen by ecologists than taxonomists). Finer-grained taxonomy and the current state of flux in fresh-

water diatom nomenclature appear to offer difficult hurdles for ecologists. The formal structures of our discipline help to perpetuate the gulf between taxonomists and ecologists. At meetings of the international society, oral presentations are arranged to separate presentations by ecologists and taxonomists; the two groups usually meet as they pass by each other going into/out of their respective sessions.

The divide between taxonomy and ecology is reflected not only in the outright absence of taxonomists in the area of ecology, but in the approaches the two groups have to taxonomy. Although, of course, there are exceptions to the stereotypes/generalizations I offer here, I would suggest that the goal of most taxonomists is what I call “correct taxonomy,” that is trying to understand the morphological variability through the ontogeny of the cell and cell cycle (Kocielek and Williams 1986), what the circumscribed taxon should be called in the context of other taxa. Assignment of the taxon under study within the Linnaean hierarchy not only offers an information storage-retrieval system (so that other data, including ecological data) can be compared and used in a wide range of studies, including comparative autecology, comparisons across space and time, alien species), but also predictive value so the hierarchy system should express the phylogenetic/evolutionary position of the taxon (Kocielek 1998). These typical taxonomic studies are usually organized and presented in stylized formats and with jargon, which appear arcane to ecologists. The back-and-forth that can result from such studies suggest more uncertainty than certainty (recall the numerous exchanges related to the proposal of the genus *Naviculadicta* — e.g., Moser et al. 1995, Kocielek 1996). The result of these debates is a wait-and-see stance from ecologists using the taxonomy, such that the impact of much of the primary literature is delayed unnecessarily. Even when the fervor of discussion has died down, and an approach has more or less been settled upon, some have found it difficult to embrace the consensus (e.g., Camburn and Charles 2000).

To achieve their research agenda, ecologists, on the other hand, focus attention on “consistent” taxonomy, making sure that the entities they encounter in the light microscope can be reliably applied to their respective group, hopefully representing some “real” biological entity. Ecologists face the challenge to avoid “shoe-horning” specimens into already-established taxon names, and to ensure their “consistent” grouping have some biological reality.

Another way taxonomists and ecologists are separated relates to their search for places to conduct their research programs. Ecologists, for the most part, seem to be attracted to systems that have been in some way impacted, usually by the activities of human beings. A driver towards these systems and their related questions may be funding, as governments (locally, regionally, nationally and internationally) seek understanding to possible impacts and remediation required. Taxonomists tend to seek out non-impacted situations to explore and conduct their research programs. It is usually these places that support native and undescribed taxa (e.g., Moser et al. 1995, 1998; Metzeltin and Lange-Bertalot 1998), and it has been suggested that an understanding of the biogeography of freshwater diatoms has been clouded by the impacts of the human species on the distribution of species (Kocielek and Spaulding 2000). Due to human disturbance, taxonomists are less likely to encounter species that might bear on the questions they pose. Thus, an issue so basic as where we work helps to divide taxonomists and most ecologists. It should be noted, however, that as ecologists seek to understand “pristine” or “unimpacted” situations, and the structure of communities found in those types of habitats, partnering with taxonomists in the investigation of those systems would be a wonderful setting for the marriage of taxonomy and ecology.

A common concern of those using diatoms to estimate water quality is the (in)ability to identify every individual encountered in their slides/counts. Many times the specimens are rare, or in cases of taxa where the entire population has nearly synchronized division, thus encountering many individuals, but who occupy a narrow range of variation. It is well documented that two or more

distinct taxa may overlap morphologically, especially at the small end of the size range (Stoermer et al. 1986; Theriot and Ladewski 1986; Geitler 1932). Thus, although it may be impossible for the practising ecologist to undertake studies to understand the full range of variation in a taxon (thus providing insights into the identity of the taxon), it must also be realized that closely related species share many similarities (hence the close evolutionary relationship), and thus it might be difficult to separate/identify isolated individuals. An analogy might be the difficulty to identify deciduous trees to species when leaves are off the tree, but easier when leaves and flowers are out.

Thus, whereas the current state of ecological and taxonomic research is of two nearly independent fields, their interrelationships are at best utilitarian, with any dependency in terms of relationships driven by taxonomists supporting ecologists with flora (rare, actually) or serving as “hired gun” identifiers of individual or groups of species.

We believe that this separation of disciplines does not have a long, sustainable future. Integration of the two disciplines is a goal worth pursuing, with the payoffs of a more rigorous, robust enterprise (more students, more positions, research impacts and more funding) that approaches answers to questions posed by ecologists and taxonomists. Areas that are and should integrate these approaches include paleolimnology-done successfully, evolutionary ecology (especially of ecologically pristine areas), conservation biology, co-evolution, and biogeography.

TAXONOMIC RESOLUTION AND ITS IMPACTS ON ECOLOGICAL INTERPRETATIONS

The interplay between taxonomy and ecology perhaps finds no closer relationship, the marriage is not more intimate, than the use of diatoms in the assessment of ecological conditions. A myriad of approaches has evolved since the early ideas of Kolkwitz and Marsson (1908) to apply diatoms to understanding freshwater ecology in particular, especially focused on human impacts (pollution). Excellent overviews of these approaches can be found in Patrick and Roberts (1979), Cholnoky (1968) and Stoermer and Smol (2001).

In quantitative approaches, early workers suggested robust analyses (robust in the sense of statistics/mathematical models) required enumeration of thousands (in some cases tens of thousands) of valves to achieve reliable results (e.g., Patrick et al. 1954; Hohn 1961; Hohn and Hellerman 1963; Patrick 1968). Since the days of these extensive identification and enumeration methods, efforts were made to save time in the analysis of samples and to essentially reduce/minimize cost (because many of these studies were by now in the U.S. being funded by government agencies) but derive “correct” assessments of water conditions. This has led to a variety of approaches where counts are reduced to a certain number of valves (e.g., Stevenson and Pan 2001; 300–600/sample seems to be settled upon without too much debate) or until no new taxa have been encountered (e.g., Charles et al. 2002; assuming richness plays some role in the analysis/understanding of water quality).

Although the effort has focused on reducing the number of valves to count (yet still achieving a correct assessment), few studies have looked at ways to reduce taxonomic resolution and still achieve a “correct” understanding of water quality. In other words, does all the “fuss” made by taxonomists to identify and separate taxa at the level of species, variety and form (and this is being done with renewed vigor-e.g. Lange-Bertalot and Metzeltin 1996; Reichardt 1999 as good examples) contribute in a substantive way to our understanding of water quality?

In the era when scientists were exploring myriads of ways to apply diatoms to water quality studies, complete data sets were often published (e.g., Hohn and Hellerman 1963; Patrick 1968; Patrick and Roberts 1979), as opposed to the summary statistics and data plots seen in most “modern” analyses.

To explore whether taxonomic resolution, i.e. coarse or fine-grained taxonomy, mattered in the interpretation of ecological data, we selected data sets published by Patrick (1968) on Darby Creek, Pennsylvania (USA). For each data set, we calculated species richness and Shannon-Wiener diversity, for three conditions, including the data set as presented (with identifications made by Patrick and finest taxonomic resolution presented in the paper at that time (what we have termed “ALL”) and two levels of reduced taxonomic resolution. In one case, we subsumed all subspecific epithets into the species (“SPECIES”) and then all species and subspecific epithets subsumed into genera (“GENUS”). The richness and diversity calculations were then ranked for each of the 8 stations based on the three different levels of taxonomic resolution. We then made the assumption that the complete or “ALL” dataset, with the finest level of taxonomic resolution most closely representing the relative ecological conditions of the eight samples. We then compared these relative relationships with those derived from approaches with more coarse-grained taxonomies, to see how well they might serve as proxies for the finest-level of taxonomic resolution. We should note here that

TABLE 1. Comparison of Richness and Shannon-Weiner Diversity including all taxa.

Sample	Richness	Diversity
Sample 1		
ALL	105	4.6555
SPECIES	88	4.3523
GENUS	22	2.6942
Sample 2		
ALL	104	4.6967
SPECIES	88	4.4337
GENUS	21	2.7002
Sample 3		
ALL	103	4.9641
SPECIES	87	4.6687
GENUS	20	2.8527
Sample 4		
ALL	111	4.6429
SPECIES	95	4.366
GENUS	23	2.5449
Sample 5		
ALL	108	4.8087
SPECIES	94	4.4895
GENUS	21	2.776
Sample 6		
ALL	101	4.8705
SPECIES	85	4.5502
GENUS	21	2.747
Sample 7		
ALL	107	4.7037
SPECIES	92	4.3687
GENUS	19	2.6464
Sample 8		
ALL	112	4.517
SPECIES	98	4.2581
GENUS	23	2.4761

the finest-grained taxonomy applied in 1968 probably does not represent the finer distinctions made today.

In Table 1 are listed the richness and diversity measures for the eight samples provided in Patrick (1968) for “ALL,” “SPECIES” and “GENUS.” The eight samples are then ranked from most to least rich, and from most to least diverse in Table 2. The richness and diversity measures are provided for pennate taxa only in Table 3. Ranking of the pennate taxa measures is provided in Table 4.

The data suggest that the samples were relatively rich, in the data including pennate and centric taxa, with total taxa numbers ranging from 101 to 112 in the ALL samples, 84-98 taxa in the SPECIES samples and 19-23 taxa in the GENUS samples. Diversity ranged from 4.5170 to 4.9641 in ALL samples 4.2581 to 4.6687 in SPECIES samples and 2.4761 to 2.8527 in the GENUS samples. In the rankings, sample 8 was the richest in all calculations, whereas sample 6 (ALL, SPECIES) and sample 7 (GENUS) were poorest in terms of taxa. Interestingly, in terms of diversity, sample 3 was most diverse in each of the three sample calculations, whereas sample 8 (the richest in terms of number of taxa) was the least diverse in all three calculations. Assuming the ALL samples best approximated the

TABLE 2. Ranking of samples by ALL, SPECIES only and GENUS only for Richness and Shannon-Weiner Diversity with all taxa included. “#shared” shows the number of rankings that are in agreement with All taxa.

Richness All	Richness Species	Richness Genus	Diversity All	Diversity Species	Diversity Genus
8	8	8	3	3	3
4	4	4	6	6	5
5	5	1	5	5	6
7	7	5	7	2	2
1	1	6	2	7	1
2	2	2	1	1	7
3	3	3	4	4	4
6	6	7	8	8	8
#shared with ALL		4 out of 8		6 out of 8	3 out of 8

“true” condition, SPECIES rankings of richness matched exactly the ALL calculations, whereas GENUS matched only 50% of the rankings. For diversity

TABLE 3. Comparison of Richness and Shannon-Weiner Diversity including pennate taxa only.

Sample	Richness	Diversity
Sample 1		
ALL	94	4.3976
SPECIES	79	4.0794
GENUS	19	2.2934
Sample 2		
ALL	95	4.4671
SPECIES	80	4.1681
GENUS	18	2.2619
Sample 3		
ALL	95	4.7224
SPECIES	79	4.389
GENUS	17	2.4439
Sample 4		
ALL	102	4.3962
SPECIES	86	4.0926
GENUS	20	2.1704
Sample 5		
ALL	100	4.6403
SPECIES	86	4.2801
GENUS	18	2.4285
Sample 6		
ALL	93	4.6821
SPECIES	78	4.3588
GENUS	18	2.578
Sample 7		
ALL	99	4.4825
SPECIES	83	4.0871
GENUS	16	2.2709
Sample 8		
ALL	102	4.262
SPECIES	88	3.9695
GENUS	20	2.0455

TABLE 4. Ranking of samples by ALL, SPECIES only and GENUS only for Richness and Shannon-Weiner Diversity with pennate taxa only included. “#shared” shows the number of rankings that are in agreement with All taxa.

Richness All	Richness Species	Richness Genus	Diversity All	Diversity Species	Diversity Genus
8	8	8	3	3	6
4	4	4	6	6	3
5	5	1	5	5	5
7	7	2	7	2	1
2	2	5	2	4	7
3	1	6	1	7	2
1	3	3	4	1	4
6	6	7	8	8	8
#shared with ALL	6 out of 8	2 out of 8		4 out of 8	3 out of 8

in ALL, 79–88 in SPECIES and 16–20 in GENUS. Diversity ranged from 4.2620 to 4.7224 in ALL, from 3.9695 to 4.3890 in SPECIES and from 2.0455 to 2.4439 in GENUS. In the rankings, data for pennates only mirrored the total taxon scores, while sample 8 being the most rich, and sample 6 being least rich in ALL and SPECIES and sample 7 least rich in the GENUS calculation. Likewise, sample 3 was the most diverse and sample 8 (the most species rich) was least diverse. Order of ranking of samples in terms of richness, 6 of the 8 rankings of SPECIES were the same as ALL, whereas only 2 of 8 were the same between GENUS and ALL. Order of ranking of samples in terms of diversity, as in pennate and centric taxa, showed less correspondence between SPECIES and ALL (4 out of 8) and GENUS and ALL (3 out of 8).

These data seem to suggest that even modest changes in taxonomic resolution can lead to large changes in the relative ranking of samples (up to 50% difference). In other words, reduced taxonomic resolution does not provide accurate prediction of relative rankings of water condition. The surprising result of an inverse relationship between species richness and diversity suggest even the most common measures of water quality analysis may require further critical evaluation. Further analysis is needed, with robust statistical power, on the impacts of reduced taxonomic resolution on predicting the relative rankings of water conditions.

CREATING MODERN TAXONOMIC TOOLS FOR A LARGE, INTERNATIONAL USER COMMUNITY

The workshop discussed at length ways in which taxonomic information can best be conveyed to the broad community of diatomists, serving both taxonomists and ecologists (and others as well). Praise was evident for projects like the Süßwasserflora (Krammer and Lange-Bertalot 1986–1991), with its great taxonomic and geographic breadth, detailed taxonomic information, and incredible photo documentation. A second project also hailed by the workshop participants, though more restricted in scope, was the series on diatoms from the Baltic Sea (Snoeijs and co-workers,

ty, SPECIES matched ALL in less than 40% of the rankings.

In data including pennate taxa only, richness ranged from 93–102 taxa

1993–1998). The project succinctly brings together illustrations with listings of important literatures and helpful comments into a common, useful format. It also represents a collaboration of scientists from different labs, countries and perspectives.

Shortcomings of traditional floras include the lack of tying images or distributions explicitly to specimens in publicly accessible collections, uncertainty or lack of studies documenting synonymies, lack of detailed geographic summaries, the static nature of data and the high cost of the published volumes.

Given the limited number of formally trained taxonomists and systematists worldwide (Kociolek and Stoermer 2001) and the increased possibilities for interaction and collaboration afforded by the internet, many workshop participants saw the opportunities and benefits of developing an on-line flora. This concept has been discussed in part by Kociolek (accepted). Such a flora could also be linked to/integrated into other information systems that are already in place or in development that offer templates for achieving additional goals (offering the ability for users to provide comments and feedback, allowing the flora to create dialogue and be a dynamic entity for several possible communities; see one example dealing with the freshwater diatoms of south Florida (and the system in place at Academy of Natural Science, Philadelphia [ANSP] as current examples). The call for on-line tools such as floras was recently presented in *Science* (Wheeler et al. 2004).

Information that can be an integral part of an on-line flora include name (linked to databases on nomenclature), description, important references (linked to on-line literature databases), verified distributions (linked to collection/herbarium databases), reported distributions (linked to literature databases), images (linked to image databases), types (linked to collection databases) and the person(s) responsible for the entry information. There is currently being developed enough information infrastructure available on-line such that an on-line flora is possible. It is time for members of the diatom community to work towards producing this much-needed tool—a tool that would serve both taxonomists and ecologists.

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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 (Jousé 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

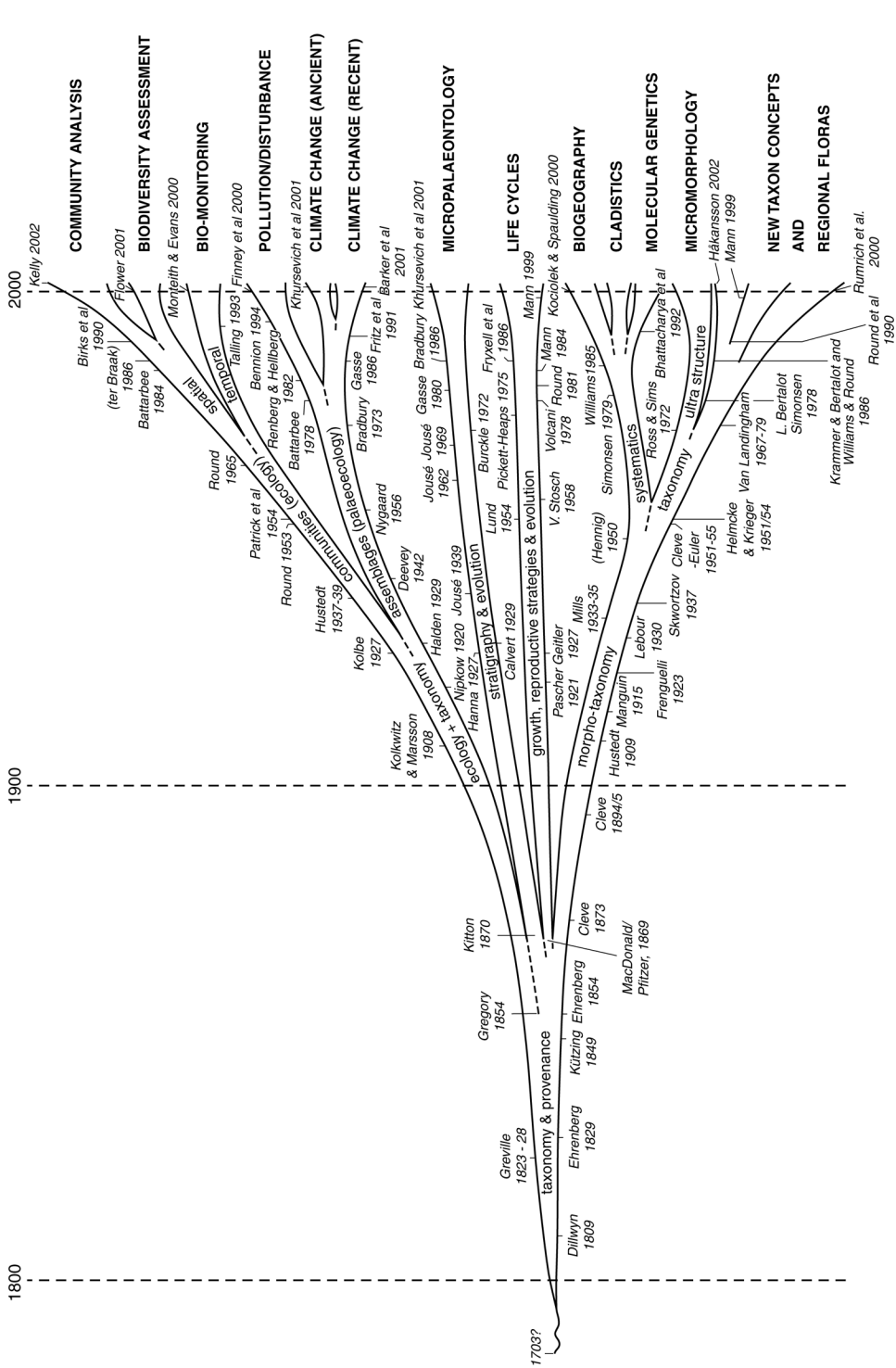


FIGURE 1. A summary diagram indicating trends in the diversification of diatom research during the past two centuries. Note that, i. several important and relevant but non-diatom references are indicated in parenthesis, ii. that the ~2000 AD array of diatom research areas is not exhaustive (see Stoermer 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/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.criticula.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 Izmeteva 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 Bolshoe in the Khamar Daban Mountains above Lake Baikal, the surface sediment is dominated by the plankton diatom *Pliocenicus 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 Bolshoe 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 with in 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):

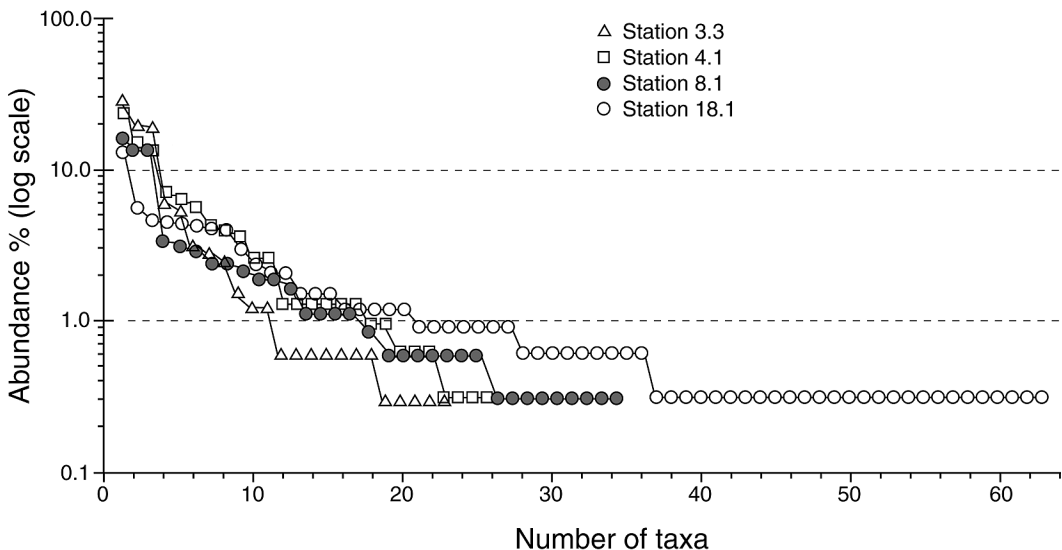


FIGURE 2. Relative abundance rank curves for diatom taxa in several shallow water epilithon samples selected from collections made from 51 sampling stations around Lake Baikal in 1997/98 (see Flower et al. 2004).

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 l 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 l

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).

Shore Zone	WSB	WMB	WNB	ENB	EMB	ESB
	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
Station scores	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
Mean scores	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-

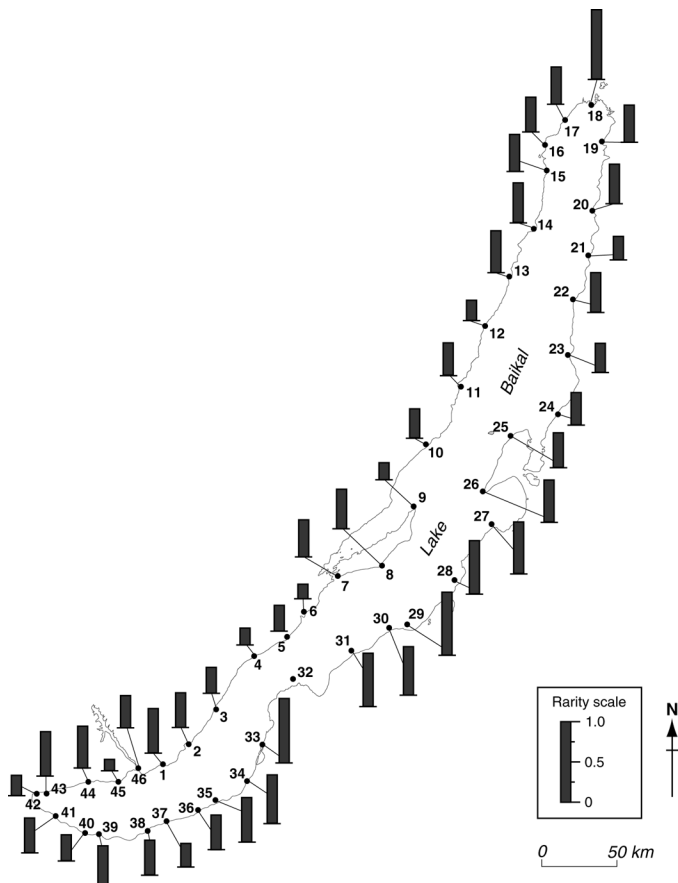


FIGURE 3. Diatom rarity index (see text) values as histograms calculated from shallow water epilithon samples from Lake Baikal (collected in 1997/98) from around the lake (see Flower et al. 2004).

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

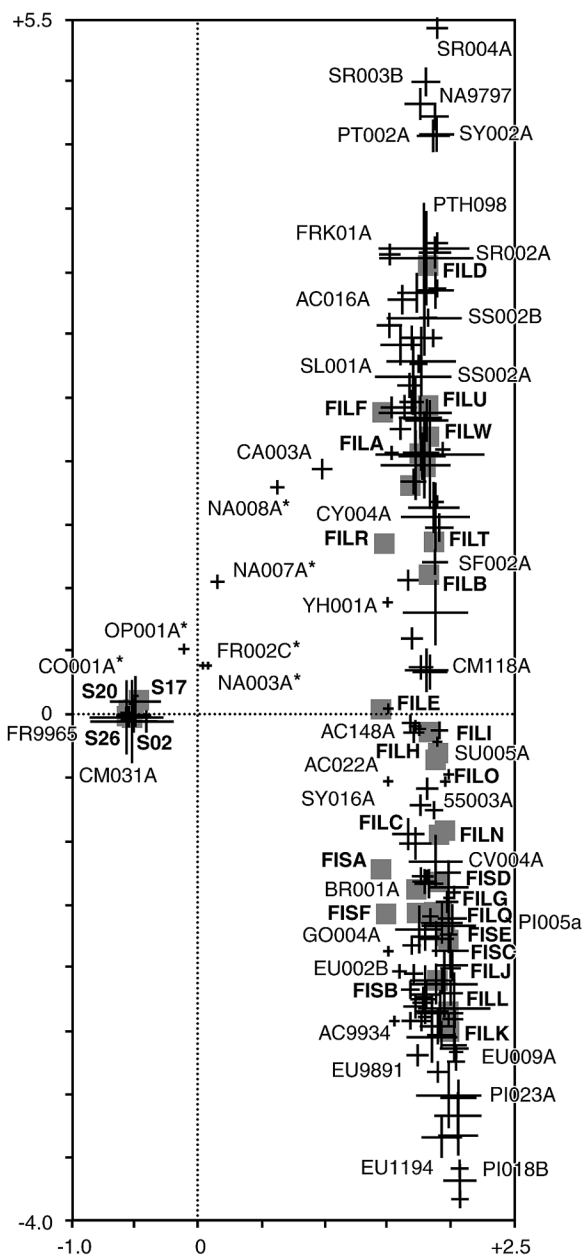


FIGURE 4. Correspondence analysis ordination of a combined data set of diatom taxa (shown as selected alpha-numeric taxon codes and crosses proportional to frequency abundances) and sites (shown as squares and coded with a bold S or FI prefix to indicate Siberian Lake Baikal or Falkland Islands sites). 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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Diatom (Bacillariophyta) Flora of Albanian Coastal Wetlands Taxonomy and Ecology: A Review

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The Albanian coast still features interesting and important lagoons and other wetlands, characterised by high biodiversity. The present paper focuses on their diatom flora: taxonomy and ecology. The checklist of hitherto identified taxa contains about 430 taxa observed in different coastal habitats, e.g., Butrinti, Karavasta, and Lezha. From the diatom structure, an evaluation of the ecological values and the trophic state of some coastal ecosystems can be made. In some of these (e.g., Butrinti), diatom and peridinophyte blooms, formed by potentially toxic species (e.g., *Pseudonitzschia seriata*, *Prorocentrum micans*, and *P. minimum*), were observed during the summer. The blooms were probably the result of the limited water exchange and were enhanced by other environmental factors (i.e., temperature, nutrients).

Studies on the ecology and taxonomy of brackish water diatoms should always be interrelated with and supported by integrated environmental programs. In the existing programs dealing with coastal wetlands, the ecological aspect is always manifestly important. However, the ecological goals cannot be satisfactorily achieved if the need for a basic taxonomic approach is neglected, which is often the case. Recently, numerous geobotanical and ecological studies of the diatom flora of lagoons from regions with different climatic conditions have been made (e.g., Miho 1994; Danielidis 1980; Witkowski 1991; Bak et al. 2001; Trobajo 2003). Similarly to other Mediterranean countries, Albania features a high diversity of species and sensitive habitats, which are rather poorly known and remain exposed to a significant impact of human activity (NEA/AKM 1999).

Biological zonation and/or the natural trophic/saprobic status of coastal lagoons can be established by studying the taxonomy and ecology of the diatom assemblages present (Miho 1994; Miho and Mitrushu 1999; Bak et al. 2001; Silvestre et al. 2002; Trobajo 2003). Such studies provide a substantial aid in exploration of biodiversity and functioning of food webs in coastal areas (Essink, 2003) and prove useful in assuring and strengthening further efforts towards their protection, restoration and sustainable use.

Publications on microscopic algae in Albania began with sporadic taxonomic surveys by foreign algologists, e.g., Forti (1902) in Shkodra Lake, Beck (1904) in Prespa Lake, Protic (1907) in brackish water habitats of Vlora, Krenner (1926) in the Drini River and Uherkovic (1963) in Shkumbini and some other rivers. Albanian studies were initiated in the 1980s. During 1987–1991, Miho (1994, 1996) surveyed the phytoplankton in Butrinti lagoon. These were expanded by research on the relationship between microalgae species composition and the trophic status of the habitats studied (e.g., Ohrid and Prespa lakes, Shkumbini and other rivers, Lezha and Vlora

lagoons, glacial lakes, e.g., Miho 1998a, 1998b; Miho and Mitrushi 1999; Miho and Dedej 1999; Miho and Lange-Bertalot 2001, 2003; Miho, Caka, and Carcani [in press]; Cullaj et al. 2003). Dedej (1994, 1995) provided also some preliminary data on the phytoplankton of the Durrresi and Karavasta regions. Recently, Rakaj (2002), Rakaj and Kashta (1999) and Rakaj et al. (2000, 2001) have reviewed the Lake Shkodra phytoplankton. Some other publications, i.e., those by Hustedt (1945), Jurilj (1954) and Vilicic et al. (2002) are important taxonomic contributions, particularly with respect to diatoms.

The present paper reviews the diatom flora of the Albanian coastal wetlands, and is an example of how taxonomy and ecology can be mutually supportive. In addition to the floristic composition, information on the ecological and trophic status of various coastal wetlands is provided.

GENERAL BACKGROUND

Albania is a small country that extends between a high mountain range and the Adriatic Sea, bordering Montenegro and Kosovo to the north, the Republic of Macedonia to the east and Greece to the south (Fig. 1). The country features large wetland areas surrounded by evergreen hills along the Adriatic coast; in addition, almost two-thirds of the country's surface area is covered by high mountain ranges (up to 2700 m) separated by valleys. The Albanian coast is about 427 km long, 273 km along the Adriatic Sea and 154 km along the Ionian Sea (Kabo 1990–91).

The low accumulative Adriatic coast extends from the Buna/Bojana delta to Vlora Bay (Fig. 1) and is characterised by the presence of fluvial deltas, inlets and lagoons, beaches, coastal sand bars, rocky promontories, submerged caves, sandy dunes and extended inland bays. Estuaries of major rivers intersect the coast: Drini, Buna, Mati, Ishmi, Shkumbini, Semani, and Vjosa that run westwards from the country's interior (Kabo 1990–91). The rivers are major water conduits not only for Albania, but also for the whole eastern Adriatic Sea. In their eastern sections they are torrential and erosive, whereas in the Western Coastal Plain they generally form wide meandering beds.

In contrast, the Ionian coast is steep, mountainous and rocky, intersected only by a few small rivers, such as the Bistrica and Pavlla. The coast also features some small wetlands and islets. The region is characteristic in its high diversity of habitats and species. In addition, it supports active aquaculture and fisheries, while urbanisation and industrial activities are limited. Butrinti, a wetland complex, unique in its biodiversity and aquaculture, is situated in the southern part (Fig. 1).

COASTAL WETLANDS AND THEIR ECOLOGICAL VALUES

Despite reclamation for agricultural purposes during the past decades, Albania still has about 109 km² of coastal wetlands or lagoons. Kabo (1990–91) described the main hydrological characteristics of Albanian lagoons, and the ecology has been reviewed by Peja et al. (1996). The most important coastal wetlands are Karavasta, Narta, Lezha, and Patoku on the Adriatic, and Butrinti on the Ionian coast (Fig. 1). The lagoons extend along the coastline and are separated from the sea by rather narrow sandy spits, which continuously change in size and shape. They are generally characterised by brackish waters, being connected with the sea through one or more channels.

Generally, wetlands display a large number of biotopes with enormous diversity of aquatic flora and fauna. Moreover, they are important especially for wintering of migratory birds (more than 70 species; NEA/AKM 1999). Some of these wetlands, e.g., Narta and Lezha, are partly protected. Regarding richness in habitats, flora and fauna (especially globally threatened water birds, i.e., the Dalmatian pelican) Karavasta and Divjaka National Park area have recently been designated Ramsar sites (Ramsar 1971, convention on wetlands [see <http://www.ramsar.org/>

profiles_albania.htm>]). Wetland areas have a very substantial economic potential for tourism, as breeding and refuge habitats for fish, and as valuable aquaculture sites. According to Peja et al. (1996), up to 6,000 kg of fish has been annually harvested during periods of high productivity.

Karavasta lagoon (surface area 43 km²), situated between the Semani and Shkumbini deltas, is the largest of Albania. It is connected with the sea through three short channels. Divjaka forest (12 km²) spreads out in the northwest of the lagoon (Kabo, 1990–91). It is a typically dune forest, bordered by brackish or freshwater, where pines (*Pinus halepensis* and *P. pinea*) grow up in old dunes, mixed with shrubs, grasses or reeds near lagoon shores. The lagoon system of Lezha is 10–15 km long and 3 km wide with a total area of about 22 km², 11.6 km² consisting of lagoons (Ceka, Merxhani, and Kenalla), 2 km² forests (Vaina and Kune) and 7 km² of wetlands. Their origin is related to deltaic processes of the Drini River. Narta, situated in the southern part of the Vjosa delta, covers 42 km² and connects with the sea via two channels. All these lagoons are shallow and fluvial in origin. Butrinti (16 km²) is one of the most interesting lagoons of tectonic origin. Due to its relatively great depth (averaging 14 m), its water column is permanently stratified. Its bottom is characterized by anaerobic decomposition. However, during the past few decades, the lagoon has been used intensively in aquaculture of mussels (*Mytilus galloprovincialis*) (up to 2,000 to 4,500 ton gross product/year).

The wetlands are, however, very sensitive ecosystems that were under strong impact in the past due to the extensive agricultural reclamation and unsustainable industry. At present, the western lowland supports densely populated industrial centres, intensive agriculture and tourism.

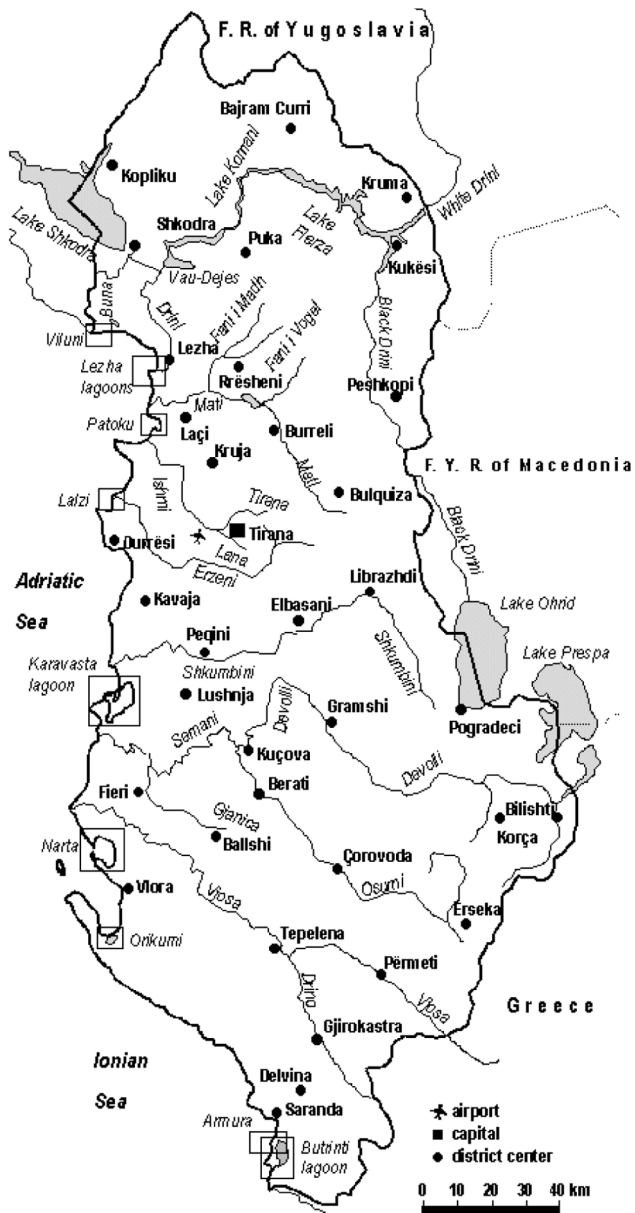


FIGURE 1: Location of Albanian coastal wetlands.

Therefore, some riverine waters (i.e., of Ishmi, Tirana, Lana, Gjanica, etc.) are heavily loaded with urban and industrial sewage discharged directly to rivers that transport this load to the sea. Moreover, high levels of heavy metals have been found in Vlora and Durresi bays, Mati delta, etc. Petroleum industry in Fieri and Vlora also result in an adverse ecological impact on the Semani and Vjosa deltas and their related lagoons. Coastal dune forests are under pressure of touristic development. Also, the high rate of erosion caused by excessive woodcutting, overgrazing or firing in reative shallow water basins, further increases the amount of suspended matter transported to the sea by the rivers (Cullaj et al. 2003; UNEP 2000).

DIATOMS: TAXONOMIC APPROACH

The survey of recent publications on Albanian waters, including the lakes on its borders, shows the number of diatom species to exceed 1 200. The most interesting area seems to be Lake Ohrid with about 550 species (Miho and Lange-Bertalot 2003), of which more than 100 are endemic or rarely occurring species. In their 1999–2000 study of Albanian freshwater diatom flora, Miho and Lange-Bertalot identified 900 taxa, including some whose distribution is poorly known (Miho and Lange-Bertalot 2001, 2003). Some of these (*Aneumastus albanicus*, *A. rosettae*, *A. humboldtianus*, *Navicula pseudoppugnata*, *N. parahasta* *N. hastatula*, and *Cymbopleura albanica*, *C. lura* and *C. lata* var. *lura*) have recently been described as new to science in Lange-Bertalot (2001) and Krammer (2003), respectively.

Altogether, more than 430 diatom taxa were identified in the brackish water coastal wetlands, either published or presented here for the first time. Of this group, 365 taxa are pennate and 65 are centrics. More than 160 taxa were found in Butrinti and about 115 in Karavasta, representing two ecosystems with the highest number of taxa. The checklist of the species identified is given in table 1. Despite the efforts to avoid synonyms or changed names of longer established taxa, some *taxa* might be recorded here twice under different names and some identifications may not be correct. Selected taxa (13 taxa in 25 figures), either the most abundant ones or those taxonomically interesting, are illustrated in Plates I and II. The data from this compilation represent the first step to shed light on the diatom flora of this Mediterranean area, hitherto unknown. About 240 taxa have already been published, whereas about 110 were not recorded before in this area; therefore, about 80 taxa have not been observed in Albanian samples examined previously.

Vilicic et al. (2002) have already published a checklist of phytoplankton taxa in the Eastern Adriatic Sea, referring to the Croatian coast. In all, 888 taxa were reported, of which 518 were diatoms (330 pennates and 174 centrics). The data refer to naturally eutrophic areas (bays, estuaries), harbours, etc. However, only 118 taxa were also included in the Albanian checklist reported here. Probably, the difference in comparison with the Croatian checklist could be due to the fact that many of the Albanian samples were of periphyton. In addition, the various habitats differ in relation to their ecology.

Protic (1907) provided the first data on some brackish habitats from the Albanian coast (in Orikumi and Narta: Vlora region). His list included 196 species, 107 of which were diatoms. When dealing with phytoplankton of Butrinti, Miho (1994, 1996) reported 90 species, 60 of which were diatoms. This was the first ecological approach to study an important habitat, at that time intensively used for aquaculture. The diatom genus *Nitzschia* was represented by the highest number of species; however, centrics, especially *Chaetoceros* spp. and *Cyclotella* aff. *choctawhatcheeana*, were the most abundant. The difficulty in their identification was the principal taxonomic problem. As a matter of fact, more than 40 taxa in Table 1 are not fully determined. Other abundant species included *Pseudonitzschia seriata*, *Nitzschia capitellata* and *Thalassionema nitzschioides*. They

were accompanied by peridiniophytes, e.g., *Prorocentrum micans*, *P. minimum*, *Scrippsiella* sp., *Ceratium fusus*, *C. pulchellum*. In the three Lezha lagoons (Ceka, Merxhani, Kenalla), about 90 phytoplankton species were recorded in July 1996 (Miho and Mitrushi 1999). A relatively high diversity was observed in Merxhani where *Chaetoceros* spp., *Amphora holsatica*, *Nitzschia sigma*, *Entomoneis paludosa*, *Cerataulus turgidus*, *Melosira nummuloides*, *Grammatophora oceanica*, *Pleurosigma angulatum* and *Striatella unipunctata* were observed as abundant species. In Ceka, an algal bloom was observed, dominated by *Nitzschia reversa*, *Peridinium* spp., *Gonyaulax monacantha*, and *Prorocentrum minimum*. Kenalla, a relatively deep pond close to the shallow lagoon of Merxhani, supported large populations of the centric diatom *Chaetoceros muelleri*, associated with abundant filamentous blue-green algae, e.g., *Anabaenopsis circularis*, *Oscillatoria* sp., and a small peridiniophyte *Gymnodinium* sp.

Occasional surveys were also carried out in other Albanian wetlands, i.e., Saranda, Karavasta, Narta, Patoku, Viluni and Durresi (Lalzi) (Miho 1998b). In Karavasta, 65 diatom species were identified. In this locality, again, pennates represented by the genera *Fragilaria* and *Cocconeis* prevailed. In 1992–93, more than 75 diatoms were identified in the Orikumi wetland, where pennates also dominated. In a recent assessment of different habitats of Butrinti, Armura and Saranda Harbour, spanning the period of 1998–2000, over 200 epiphytic diatoms were identified. These included 28 centric species, represented by *Cyclotella* (6 species), *Actinocyclus* (5), and *Chaetoceros* (4), as well as 178 pennates, including, e.g., *Nitzschia* (25 species), *Mastogloia* (20), *Amphora* (14) and *Navicula* (12). The most abundant taxa included *Cyclotella* cf. *choctawhatcheeana*, *Achnanthes brevipes*, *Amphora* cf. *tomiakae*, *A. coffeaeformis*, *Bacillaria paxillifer*, *Cocconeis placentula*, *C. scutellum*, *Staurosira construens*, *Mastogloia crucicula*, *Nitzschia coarctata*, *N. constricta*, *Pleurosigma formosum* and *Thalassionema nitzschioides*.

Certain species, interesting either from an ecological or taxonomical point of view, are presented below. Some of them represent the dominant organism, whereas others are poorly known.

Cyclotella aff. *choctawhatcheeana* Prasad (Plate 1: Figs. 1–9) was abundant in the phytoplankton of Butrinti (Miho 1994) where it was responsible for an autumn bloom. The species occurred as solitary cells or colonies and was present in the water column throughout the growing season. *C.* aff. *choctawhatcheeana* occurred in combination with various *Chaetoceros* species. In other Albanian lagoons (Orikumi, Karavasta) the distribution was scarce and represented by single cells only. Albanian specimens belong to the *Cyclotella caspia* group and are closely related to *C. choctawhatcheeana* Prasad; however, some characters differ from the descriptions given by Prasad (1991), Wendker (1991), and Hakansson et al. (1993). Unlike *C. choctawhatcheeana*, the Albanian specimens possess 1–3 fulcra in the middle; the transapical striae were radiate but finer, about 30–40/10 µm, and measured 5–15 µm.

Chaetoceros spp. (Plate 1: Figs. 10–14): the species belonging to the genus *Chaetoceros* occurred abundantly in the phytoplankton of the lagoons, especially in Butrinti, Orikumi, and Merxhani. However, due to their very fine structure, it was not easy to identify the most common species. Nevertheless, as shown by Miho (1994), *Ch. wighamii* Brightwell seems to be the most abundant, characterised by very small colony-forming cells with very fine setae.

Actinocyclus cf. *subtilis* (Gregory) Ralfs (Plate 2: Fig. 2) was found in brackish and almost marine waters, e.g., Butrinti and Armura Bay (Saranda). Based on their overall morphology, our specimens resembled *A. subtilis* (Gregory) Ralfs. However, they differed from this in having a generally larger valve diameter (exceeding 68 µm) and denser areolation of the striae (more than 16 puncta/10 µm). The taxon appears to have morphologically distinct valves; according to the species description by Witkowski et al. (2000), *A. subtilis* valve diameter is smaller and the striae possess a coarser areolation (about 12/10 µm).

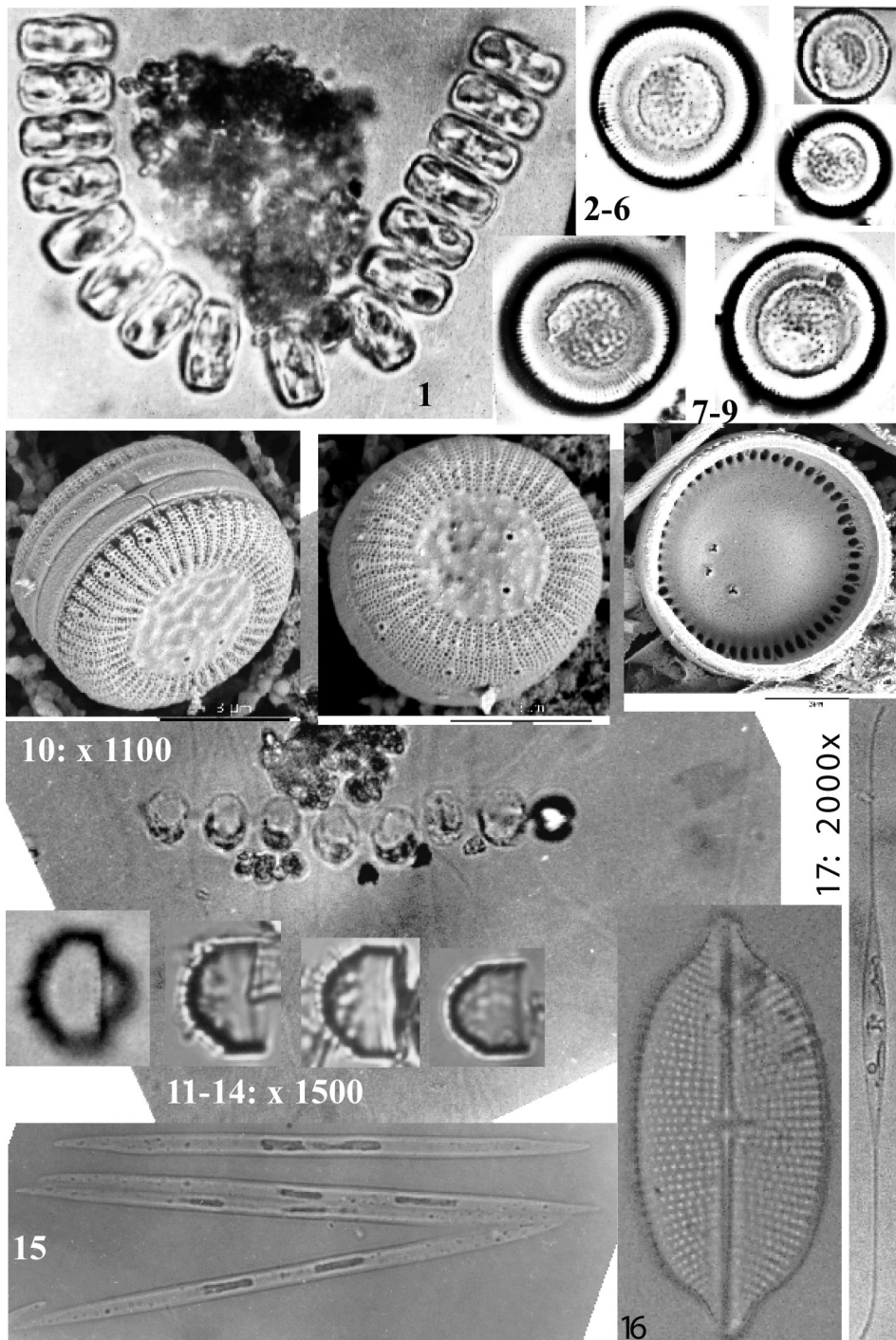


PLATE I. Figs. 1-9: *Cyclotella* aff. *choctawhatcheeana* Prasad; Figs. 10-14: *Chaetoceros* sp. diverse (cf. *Ch. wighamii* Brightwell); Fig. 7-9, SEM, bar = 3 μ m); Fig. 15: *Pseudonitzschia seriata* Cleve; Fig. 16: *Navicula* cf. *besarensis* Giffen; Fig. 17: *Nitzschia reversa* W. Smith. (Figs. 1-6, 11-16: 1500x; Figs. 7-9: SEM, bar=3 μ m; Fig. 10: 1100x; Fig. 17: 2000x.)

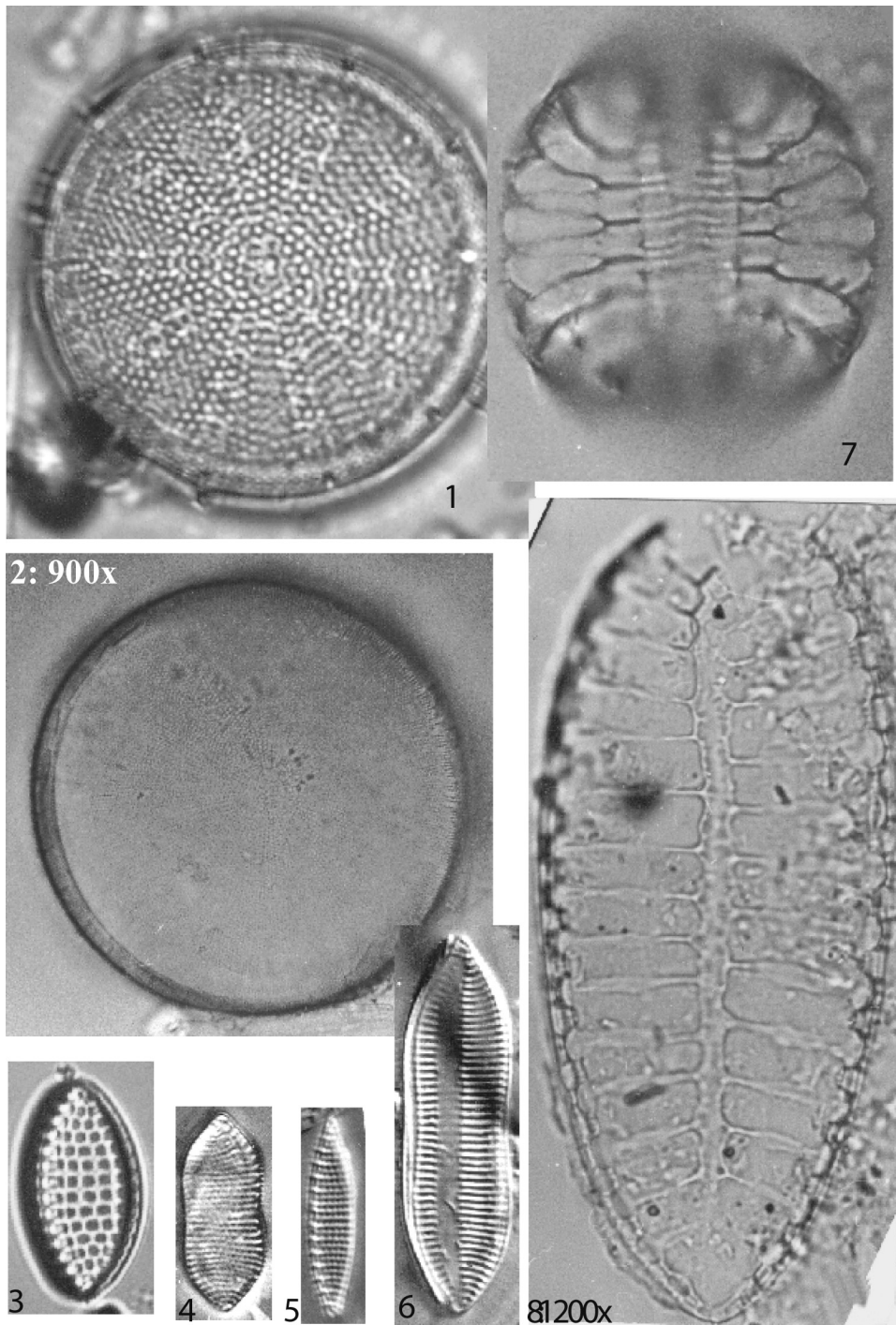


PLATE II. Fig. 1: *Actinocyclus* cf. *ochotensis* Jouse; Fig. 2: *A.* cf. *subtilis* (Gregory) Ralfs; (900x) Fig. 3: *Nitzschia granulata* Grunow; Fig. 4: *N. coarctata* Grunow; Fig. 5: *N. constricta* (Kützing) Ralfs; Fig. 6: *Campylodiscus* cf. *simulans* Gregory; Fig. 6: *Surirella* cf. *fluminensis* Grunow. (Figs. 1, 3–7: 1500x; Fig. 2: 900x; Fig. 8: 1200x.)

Campylodiscus cf. *simulans* Gregory (Plate 2: Fig. 7) was found in Butrinti and Saranda Bay. The morphology seems to be intermediate between that of *C. simulans* Gregory (Schmidt's Atlas: Tafel 17, Figs. 12–14) and *C. thuretii* var. *baldjikiana* Grunow (Plate 51, Figs. 16–21).

Surirella cf. *fluminensis* Grunow (Plate 2: Fig. 8) is a poorly known species. The morphology appears to be similar to that of the specimen drawn in Schmidt's Atlas (Plate 5: Fig. 6). Specimens were 44–62 μm long and 23–27 μm broad with 8 ribs/100 μm . The axial area was relatively narrow. These organisms were frequent in Karavasta and scarce in other Albanian lagoons.

Nitzschia reversa W. Smith was found to form blooms in Ceka lagoon (Lezha) (Plate 1: Fig. 17). It is characterised by sigmoid valve shape (35–95 μm long and 2.5–3.5 μm broad) and a very fine striation (not resolvable in LM). It was smaller and finer than the specimens from the type population characterized in Witkowski et al. (2000) or Proshkina-Lavrenko (1955).

Pseudonitzschia seriata Cleve (Plate 1: Fig. 15) was very abundant in Butrinti lagoon. During late spring and summer of 1987 it was observed to form a bloom (Miho 1994).

DIATOMS: ECOLOGICAL APPROACH

Guelorget and Perthuisot (1984) have proposed a biological zonation system for lagoons, based on their 'confinement', a hydrological parameter linked mainly to exchange/renewal of the water. It can be based on benthic communities, where each community characterizes one of the six defined zones. Therefore, each zone has its own specific richness, density, biomass, productivity (including phytoplankton), etc. Hence, based on the composition of the microalgae, such zonation could be drawn up, and as a consequence a diagnosis of the biological and economic potential of a lagoon could even be made. Here, some preliminary insights into biological zones that prevail in Albanian lagoons are presented, based on the algal assemblages.

Butrinti ranks among typical meromictic water bodies; therefore, optimum conditions for phyto-benthos are to be found in some borderline locations, dominated by *Enteromorpha prolifera* (Miho 1994, 1996). The remaining part of the bottom is affected by anaerobic conditions, characterized by high rates of organic matter sedimentation and decomposition. Thus, the primary production is virtually due to the phytoplankton of the upper layers (5–7 m depth), which was dominated by one or two species of centric diatoms (often accounting for more than 90% of the primary producers). The seasonal pattern involved a very pronounced peak in spring (up to 44,000 cells/ml in March 1991) and a smaller one in the autumn. A phytoplankton decline, accompanied by a relative increase in peridiniophyte abundance, was recorded in the summer.

Intensive growth of phytoplankton, mainly by the neritic forms of the centric diatoms mentioned, shows that the upper layers of Butrinti mainly belong to zone 3. According to Dutrieux and Guelorget (1988) this zone is characterized by limited impact of hydrodynamic conditions; the organic matter content increases in both sediment and water, although the overall living conditions remain good. It represents a habitat favourable for shellfish reproduction, as evidenced by profusion of *Mytilus galloprovincialis* everywhere in Butrinti. However, being permanently stratified with anoxic bottom waters, the lagoon poses a potential risk to aquaculture.

Centric diatoms were the most abundant in Orikumi (Miho and Dedej 1999). The phytoplankton structure seemed to be similar to that in Butrinti, but the cell density was much lower. However, the increase of peridiniophytes was observed in summer as well. Taking the species composition into account, even Orikumi seems to represent predominantly zone 3, with similar features of surface waters in Butrinti, related to shellfish production. However, it is worth mentioning that the coastal wetland at Orikumi is exposed to one of the strongest human impacts among the Albanian lagoons. Its area was extremely reduced by land reclamation about 35 years ago. Consequently, its biological characteristics were significantly altered.

To obtain a complete zonation view for each lagoon a more detailed approach of their physico-chemical and biological features would be necessary. A small number of phytoplankton samples from Narta, a large and very shallow lagoon (the depth ranges from 0.3 to 1 m), contained a few species only. This water body is characterized by a very limited connection with the sea and slow water exchange, belonging mainly to zone 6. After Dutrieux and Guelorget (1988) it does not support intensive phytoplankton growth, and its use for intensive aquaculture is rather limited; therefore, the lagoon could be suitable for traditional fishing.

Pennate diatoms were most abundant in Karavasta. Unlike in other lagoons (Butrinti or Ceka), blooms or intensive growth of peridinophytes were not observed there. In agreement with Guelorget and Lefebvre (1993), zones 4 and 5 seem to prevail within the lagoon, characterised by a high productivity, mostly attributable to phytoplankton. Therefore, it may be used mainly in an extensive way for farming detritivorous fish species (e.g., mullet) or penaeid shrimps (Dutrieux and Guelorget 1988). Similar characteristics seem to be typical of Patoku and Ceka (Lezha). As indicated by the diatom flora, dominated by centrics, Merxhani lagoon shows a relatively good water exchange with the sea, characteristic of zone 3.

During April-June 1987, an abnormal bloom of *Pseudonitzschia seriata* was observed in Butrinti, followed by a bloom of *Prorocentrum micans* and *P. minimum* (Miho 1994), both known to produce toxins (Hallegraeff 1995). Algal bloom was observed also in Ceka (Lezha; spring-summer 1992), where *Nitzschia* spp. or *Prorocentrum* spp. and *Gonyaulax* spp. were dominant. This indicates conditions of stress, ensuing probably due to a combination of climate, the very limited water circulation in the lagoon and restricted water exchange with the sea. According to Marasovic (1989), the very high evaporation rate accompanied by increasing water temperature and salinity may contribute to the environmental stress as well. These critical conditions allow the presence of only a few species, with extremely dense growth.

Parameters important in evaluation of the trophic status and other ecological features of a habitat may include the diversity index (Shannon and Weaver 1949) and/or dominance index (McNaughton 1967). In Butrinti, the diversity index was higher in marine habitats (varying from 1.9 to 3.4 in the littoral zone) than within the lagoon (ranging from 0.6 to 2.5; Miho 1994, 1996). In lagoon habitats, contributions of the two dominant species were very high (up to 92.4 % in Butrinti) and showed a strong seaward decrease (27.8% in Armura or 30.3% in Saranda). Generally, even the number of species was higher in the littoral marine habitats than in the lagoons, where the water exchange was limited. Armura, Butrinti (northern part), Karavasta, and Merxhani were the most distinct habitats in terms of species richness and trophic status.

CONCLUDING REMARKS

Albanian coastal wetlands, exemplified by the habitats studied in Butrinti, Armura, Karavasta, Orikumi and Merxhani show a high diversity of diatoms. The species composition found in some lagoons provides evidence of relatively good water exchange with the sea and favourable conditions of the natural environment. Stress conditions were observed in some other localities. Algal blooms were sporadically observed in Butrinti and Ceka, especially during the summer. The blooms were formed by pennate diatoms, e.g., *Pseudonitzschia seriata* and *Nitzschia reversa*, and by a few peridinophytes some of which are known to produce neurotoxins. Highly stressing conditions seem to prevail for an extended period of time in Narta and Kenalla pond (Lezha). The eutrophic status and related stressing conditions there are probably the result of limited water exchange with the sea. Moreover, the Albanian coast and the wetlands continue to be endangered by tourism, urban and industrial wastewater pollution, etc.

Potentially, the Albanian coast is a valuable environmental asset, but there is an urgent need of responsible protection and management.

Taking appropriate measures in important and sensitive watershed areas will help to prevent damage to biodiversity and other natural values. Studies of the structure of diatom floras would provide additional information leading toward a better ecological approach of coastal ecosystems.

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Appendix

TABLE 1. Checklist of Diatoms Found in Albanian Coastal Wetlands

Key: A: Armura; B: Butrinti; C: Ceka; D: Durresi; K: Karavasta; Ke: Kenalla; L: Lalzi; Le: Lezha; M: Merxhani; N: Narta; O: Orikumi; P: Patoku; S: Saranda; VI: Vlora; V: Viluni (see Fig. 1).

Note: The taxa labeled with 'VI' were reproted by Protic (1907), 'D' and partly 'K' by Dedej (1994, 1995), 'A, B, C, L, Le, K, Ke, M, O, P, S, V' by Miho (1994, 1996), Miho and Dedej (1999), and Miho and Mitrush (1999); data for unlabeled taxa are from the unpublished notes of A. Miho.

Bacillariophyceae: Centricae	<i>stolterfothii</i> Peragallo [B]
<i>Actinocyclus</i> cf. <i>subtilis</i> (Gregory) Ralfs [S]	<i>Hemiaulus hauckii</i> Grunow [B, D, M]
<i>Actinocyclus ochotensis</i> Jouse [A]	<i>Hyalodiscus radiatus</i> (O'Meara) Grunow [B, D, K, Le, O, P, V]
<i>Actinocyclus octonarius</i> Ehrenberg (= <i>A. ehrenbergii</i> Ralfs) [B]	<i>Hyalodiscus scoticus</i> (Kützing) Grunow [B]
<i>Actinocyclus subtilis</i> (Gregory) Ralfs [A, B, S]	<i>Leptocylindrus adriaticus</i> Schroeder [B, K, O]
<i>Actinoptychus senarius</i> (Ehrenberg) Ehrenberg [B]	<i>Leptocylindrus minimus</i> Grunow [B]
<i>Actinoptychus splendens</i> (Shadbolt) Ralfs [M]	<i>Melosira moniliformis</i> (Mueller) Agardh var. <i>moniliformis</i> [B, Le, M, O, P, V]
<i>Amphitetras antediluviana</i> Ehrenberg [B, K, O]	<i>Melosira nummuloides</i> Agardh [B, K, Ke, M, O, P]
<i>Asteromphalus heptactis</i> (Brébisson) Ralfs [B, M]	<i>Melosira sol</i> (Ehrenberg) Kützing [S]
<i>Asteromphalus robustus</i> Castracane [B]	<i>Melosira varians</i> Agardh [B, K, VI]
<i>Aulacoseira ambigua</i> (Grunow) Simonsen [B]	<i>Odontella aurita</i> (Lyngbye) Brébisson [B, K]
<i>Aulacoseira granulata</i> (Ehrenberg) Simonsen [B, K]	<i>Odontella mobiliensis</i> (Bailey) Grunow [B, K]
<i>Aulacoseira islandica</i> (Mueller) Simonsen [L]	<i>Porosira</i> cf. <i>pseudodenticula</i> (Hustedt) Jouse [A]
<i>Bacteriastrum furcatum</i> Shadbolt [B, Ke]	<i>Proboscia alata</i> (Brightwell) Sundstroem (= <i>Rhizosolenia alata</i> Brightwell) [B, D, K, M, O]
<i>Bacteriastrum delicatulum</i> Cleve [B; Ke]	<i>Pseudosolenia calcar-avis</i> (Schultze) Sundstroem [B, D]
<i>Biddulphia pulchella</i> Gray [A, B]	<i>Rhizosolenia imbricata</i> var. <i>shrubsolleyi</i> (Cleve) Schroeder [B]
<i>Cerataulina pelagica</i> (Cleve) Hendey [K]	<i>Skeletonema costatum</i> (Greville) Cleve [K]
<i>Cerataulina bergonii</i> (Peragallo) Schuett [B, D]	<i>Thalassiosira lacustris</i> Grunow var. <i>lacustris</i> [B, K]
<i>Ceratulus turgidus</i> (Ehrenberg) Ehrenberg [B, C, K, M, P]	<i>Triceratium favus</i> Ehrenberg [B]
<i>Chaetoceros affinis</i> Lauder [B]	<i>Triceratium reticulum</i> Ehrenberg [S]
<i>Chaetoceros atlanticus</i> Cleve [B, K]	
<i>Chaetoceros atlanticus</i> var. <i>neapolitana</i> (Schroeder) Schuett [B, K, M]	Bacillariophyceae: Pennatae
<i>Chaetoceros decipiens</i> Cleve [B]	<i>Achnanthes brevipes</i> Agardh var. <i>brevipes</i> [B, K]
<i>Chaetoceros densus</i> Cleve [B, Le]	<i>Achnanthes brevipes</i> var. <i>angustata</i> (Greville) Cleve [B, P]
<i>Chaetoceros diversus</i> Cleve [B, D]	<i>Achnanthes brevipes</i> var. <i>intermedia</i> (Kützing) Cleve [B, K, M, O, P, V]
<i>Chaetoceros insignis</i> Proshkina-Lavrenko [D]	<i>Achnanthes</i> cf. <i>groenlandica</i> (Cleve) Grunow [S]
<i>Chaetoceros lorenzianus</i> Grunow [D]	<i>Achnanthes delicatula</i> (Kützing) Grunow var. <i>delicatula</i> [B]
<i>Chaetoceros muelleri</i> Lemmermann [Ke]	<i>Achnanthes exigua</i> Grunow [B]
<i>Chaetoceros peruvianus</i> Brightwell [D]	<i>Achnanthes exilis</i> Kützing [VI]
<i>Chaetoceros subtilis</i> Cleve [B]	<i>Achnanthes hungarica</i> Grunow [K]
<i>Chaetoceros teres</i> Cleve [D]	<i>Achnanthes lanceolata</i> (Brébisson) Grunow agg. [B]
<i>Chaetoceros tortissimus</i> Grunow [B]	<i>Achnanthes longipes</i> Agardh [B, K, M, P, V]
<i>Chaetoceros wighamii</i> Brightwell [B]	<i>Achnanthes minutissima</i> Kützing [B, D, K, M, N, VI]
<i>Coscinodiscus</i> cf. <i>curvatulus</i> Grunow var. <i>minor</i> [B]	<i>Achnanthes separata</i> Hustedt [A, S]
<i>Coscinodiscus nodulifer</i> Schmidt [B, K]	<i>Achnanthes parvula</i> Kützing [S]
<i>Cyclotella</i> aff. <i>choctawhatcheeana</i> Prasad [B, O, K]	<i>Adlafia minuscula</i> Grunow (Lange-Bertalot) [Le]
<i>Cyclotella</i> cf. <i>hustedti</i> Jurilj [B]	<i>Amphipleura pellucida</i> (Kützing) Kützing [B, D, K, VI]
<i>Cyclotella meneghiniana</i> Kützing [B, Le, O, D]	<i>Amphora angularis</i> Gregory [VI]
<i>Cyclotella ocellata</i> Pantocsek [B, O]	<i>Amphora angularis</i> var. <i>lyrata</i> Van Heurck [VI]
<i>Cyclotella radiosa</i> (Grunow) Lemmermann [B, K]	<i>Amphora arenaria</i> Donkin [A]
<i>Cyclotella striata</i> (Kützing) Grunow [B, P]	<i>Amphora</i> cf. <i>granulata</i> Gregory [S]
<i>Cymatosira lorenziana</i> Grunow [S]	<i>Amphora</i> cf. <i>tomiakae</i> Witk., Lange-Bert. and Metz. [B, S]
<i>Dactyliosolen blavyanus</i> (Peragallo) Hasle [B, D, M, O]	
<i>Dactyliosolen fragilissimus</i> (Bergon) Hasle [B, D, K, M, O]	
<i>Guinardia flaccida</i> (Castracane) Peragallo [K]	
<i>Guinardia striata</i> (Stolterfoth) Hasle (= <i>Rhizosolenia</i>	

- Amphora coffeaeformis* (Agardh) Kützing [B, C, K, O, P]
Amphora commutata Grunow [VI]
Amphora costata W. Smith [S]
Amphora holsatica Hustedt [B, D, Le, O, P]
Amphora inflata Grunow [K]
Amphora kolbei Aleem [A, S]
Amphora laevis Gregory [K]
Amphora laevis Gregory [S]
Amphora lineolata Ehrenberg [B, K, Ke, M, VI]
Amphora lybica Ehrenberg [B, D, K, O]
Amphora marina (W. Smith) Van Heurck [A, B]
Amphora ovalis (Kützing) Kützing [K, Le, O, VI]
Amphora ovalis var. *affinis* Kützing [VI]
Amphora pediculus (Kützing) Grunow [B, K, Le, VI]
Amphora pseudohyalina Simonsen [S]
Amphora robusta Gregory [B, K, Le, P]
Amphora salina W. Smith [VI]
Aneumastus tusculus (Ehrenberg) Mann [Le, VI]
Brachysira serians (Brébisson) Round and D.G. Mann [VI]
Ardissonia crystallina (Agardh) Grunow (Agardh) Kützing [A, B]
Ardissonia fulgens (Greville) Grunow [B, K, Le, P, S]
Asterionellopsis glacialis (Castracane) Round [K]
Bacillaria cf. *socialis* (Gregory) Ralfs [S]
Bacillaria paradoxa Gmelin [B, D, K, Le, P]
Berkeleya scopulorum (Brébisson) Cox [S]
Caloneis amphisbaena (Bory) Cleve [B, K]
Caloneis amphisbaena var. *subsalina* Van Heurck [VI]
Caloneis bicuneata (Grunow) Wolle [B]
Caloneis liber (W. Smith) Hendey [B]
Caloneis silicula (Ehrenberg) Cleve agg. [B, D, K, VI]
Caloneis westii (W. Smith) Hendey [B, K, P]
Campylodiscus bicostatus W. Smith [B, K, O]
Campylodiscus cf. *simulans* Gregory
Campylodiscus clypeus Ehrenberg [B, K, O, VI]
Campylodiscus echeinis Ehrenberg [B, K, Le, P]
Campylodiscus levanderi Hustedt [B, K]
Campylosira cymbelliformis (Schmidt) Grunow [VI]
Cavinula cocconeiformis (Gregory) Mann and Stickle [B, K]
Cocconeis costata Gregory [B, K, O]
Cocconeis guttata Hustedt [S]
Cocconeis molesta Kützing [K, Le]
Cocconeis neodiminuta Krammer [B, K, O]
Cocconeis pediculus Ehrenberg [B, O, VI]
Cocconeis placentula (Ehrenberg) Hustedt agg. [VI]
Cocconeis placentula Ehrenberg var. *placentula* [B, K, O]
Cocconeis placentula var. *euglypta* (Ehrenberg) Cleve [B, K, Le, P]
Cocconeis placentula var. *lineata* (Ehrenberg) Van Heurck [Le]
Cocconeis scutellum Ehrenberg [B, K, Le, P]
Cocconeis pseudomarginata Gregory [B, A]
Craticula cuspidata (Kützing) Mann [B, D, K, O]
Craticula halophila (Grunow) D.G. Mann [B, D, K, Le, V]
Ctenophora pulchella (Ralfs ex Kützing) Williams and Round (= *Fragilaria pulchella* (Ralfs) Lange-Bertalot [B, Le, K, O])
Cylindrotheca cf. *gracilis* (Brébisson) Grunow [B, K, P]
- Cylindrotheca closterium* (Ehrenberg) Reimann and Lewin (= *Nitzschia closterium* (Ehrenberg) W. Smith) [B, D, K, M, P]
Cymatopleura elliptica (Brébisson) W. Smith [B, VI]
Cymatopleura solea (Brébisson) W. Smith [B, VI]
Cymbella affinis Kützing agg. [B, K, O, P]
Cymbella ampicephala Naegeli var. *ampicephala* [B]
Cymbella aspera (Ehrenberg) Peragallo [VI]
Cymbella cistula (Ehrenberg) Kirchner agg. [VI]
Cymbella cymbiformis Agardh var. *cymbiformis* [VI]
Cymbella delicatula Kützing [VI]
Cymbella ehrenbergii Kützing [VI]
Cymbella helvetica Kützing [B, P, VI]
Cymbella lanceolata (Ehrenberg) Kirchner [VI]
Cymbella pusilla Grunow [VI]
Cymbella tumida (Brébisson) Van Heurck [K, P, VI]
Cymbella turgida (Gregory) Cleve [B]
Delphineis cf. *livingstonii* Prasad [S]
Denticula tenuis Kützing [VI]
Diatoma anceps (Ehrenberg) Kirchner [VI]
Diatoma ehrenbergi Kützing [Le]
Diatoma hyemalis (Riith) Heiberg [VI]
Diatoma tenuis Agardh (= *D. elongatum* (Lyngbye) Agardh) [O]
Diatoma vulgare Bory var. *vulgare* [B, VI]
Diatoma vulgare var. *tenuis* Van Heurck [VI]
Dimerogramma minor (Gregory) Ralfs [S]
Diploneis cf. *interrupta* (Kützing) Cleve [S]
Diploneis cf. *littoralis* (Donkin) Cleve [B, S]
Diploneis cf. *mirabilis* Koenig [A]
Diploneis cf. *smithii* var. *dilatata* (Peragallo) Terry
Diploneis didyma (Ehrenberg) Cleve [B, Le, K, O, P]
Diploneis domblittensis Cleve [B]
Diploneis elliptica (Kützing) Cleve (= *Navicula elliptica* Kützing) [VI]
Diploneis marginestriata Hustedt [B]
Diploneis oblongella (Naegeli) Cleve-Euler [B]
Diploneis ovalis (Hilse) Cleve [B, Ke]
Diploneis smithii var. *pumila* (Grunow) Hustedt [B, K, P]
Diploneis subovalis Cleve [B, M]
Diploneis vetula (Schmidt) Cleve [A]
Diploneis subcincta (Schmidt) Cleve [B]
Encyonema caespitosum (Kützing) Grunow [VI]
Encyonema prostratum (Berkeley) Cleve [VI]
Encyonema ventricosum Kützing [B, VI]
Encyonopsis minuta Krammer and Reichardt [S]
Entomoneis paludosa (W. Smith) Reimer [B, K, Le, O, P]
Entomoneis alata (Ehrenberg) Ehrenberg [B, S]
Epithemia adnata (Kützing) Brébisson [B, K, O, VI]
Epithemia smithii Carruthers [B]
Epithemia sorex Kützing [B, K, O, VI]
Epithemia turgida (Ehrenberg) Kützing [VI]
Epithemia turgida var. *granulata* (Ehrenberg) Grunow [Le]
Eunotia arcus Ehrenberg [VI]
Eunotia cf. *exigua* (Brébisson) Rabenhorst [Le]
Eunotia flexuosa (Brébisson) Kützing [VI]
Eunotia pectinalis (Dillwyn) Rabenhorst [VI]
Eunotia praerupta Ehrenberg [B, K, O]
Fallacia versicolor (Grunow) Mann [S]

- Fragilaria affinis* Kützing [K]
Fragilaria capucina Grunow var. *capucina* [VI]
Fragilaria capucina var. *perminuta* (Grunow) Lange-Bertalot [B]
Fragilaria crotonensis Kitton [B, D, K]
Fragilaria dilatata (Brébisson) Lange-Bertalot (= *F. capitata* (Ehrenberg) Lange-Bertalot) [VI]
Fragilaria fasciculata (Agardh) Lange-Bertalot [B, K, Le, O, P, V]
Fragilaria investiens (W. Smith) A. Cleve [B]
Fragilaria laevis Oestrup [B, S]
Fragilaria pinnata Ehrenberg gr. [B, K, O, P]
Fragilaria ulna (Nitzsch) Lange-Bertalot agg. [B, Le, O, P]
Fragilaria ulna (*Synedra*) var. *longissima* Van Heurck [VI]
Fragilaria ulna (*Synedra*) var. *oxyrhynchus* (Kützing) Van Heurck [VI]
Fragilaria (*Synedra*) *ulna* var. *subaequalis* Grunow [VI]
Fragilaria virescens Ralfs [VI]
Frustulia cf. *weinholdii* Hustedt [B]
Gomphonema acuminatum Ehrenberg [Le, VI]
Gomphonema angustatum (Kützing) Rabenhorst [VI]
Gomphonema angustum Agardh [VI]
Gomphonema constrictum Ehrenberg [VI]
Gomphonema gracile Ehrenberg [Le]
Gomphonema minutum (Agardh) Agardh agg. [B, K, O]
Gomphonema olivaceum (Horn.) Brébisson var. *olivaceum* [B, K, O, VI]
Gomphonema olivaceum var. *calcareum* (Cleve) Cleve [B, K, O]
Gomphonema olivaceum var. *staurophorum* Pantocsek [B, D, K]
Gomphonema parvulum (Kützing) Grunow [Le, VI]
Gomphonema pseudotenellum Lange-Bertalot [Le]
Gomphonema truncatum Ehrenberg [B, D, K, Le, O]
Grammatophora angulosa Ehrenberg var. *angulosa* [B, Le]
Grammatophora macilenta W. Smith [B, K, V]
Grammatophora oceanica (Ehrenberg) Grunow var. *oceanica* [B, K, Le, N, O, P, V]
Gyrosigma acuminatum (Kützing) Rabenhorst var. *acuminatum* [B, K, Le, N, P, V]
Gyrosigma attenuatum (Kützing) Rabenhorst [B, K, O]
Gyrosigma arcuatum (Donkin) Sterrenburg
Gyrosigma balticum (Ehrenberg) Rabenhorst [B, K, Le, N, O, P, V]
Gyrosigma cf. *obscurum* (W. Smith) Griffith and Henfrey [B]
Gyrosigma cf. *peisonis* (Grunow) Hustedt [Le]
Gyrosigma cf. *wansbecki* (Donkin) Cleve [Le]
Gyrosigma compactum (Grev.) Cleve [B, S]
Gyrosigma fasciola (Ehrenberg) Griff. and Henf. [B, K, Le, N, O, P, V]
Gyrosigma strigilis (W. Smith) Cleve [B, K, Le, P]
Hantzschia amphioxys (Ehrenberg) Grunow [B, VI]
Hantzschia amphioxys fo. *capitata* Hustedt [B]
Licmophora cf. *grandis* (Kützing) Grunow [B, K]
Licmophora cf. *hyaline* Kützing [B, K]
Licmophora ehernberghii (Kützing) Grunow [B, K]
Licmophora flabellata var. *splendida* W. Smith [K]
Licmophora remulus Grunow [B, K, Le, N, O, P, V]
- Licmophora dalmatica* (Kützing) Grunow [VI]
Licmophora flabellata (Carmichael) Agardh
Licmophora gracilis (Ehrenberg) Grunow
Licmophora paradoxa (Lyngbye) Agardh [A, S]
Lyrella amphorooides D.G. Mann [S]
Lyrella cf. *clavata* (Gregory) D.G. Mann [M]
Lyrella lyra (Ehrenberg) Karayeva [B, K]
Lyrella spectabilis (Gregory) D.G. Mann [A, S]
Lyrella sulcifera (Hustedt) Witkowski [B, K, O, P, Le]
Mastogloia angulata Lewis [B, K, O, P, Le]
Mastogloia binotata (Grunow) Cleve [B]
Mastogloia braunii Grunow [B, K, O, VI]
Mastogloia cf. *adriatica* Voigt [B]
Mastogloia cf. *baldjikiana* Grunow [B, K]
Mastogloia cf. *biocellata* (Grunow) Nov. and Muft. [B]
Mastogloia cf. *labuensis* Cleve [B]
Mastogloia cf. *recta* Hustedt [B]
Mastogloia crucicula (Grunow) Cleve [B, K, O]
Mastogloia cuneata (Meister) Simonsen [B]
Mastogloia dansei Thwaites [VI]
Mastogloia grunowii A. Schmidt [B]
Mastogloia ignorata Hustedt [B]
Mastogloia lanceolata Thwaites [A]
Mastogloia laterostrata Hustedt [B]
Mastogloia ovalis A. Schmidt [A]
Mastogloia paradoxa Grunow [B]
Mastogloia pseudoexigua Cholonyk [B]
Mastogloia pseudolatecostata Yohn and Gibson [A]
Mastogloia pumila (Grunow) Cleve [B]
Mastogloia pusilla (Grunow) Cleve [B]
Mastogloia robusta Hustedt [B]
Mastogloia smithii Thwaites var. *smithii* [B]
Mastogloia smithii var. *lacustris* Grunow [B, D, K, O]
Mastogloia splendida (Gregory) Cleve [B]
Mastogloia vasta Hustedt [B]
Navicula agnita Hustedt [A]
Navicula arenaria Donkin [B, S]
Navicula cf. *besarensis* Giffen [S]
Navicula cf. *heimansii* Van Dam et Kooyman [B]
Navicula cf. *indulgens* Simonsen [B]
Navicula cf. *johanrossii* Giffen [S]
Navicula cf. *subhamulata* Grunow [Le]
Navicula cincta (Ehrenberg) Kützing [VI]
Navicula cluthensis Gregory var. *cluthensis* [P, V]
Navicula cryptocephala Kützing [D, K, VI]
Navicula cryptotenelloides Lange-Bertalot [B]
Navicula dealpina Lange-Bertalot [VI]
Navicula digitoradiata (Gregory) Ralfs [VI]
Navicula distans (W. Smith) Ralfs [VI]
Navicula duerrenbergiana Hustedt [B]
Navicula erifuga Lange-Bertalot [A]
Navicula granulata Bailey [C, Ke, V]
Navicula gregaria Donkin [B, S, V]
Navicula integra W. Smith [VI]
Navicula monilifera Cleve [B, K]
Navicula oblonga (Kützing) Kützing [B, K, O, VI]
Navicula pavillardii Hustedt [B, C]
Navicula peregrina (Ehrenberg) Kützing [VI]
Navicula perminuta Grunow [B]

- Navicula perrhombus* Hustedt [B]
Navicula phyllepta Kützing [B, K, O, P, Le]
Navicula phylleptosoma Lange-Bertalot [B]
Navicula pseudosilicula Hustedt [VI]
Navicula radiosa Kützing [V, VI]
Navicula recens (Lange-Bertalot) Lange-Bertalot [Le]
Navicula rhynchocephala Kützing [B, VI]
Navicula rolandii Lange-Bert. and Witk. [O]
Navicula salinarum Grunow [B, K, O, VI]
Navicula salinicola Hustedt [A, B, S]
Navicula termes Ehrenberg [VI]
Navicula tripunctata (Mueller) Bory [B, Le]
Navicula veneta Kützing [B, K]
Navicula viridula (Kützing) Ehrenberg [VI]
Neidium iridis var. *affinis* Ehrenberg [VI]
Neidium iridis var. *amphirhynchus* Ehrenberg [VI]
Nitzschia acicularioides Hustedt [S]
Nitzschia amphibia Grunow [B]
Nitzschia angularis W. Smith [A, S]
Nitzschia cf. *filiformis* var. *conferta* [Le]
Nitzschia cf. *graeffii* Grunow [S]
Nitzschia cf. *plana* W. Smith [B, S]
Nitzschia cf. *prolongata* Hustedt [B]
Nitzschia cf. *splendida* Kützing [B, K]
Nitzschia capitellata Hustedt [B, K, O]
Nitzschia circumscuta (Bailey) Grunow [B, D, K, P, Le, V]
Nitzschia clausii Hantzsch [B]
Nitzschia coarctata Grunow [B, K, O, P, Le]
Nitzschia communis Rabenhorst [VI]
Nitzschia commutata Grunow [VI]
Nitzschia compressa (Bailey) Boyer var. *compressa* [B, D, K, O, P, Le]
Nitzschia constricta (Kützing) Ralfs [B, D, K, O, P, Le]
Nitzschia denticula Grunow (= *Denticula Kützingii* Grunow) [B, K, O, P]
Nitzschia dissipata (Kützing) Grunow [B]
Nitzschia dissipata var. *media* (Hantzsch) Grunow [Le]
Nitzschia distans var. *tumescens* Gregory [K]
Nitzschia filiformis (W. Smith) Hustedt [A, B, S]
Nitzschia flexoides Geitler [B]
Nitzschia fossilis Grunow [Le]
Nitzschia granulata Grunow [B, Le]
Nitzschia hungarica Grunow [VI]
Nitzschia incospicua Grunow [B]
Nitzschia lacuum Lange-Bertalot [A, B, S]
Nitzschia lanceola var. *minutula* Grunow [B]
Nitzschia lanceolata W. Smith [B]
Nitzschia linearis (Agardh) W. Smith [VI]
Nitzschia littoralis Grunow [S]
Nitzschia longissima (Brébisson) Ralfs [B, D, K, Le, V]
Nitzschia macilenta Gregory [B]
Nitzschia microcephala Grunow [Le]
Nitzschia palea (Kützing) W. Smith [B, K, Le, VI]
Nitzschia panduriformis Gregory [A]
Nitzschia pararostrata (Lange-Bertalot) Lange-Bertalot [B]
Nitzschia recta Hantzsch [B]
Nitzschia reversa W. Smith [Le, O]
Nitzschia scalpelliformis Grunow [V]
Nitzschia sigma (Kützing) W. Smith [B, K, Le, VI]
Nitzschia sigma var. *sigmatiella* Grunow [D, K, Le, P, V]
Nitzschia sigmoidea (Nitzsch) W. Smith [VI]
Nitzschia paleacea (Grunow) Grunow [VI]
Nitzschia vitrea var. *salinarum* Grunow [VI]
Ophephora mutabilis (Grunow) Sabbe and Vyverman [B]
Parlibellus berkeleyi (Kützing) Cox [A, S]
Parlibellus cruciculoides (Brock.) Witk., Lange-Bert. and Metzeltin [S]
Parlibellus protracta (Grunow) Witk., Lange-Bert. and Metzeltin [A, Le, S]
Parlibellus rhombicula (Hustedt) Witk., Lange-Bert. and Metzeltin [S]
Petronis humerosa (Brébisson) D.G. Mann [B, K, M]
Pinnularia appendiculata (Agardh) Cleve [VI]
Pinnularia gibba Ehrenberg [VI]
Pinnularia legumen (Ehrenberg) Ehrenberg [VI]
Pinnularia major (Kützing) Rabenhorst [VI]
Pinnularia microstauron var. *brebissonii* (Kützing) Mayer [VI]
Pinnularia nobilis (Ehrenberg) Ehrenberg [VI]
Pinnularia pulchra Oestrup Ehrenberg [VI]
Pinnularia tabellaria Ehrenberg [VI]
Placoneis elginensis (Gregory) Cox [VI]
Placoneis gastrum var. *signata* (Hustedt) [B, K]
Plagiotropis gibberula Grunow [S]
Plagiotropis lepidoptera (Gregory) Kuntze [A, B, V]
Pleurosigma angulatum (Quekett) W. Smith [B, K, Le, O, P, V]
Pleurosigma cf. *rostratum* Hustedt [M]
Pleurosigma elongatum W. Smith [B, D, K, Le, O, P, V]
Pleurosigma formosum Peragallo [B, K, Le, O, P, V]
Pleurosigma salinarum Grunow [S, Le]
Pseudonitzschia delicatissima (Cleve) Peragallo [D]
Pseudonitzschia seriata (Cleve) Peragallo [B, K, Le, O, P, V]
Pterodictyon gemma (Ehrenberg) D.G. Mann [B, K, P]
Rhabdonema adriaticum Kützing [B, K, Le, O, P, V]
Rhoicosphenia abbreviata (Agardh) Lange-Bertalot [B, VI]
Rhoicosphenia marina (W. Smith) M. Schmidt [B]
Rhopalodia acuminata Krammer [A, S]
Rhopalodia brebissonii Krammer [B]
Rhopalodia cf. *constricta* (W. Smith) Krammer [A]
Rhopalodia cf. *gibberula* (Ehrenberg) Mueller [B, K]
Rhopalodia gibba (Ehrenberg) Mueller [B, K, Le, O, P, VI]
Rhopalodia gibba var. *minuta* Krammer [A, S]
Rhopalodia musculus (Kützing) Mueller [B, D, K, Le, O, P, V]
Sellaphora bacillum (Ehrenberg) Mereschkowsky [VI]
Sellaphora seminulum (Grunow) D.G. Mann [VI]
Seminavis basilica Danielidis and D.G. Mann [A, B, S]
Stauroneis acuta W. Smith [VI]
Stauroneis anceps Ehrenberg [VI]
Stauroneis gregori Ralfs [VI]
Stauroneis phoenicenteron Ehrenberg [VI]
Stauroneis salina W. Smith [VI]
Staurosira brevistriata Grunow (= *Fragilaria brevistriata* Grunow, *Pseudostaurosira brevistriata* (Grunow) Williams and Round) [B, O]
Staurosira construens Ehrenberg (= *Fragilaria construens*

(Ehrenberg) Grunow [B, S]

Striatella unipunctata (Lyngbye) Agardh [B, K, Le, O, P, V]

Surirella biseriata Brébisson [VI]

Surirella brebissonii Krammer and Lange-Bertalot [B, K, O]

Surirella cf. *fluminensis* Grunow [B, K, M, P]

Surirella cf. *scalaris* Giffen [A, S]

Surirella fastuosa (Ehrenberg) Kützing [B, K, Le, O, P, V]

Surirella minuta Brébisson [VI]

Surirella ovalis Brébisson [B, K, O, VI]

Surirella spiralis Kützing [K, VI]

Surirella splendida (Ehrenberg) Kützing [VI]

Surirella striatula Turpin [B, C, K, O, P]

Synedra tabulata (Agardh) Kützing var. *tabulata* [B, K, Le]

Synedra undulata (Bailey) Gregory (= *Toxarium undulatum* Bailey) [B, Le, O]

Tabellaria fenestrata (Lyngbye) Kützing [VI]

Tabellaria flocculosa (Roth) Kützing [VI]

Thalassionema nitzschioides (Grunow) Grunow [B, D, K, Le, O]

Trachyneis aspera (Ehrenberg) Cleve [A]

Marrying Taxonomy and Ecology: An Attempt

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Freshwater diatoms present an interesting challenge in an era when biodiversity is becoming a major concern. Although tremendously useful indicators of ecological conditions, past and present, lack of taxonomic knowledge limits the potential of ecological interpretation. At the same time the ecological studies that are carried out provide less than optimal feedback to the taxonomic literature. I suggest that appropriate use of available computer-based technologies can integrate these fields to the benefit of both. I further outline the approaches taken in an early and primitive attempt to accomplish this goal, the benefits derived, and the mistakes made and inadequacies of our effort at that time. Thoughtful application of technologies now available has the potential to further integrate studies and expand eventual understanding.

The following is a discussion of an attempt to marry the fundamental approaches of systematic practice to ecological studies. The tools and approaches used are, in retrospect, quite primitive, but there is an underlying logical framework that applies to all such endeavors, in taking on any problem at any time. I hope that discussing the way we attempted to solve problems common to any taxonomically based diatom study, what worked and what didn't, and the mistakes made, will be of some value to current investigators.

I should hasten to explain that the “we” in the previous paragraph is used advisedly. I am not a programmer, so much of the development and implementation was done by other people, better equipped to deal with the intricacies of programming than I. I thank the late Dr. Vincent Noble and Dr. Edward Johnston (Johnston and Stoermer 1976) for enlightening discussions of logical structures appropriate for human — computer interactions. The initial programming was done by Dr. J.K.C. Huang and the system was brought to its most advanced state largely through the efforts of Theodore and Barbara Ladewski (Ladewski and Stoermer 1973; Sicko-Goad et al. 1977). Numerous helpful comments and suggestions were also made by many technical staff and students, which materially helped shape the project.

THE PROBLEM

In the mid 1960s I was a young investigator faced with the rather intimidating problem of investigating the algal flora of the Laurentian Great Lakes. At the time, severe eutrophication problems were apparent in many regions of these lakes (Beeton 1965, 1969). Because of the Great Lakes' tremendous value to the economies of the United States and Canada, considerable resources were available for studies related to water quality. Many of the practical problems that beset the lakes at that time were directly related to algae. Taste and odor problems caused by diatoms in the spring (Vaughn 1961, 1962) and cyanophytes in the summer and fall (Stoermer and Stevenson

1980; Bierman and Dolan 1981; Stoermer and Theriot 1985). *Cladophora* was a nuisance in many regions of the lakes (Wolfe and Sweeney 1980) and generally unpleasant obnoxious conditions were present in many areas. Lake Erie, in particular, became a cause célèbre of the environmental activism of the day, and was widely reported in the common press to be a “dead lake.” This was somewhat problematic to biologists, as the actual problem was over-production, which eventually led to de-oxygenation of the bottom waters in certain areas of the lakes, creating so called “dead zones” where benthic invertebrates were periodically exterminated. In retrospect, the problems of the 1960s and 1970s were only the most recent in a long history of environmental catastrophes, such as epidemics of water-borne diseases (Beatty 1982; Bonner 1991) that devastated communities that drew drinking water from the lakes. For example, the great cholera epidemic of 1854 was estimated to have killed five percent of the total population of the city of Chicago. Collapse of native fish stocks began soon after western settlement of the region (Smith 1972), and culminated in total extermination of some native stocks by 1950 (Beeton 1969) and introduction of many exotic fish species.

One would rationally suppose such a valuable, but clearly damaged, ecosystem would have received careful and comprehensive study, especially considering the large number of well-known academic institutions in the region. Unfortunately, this was not the case. The ecological history of the Great Lakes, in many respects, provides a sterling example of precisely the wrong way to approach management of a large and complex ecosystem. Each successive crisis generated a wave of “directed research” centered on the apparent problem and to a lesser extent, if at all, on its root causes. “Charismatic vertebrates,” in this case fish, were the initial center of attention, and lesser attention and resources were devoted to the rest of the biota or to chemical and physical factors of the environment.

In the case of diatoms, early (in the North American context) exploratory studies were carried out by J.W. Bailey in 1839, first mentioned in 1842 (Bailey 1842a, 1842b), and sent to C.G. Ehrenberg, who more formally published them in his monumental works (Ehrenberg 1845, 1854). These collections are still maintained at the Museum für Naturkunde, Humboldt-Universität zu Berlin, and have been used in more recent studies of the Great Lakes diatom flora (Stoermer and Ladewski 1982). Early pollution studies, particularly in the area of Chicago (Thomas and Chase 1887) and Cleveland (Vorce 1881, 1882) produced collections which are still available, but the majority of taxonomic work undertaken was either un-vouchered, or the material resulting from the study has been lost. For example, studies on early fisheries declines included some work on diatoms (e.g., Ward 1896; Thompson 1896) but we have never been able to locate any of these collections.

Thus, from the beginning it was apparent that the type of supporting references and materials generally assumed to be available to ecological studies were lacking. Although this problem is obvious in the Great Lakes case, it applies to the majority of studies attempting to use diatoms as ecological indicators, as I have argued elsewhere (Stoermer 2001).

APPROACH

Collections

Early on I determined that it was absolutely necessary to maintain a consistent and reasonably well ordered reference collection. It was clear that the available literature of the time was grossly insufficient to support repeatable identifications, so the availability of a reference standard was essential. Maintenance of vouchers, once a routine part of good scientific practice, has largely been abandoned in ecological studies. Logically, it is still necessary for studies involving lesser-known

organism groups, and certainly should be a requirement for studies involving diatoms. It is sometimes argued that maintaining collections is “too expensive” for the competitive world of ecological funding. In a reasonable and logical world the functions of developing a comprehensive taxonomy might be separated, as they are in most large organisms, but this was not the case at the time I began. Although it has become much easier in recent years, due to general recognition of the biodiversity crisis, in the 1960s and 1970s it was virtually impossible to obtain direct funding for taxonomic studies of microscopic eukaryotes.

In our case, I simply made the decision that studies from our lab would be supported by vouchers, as a minimum standard of scientific practice. Our collections are in the form of lots, numbered consecutively. Each lot consists of raw material, cleaned material, and one or more slides. In some cases, we have accepted slides from other investigators and integrated them into the collection without other material, but this is a compromise to be avoided if at all possible. Because we operated primarily from ships, locality information consists of latitude and longitude and brief habitat and collection method descriptors. With the current availability of global positioning system (GPS) apparatus, there is now no excuse not to substitute this unambiguous information for references to inconstant physical landmarks and place names. In the better systems available, it is also possible to directly transcribe information electronically, avoiding the inevitable mistakes introduced by hand transcription.

Index and Pictorial Reference

When working on a system such as the Great Lakes it is easy to escape the illusion that appropriate names for all diatoms encountered exist in the literature, or the equally pernicious assumption that all names in the literature reflect biological reality. For that reason, we have always treated diatom names as entirely arbitrary. Thus, a nomenclaturally correct binomial is quite acceptable but, in our system, an arbitrary name (e.g., aff. *Navicula ambigua*) or a numerical designation (e.g., *Nitzschia* 343) is equally acceptable, if it is supported by an adequate illustration and voucher specimen. This, of course, is a compromise, recognizing the fact that it is not possible to resolve all taxonomic questions while conducting ecological studies, which furnished support for our lab at the time the system was instituted. In order to keep internal consistency, but avoid the extra time and effort necessary to directly compare specimens under a microscope, we resorted to a photographic archive. An illustration of the file used is shown in Figure 1. The elements are an epithet (upper left), one or more photographs (upper right), the dimensions of the specimen(s) (center) and coordinates of their location on a slide (in parentheses) taken from a particular microscope indicated by the letter following. Pictorial representations of specimens circled on a slide, and location of specimen(s) within a particular circle (lower left), photo magnification (lower center) and the collection number (lower right) are also provided. In our original system, additional notes were written on the back of

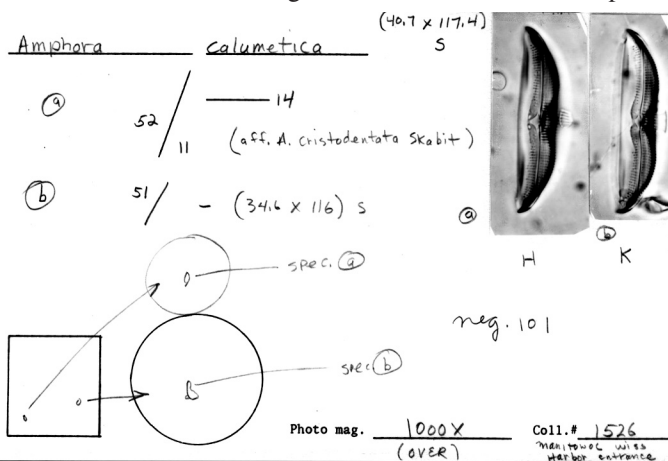


FIGURE 1. Example of card image used for specimen location and identification. See text for explanation.

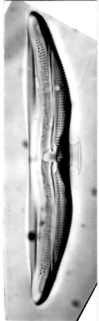
the card (Fig. 2). More than one card could be used to illustrate morphological variation and size series of any given entity (Fig. 3). Of course this is all very primitive, given the current availability of excellent databases that easily incorporate such information and are very easy to use. An example is the File-maker™ template developed by Joynt (Joynt and Wolfe 1999) that can incorporate all these features and considerably more. The really important aspect of using such a system, rather than relying entirely on the published literature is that it allow one to follow the dictum of “when in doubt, sort it out.” In the case of the Great Lakes, it was obvious that many “common species” had different morphotypes that had separate distribution patterns (Pappas and Stoermer 2001), and likely were genetically separate entities. Although separation of taxa on minor morphological variations might seem risky, in terms of supporting ecological interpretation, it is vastly less destructive than under-classification (Birks 1994). In fact, most multivariate statistical techniques will, given that identification is consistent, merely re-aggregate false separations.

See also 1565a (52.9 x 113.7) S Sta GS 13a 45°43.8'N: 86°41.6'W Lake Mich.
 # 1541a (45.5 x 117.3) Y Sta A 3 42° 05.5' N: 86° 43.0' W " "
 891 (43.9 x 124.8) S gv Rock at 70' depth Sta AG-a " "
 1279a (40.1 x 120.4) Y Sta E-1 44° 37.5' N: 86° 18. "
 * #10 1572 (36.0 x 124.1) Y Sta E-3 44° 34' 00" N: 86° 40.0' W Lake Mich.
 85.5/11 → 1574 (43.4 x 117.2) Y Sta GS-22 Lake Mich.
 ANSP - Beyer 802 (35 x 119.5) GV
 # = Amphora sp. # 10
 NLM Slide # 3376 (35.7 x 95.0) J. Frey scope Lake Mich - Sta, 1
 Slide from ANSP 46906a May 1947 L. Mich. Chicago (42.2 x 119.2) Y

FIGURE 2. Notes from reverse of card shown in Figure 1. Because *Amphora calumetica* is relatively rare, emphasis is on locating a range of specimens.

Amphora calumetica (43.4 x 117.2) Y

85.5 / 11



NEG. 60 G
 Coll. # 1574

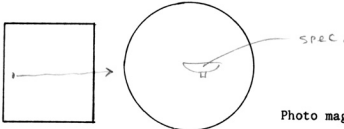


Photo mag. 1000X

FIGURE 3. Example of an ancillary card, showing largest specimen of *A. calumetica* found at the time.

Computerization

In our case, computerization began as a simple data analysis problem. When handling large data sets, verification and data integrity are always problems, and ones that humans seem to handle poorly. Remembering these were the days when computer memories were limited and storage devices primitive. We had quite a struggle with programmers to use names recognizable to humans, and let the computer do the lookup, rather than simplifying the programmer’s task by using a simple sequential list of taxa. Although this seems trivial in the modern context, I think there is an important lesson. Let computers do the simple, purely logical tasks. Save the human ability to deal with more complex tasks, perhaps aided by calculating engines, for the hard parts.

From this humble beginning, we, largely through the efforts of Theodore and Barbara Ladewski, were able to develop an integrated database system useful to both taxonomy and ecolo-

gy. The program's name, through its several incarnations, was FIDO (a programmer's play on the word "phyto"). It consisted of the following elements:

MASTERLIST — A list of all acceptable names. These could be in the form of proper Latin binomials, binomials of convenience, or simple numerical or other arbitrary designation. The important part was that in order to become part of Masterlist, any designation had to be supported by a marked specimen in the collection and a photographic illustration in the master card file. Of course, all of these functions can be incorporated in any modern database. An sample portion is shown in Figure 4.

DECKCHECK — a subprogram that checked all entries for codes not acceptable to Masterlist (coding violations, misspellings, etc.) and "suspicious" data. I am surprised at how few current databases include extended data verification protocols. It is our experience that an appreciable error rate is associated with human data entry and review, no matter how careful the analyst or transcriber, and many of these can be detected by fairly simple data screening protocols.

TAPEIT — A subprogram that wrote files for further processing and a separate permanent archive.

FETCH — A subprogram that retrieved data from the archive, either as hardcopy with summary statistics (subprogram ANALYZE) or output for further manipulation. An example of the former is shown in Figure 5. Note that summary statistics are calculated, including error estimates on counts. A separate, parallel-running system was used to collect and process chemical and physical data. This system was structured similarly to FIDO, which made merging of the databases for analysis relatively simple (Fig. 6). Examples of further manipulations include such things as distribution maps (Fig. 7) and representations of community structure based on multivariate statistical analyses (Figs. 8 and 9).

In the discussion above readers will note that almost all the design criteria were motivated by trying to bring some sort of modern taxonomic understanding to relatively large scale ecological

ACLANCVO	DIF2	11	44	Achnanthes lanceolata var. ?
ACLANCVF	DIF1	11	1432	Achnanthes lanceolata var. robusta
ACLANTOI	DIF1	11	45	Achnanthes lanceolatoides
ACLAPFON	DIF1	11	1727	Achnanthes lapponica
ACLAPPVN	DIF1	11	2338	Achnanthes lapponica var. ninnkii
ACLATEFC	DIF1	11	46	Achnanthes laterostrata
ACLAUENE	DIF1	11	47	Achnanthes lauenburgiana
ACLEMMEQ	DIF2	11	48	Achnanthes lemmermanni ?
ACLEMMER	DIF1	11	49	Achnanthes lemmermanni
ACLEVAND	DIF1	11	50	Achnanthes levanderi
ACLEWISI	DIF1	11	51	Achnanthes levisiana
ACLINERH	DIF1	11	52	Achnanthes linearis
ACLINEFC	DIF1	11	53	Achnanthes linearis fo. curta
ACLINEVF	DIF1	11	54	Achnanthes linearis var. pusilla
ACMARGIN	DIF1	11	55	Achnanthes marginulata
ACMICROC	DIF1	11	56	Achnanthes microcephala
ACHINUUI	DIF1	11	57	Achnanthes minutissima
ACHINUVC	DIF1	11	58	Achnanthes minutissima var. cryptocephala
ACHINUVR	DIF1	11	59	Achnanthes minutissima var. robusta
ACHNOLLII	DIF1	11	60	Achnanthes nollii
ACESTRU	DIF1	11	61	Achnanthes oestrupii
ACESTVL	DIF1	11	62	Achnanthes oestrupii var. lanceolata
ACEERAGA	DIF1	11	63	Achnanthes peragalli
ACEPERAVF	DIF1	11	64	Achnanthes peragalli var. fossilis
ACEINNAT	DIF1	11	65	Achnanthes pinnata
ACELOENE	DIF1	11	66	Achnanthes ploenensis
ACEFCCER	DIF1	11	67	Achnanthes procera
ACRECURQ	DIF2	11	2313	Achnanthes recurvata ?
ACSLAEVI	DIF1	11	68	Achnanthes sublaevis
ACS	DIF2	11	1738	Achnanthes sp.
ACSPECFA	DIF2	11	69	Achnanthes sp. #27
ACSPECRB	DIF2	11	1476	Achnanthes sp. #28
ACSPECAD	DIF2	11	1739	Achnanthes sp. #30
ACSPECRE	DIF2	11	1626	Achnanthes sp. #31
ACSPECAF	DIF2	11	2578	Achnanthes sp. #32
ACSPECAG	DIF2	11	2579	Achnanthes sp. #33
ACSPECAH	DIF2	11	2560	Achnanthes sp. #34
ACSPECOA	DIF2	11	70	Achnanthes sp. #1
ACSPECOE	DIF2	11	71	Achnanthes sp. #2
ACSPECOG	DIF2	11	72	Achnanthes sp. #3
ACSPECOJ	DIF2	11	73	Achnanthes sp. #4
ACSPECOE	DIF2	11	74	Achnanthes sp. #5
ACSPECOF	DIF2	11	75	Achnanthes sp. #6
ACSPECOG	DIF2	11	76	Achnanthes sp. #7
ACSPECOH	DIF2	11	77	Achnanthes sp. #8
ACSPECOI	DIF2	11	78	Achnanthes sp. #9
ACSPECOJ	DIF2	11	79	Achnanthes sp. #10
ACSPECOK	DIF2	11	80	Achnanthes sp. #11
ACSPECOL	DIF2	11	81	Achnanthes sp. #12
ACSPECOM	DIF2	11	82	Achnanthes sp. #13
ACSPECON	DIF2	11	83	Achnanthes sp. #14
ACSPECOO	DIF2	11	84	Achnanthes sp. #15
ACSPECOF	DIF2	11	85	Achnanthes sp. #16
ACSPECOG	DIF2	11	86	Achnanthes sp. #17
ACSPECOR	DIF2	11	87	Achnanthes sp. #18
ACSPECOS	DIF2	11	88	Achnanthes sp. #19
ACSPECOI	DIF2	11	89	Achnanthes sp. #20
ACSPECOJ	DIF2	11	90	Achnanthes sp. #21
ACSPECOV	DIF2	11	91	Achnanthes sp. #22
ACSPECOW	DIF2	11	92	Achnanthes sp. #23

FIGURE 4. A fragment of MASTERLIST printed in the late 1970s. Reading from the left, identity code, a major group and habitat code, two columns of numerical book keeping codes used by the program, and accepted epithets. At present, only about 20% of arbitrary numerical designations have been identified with described species.

Southern Lake Michigan, August 1971

project: SLM	survey number: 5	slide ID: 201
year: 1971	Julian day: 236 (24 Aug)	sample number: 967
station: 201	depth: 0.0 m	volume filtered: 50. ml
latitude: 42° 22.0'	longitude: 86° 18.0'	filter diameter: 2.00 cm
number of cells counted: 1463	volume of water scanned: 1.332 ml	field width: 3.0150 cm
diversity: 2.683	evenness: 0.643	number of half-rows: 6

division	number of species	cells/ml	SE	CV	% pop.
Cyanophyta (blue-green algae)	5	180.1	8.2	0.05	17.635
Chlorophyta (green algae)	16	104.0	3.0	0.03	10.185
Bacillariophyta (diatoms)	36	543.8	9.3	0.02	53.247
Chrysoophyta (chrysophytes)	4	12.6	0.4	0.03	1.230
Cryptophyta (cryptomonads)	1	4.9	0.2	0.04	0.478
Pyrophyta (dinoflagellates)	2	25.1	0.9	0.03	2.461
other	6	0.0	0.0	****	0.0
undetermined	1	150.8	1.6	0.01	14.764
total	65	1021.4	9.9	0.01	100.000

species name	cells/ml	SE	CV	% pop.	species code	type code	half-row counts (1) (2) (3) (4) (5) (6)
Cyclotella stelligera	280.0	2.5	0.01	27.409	CYSTELEI	DIR1	80 62 67 73 55 64
Undetermined flagellate spp.	150.8	1.6	0.01	14.764	FLSPP	DNS3	41 29 39 43 33 31
Anacystis thermalis	122.9	3.1	0.03	12.030	ATHTHERA	BGC1	48 18 34 29 19 28
Fragilaria crotonensis	65.6	5.4	0.08	6.425	FRCPAPUCI	DIP1	23 49 18 9 8 4
Oocystis sp. #1	58.6	2.1	0.04	5.742	OSPEPCOA	GRC2	19 2 18 21 16 8
Anabaena flos-aquae	53.1	8.7	0.16	5.195	ABFLOSA	BGP1	1 0 0 0 0 75 0
Stephanodiscus minutus	42.6	1.2	0.03	4.170	STMINUTU	DIR1	13 14 6 13 11 4
Cyclotella michiganiana	36.3	0.8	0.02	3.554	CYMICHIG	DIR1	13 10 9 8 6 6
Glenodinium sp. #1	24.4	0.8	0.03	2.392	GDSPECOA	DNS2	4 4 6 5 11 5
Asterionella formosa	19.5	1.3	0.07	1.914	ASFORMOS	DIP1	2 3 9 2 12 0
Rhizosolenia gracilis	16.8	1.2	0.07	1.640	RHGACIL	DIR1	5 11 3 5 0 0
Fragilaria capucina	12.6	1.8	0.15	1.230	FRCPAPUCI	DIP1	2 16 0 0 0 0
Crucigenia quadrata	11.2	1.9	0.17	1.094	CRQUADRA	GRC1	0 0 0 0 0 16
Nitzschia holstiana	9.1	1.5	0.17	0.889	NTHOLSA	DIP1	0 0 0 13 0 0
Dinobryon cysts	8.4	0.4	0.04	0.820	DNCYSTS	CHS3	4 1 3 1 2 1
Cyclotella comta	7.7	0.4	0.05	0.752	CYCOMTA	DIR1	4 1 1 0 3 2
Nitzschia palea	7.0	0.2	0.03	0.684	NIPALEA	DIP1	1 1 1 2 3 2
Scenedesmus sp. #2	5.6	0.1	0.03	0.547	SCSPECOB	GRC2	2 2 1 1 1 1
Cyclotella comta var. bodanica	4.9	0.3	0.07	0.478	CYCOMTVB	DIR1	1 3 1 2 0 0
Cryptomonas cyst.	4.9	0.2	0.04	0.478	CRCYST	CRS3	2 1 1 2 1 0
Nitzschia acicularis	4.9	0.1	0.02	0.478	NITACICUL	DIP1	1 1 1 1 2 1
Asterionella sp. #3	4.2	0.5	0.11	0.410	ASPEPCOC	GRC2	0 0 4 0 0 0

FIGURE 5. Example of ANALYZE output taken from a study of whole phytoplankton (diatoms and other groups) in southern Lake Michigan in 1971. Raw data are shown in right hand columns. Summarized data are shown in left columns. The large "undetermined" category consists mostly of microflagellates that cannot be satisfactorily identified with light microscopy.

projects, lacking the sort of traditional floristic and monographic support generally assumed. Perhaps more importantly, once our national science funding establishment began to awake to the fact that we are living in an ecosystem that is probably less than 20% described, this type of data base made it possible to attack some real taxonomic problems, particularly of the Great Lakes region (e.g., Theriot and Stoermer 1984, 1986).

MISTAKES AND PROBLEMS

In retrospect, it is nearly always possible to identify mistaken directions and things that should have been done differently. In our case the worst problems were partially our own fault and partially due to faults in the system. Part of the problem was that we started early in the game. Many diatomists resisted computer applications when they first became available. On the other hand, the funding agencies we dealt

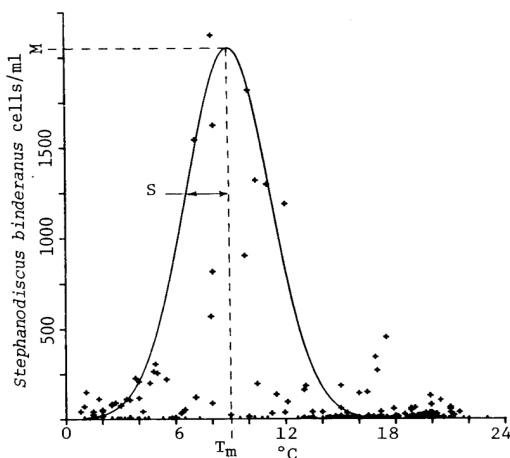


FIGURE 6. Example of data plotted from the study cited in Figure 5, in this case the absolute abundance of *Stephanodiscus binderanus* (Kütz.) Krieg relative to temperature (Stoermer and Ladewski 1976). Curve is fitted to data envelope and estimates of maximum abundance (M) and dispersion (S) are derived. Anomalous appearing points on the right come from inshore stations in the fall when populations are injected into the still warm lake from more rapidly cooling streams.

with at the time were reluctant to provide support dedicated to database development at the local project level. Some spent inordinate amounts of money on commercial database development, but most of these were put together with minimal inputs from the user community and, although they might have incorporated the latest programming tricks of the time, were hideously clumsy and inefficient to use. It has been my observation that most really useful databases incorporate a high level of specific user input, and most really successful programs are locally developed. Since computerization has become popular our national funding agencies have devoted considerable resources to development of several generations of biological databases, but most of this effort has gone to generalized systems that are not particularly appropriate for the problems faced by diatomists.

Part of the problem is the structure and economics of the computer industry. The very rapid expansion of computing power (Moore's Law) causes rapid obsolescence in microcomputers, a trend that the industry has capitalized on. It must also be said that University administrations, at least in this country, have been alert to the fact that the cost of centralized mainframe computer systems usually becomes their responsibility, whereas much of the cost of decentralized systems falls on Departments, or individual investigators. It is also a truism that the quickest way for a software company to go broke is to design a perfect product. It is economically much more rewarding to design something marginally adequate that can continue to be upgraded. All of this militates against development of a stable continuing system, and makes upgrading of a developed system very difficult, in that most resources are devoted to exploiting "exciting" new technologies, rather than adapting existing databases to them as they arise.

In the case of our system described above, we eventually became victims of the technology transition. FIDO was much more complete and easy to use than any of the early microcomputer database programs, and we continued to use it well past the transition from mainframe-based to a microcomputer-based network system. We were unable to obtain support for conversion from either local or national funding sources, so much of the data accumulated during this era exists only on hardcopy and tapes that are rapidly becoming unreadable. Part of the reason for this was that we were somewhat too clever in using "latest technologies" of the day that were specific to the University of Michigan mainframe computer system.

Perhaps the "take home" message for independent laboratories is to develop and use the sim-

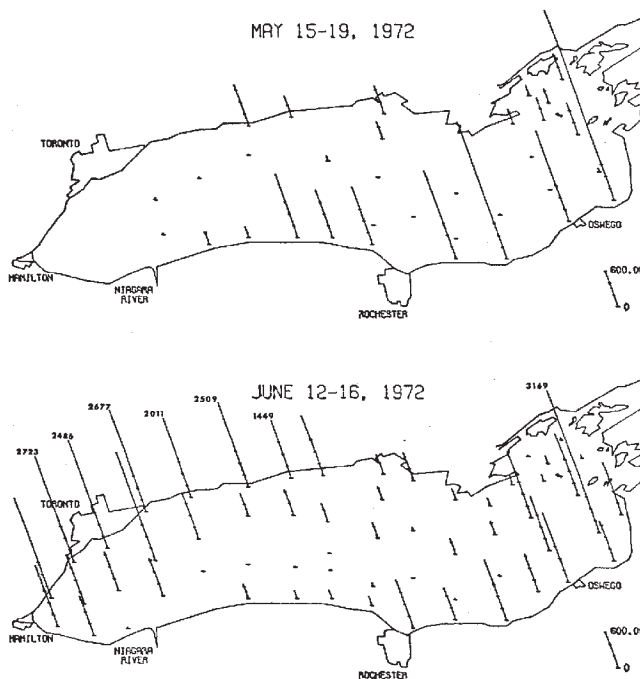


FIGURE 7. Example of species data plotted from a similar study. Distribution of *S. binderanus* in Lake Ontario in the spring of 1972. In the lower image, actual numerical values are given at the top of bars when values are too large to conveniently plot at scale used (from Stoermer et al. 1974).

plest system adequate to your specific needs, and upgrade and maintain it judiciously. Although the latest and greatest in technology is always attractive, pioneers in technology areas often suffer different, but equally painful, slings and arrows as did the geographic pioneers of past centuries. In this regard, I think the “open software” movement offers great promise.

PRESENT AND FUTURE CONSIDERATIONS

And I continue to feel that computer assisted approaches offer the best avenue for “marrying” the needs of taxonomists and ecologists. As I have discussed elsewhere (Stoermer 2001) it is foolish for ecologists to expect taxonomic treatises on diatoms of the type generally available for “higher” organisms to become available in the foreseeable future. This being the

case, it is really necessary to incorporate good taxonomic practice into routine analytical work and assure that project outputs are useful to people whose primary interests are in taxonomy and systematics. At the same time, it behooves the few people in the latter category to be more proactive in addressing the resources potentially available from ecological studies.

At present, it is quite feasible for workstations used in diatom analysis to capture and maintain not only the analysts’ taxonomic decisions, but also images of exemplar specimens such decisions are based on, the pertinent locality information, and the precise location on a slide of each specimen assigned to a given category. At the same time, the analyst should be able to address taxonomic information and identification aids, such as image analysis, directly and in real time.

Whereas the digital tools now available offer exciting possibilities, they also present some real challenges and dangers. The possibilities for enhanced data display and sharing make the possibility of “consensus floras” more attractive. Although this may be useful, and indeed necessary, in the context of a particular ecological project, such efforts can easily degenerate into lowest common denominator solutions that actually retard scientific progress in the general field, rather than advancing it. Diatomists are in a particularly difficult situation in this regard. Taxonomic information in our field is virtually exploding, but most funding agencies, both those traditionally supporting ecological research and those supporting taxonomic tend to take large organisms as their model for understanding diversity. Even at this level, there is no logical expectation of ever establishing a truly “stable” taxonomic system unless we are willing to freeze knowledge in some imperfect

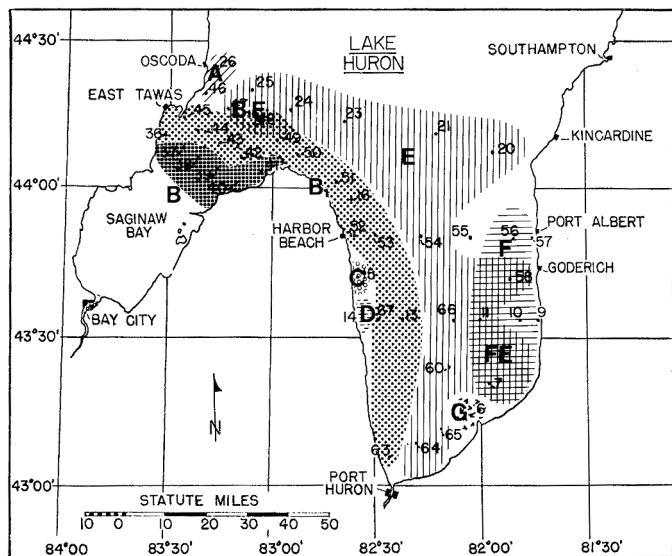


FIGURE 8. Representation of phytoplankton community structure in southern Lake Huron based on samples taken 4-8 June 1974 under west wind forcing. Associations were determined using dimensional ordination and principal components analysis (from Stoermer and Kreis 1980). Materials and phytoplankton from badly polluted Saginaw Bay are entrained by the spring thermal bar and, combined with other local shoreline sources, generate “eutrophic” associations in the western portion of the lake. Mostly agricultural and minor industrial sources from the Canadian shore, also entrained by the spring thermal bar, produce more “mesotrophic” associations in the eastern portion of the lake. The oligotrophic associations expected in a large lake of this type are only found in the offshore waters.

state. In the case of diatoms, the present state is grossly imperfect and the expectation of stability is demonstrably unscientific. Given that there are snares and pitfalls to be avoided, currently available technologies offer those bold and resourceful enough to utilize them great possibilities. These range from purely exploratory — we are still in the era where simple discovery and description probably advances the field more than any other approach — to application and incorporation of available tools for taxonomic and ecological questions.

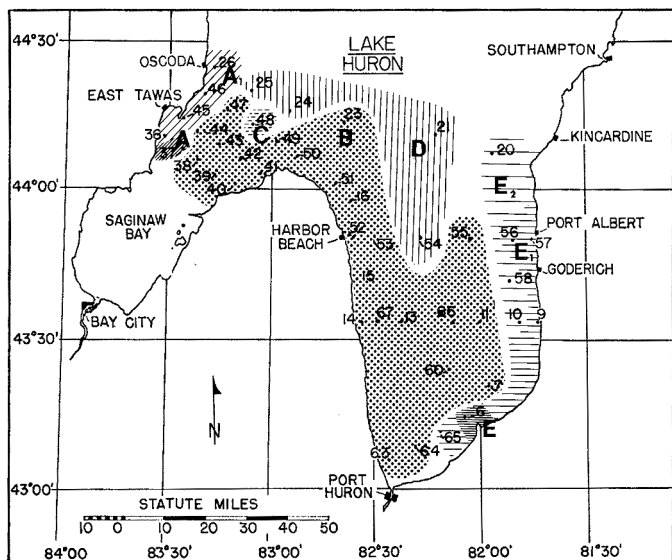


FIGURE 9. Representation of phytoplankton associations from the same study shown in Figure 8. In this case, data were collected 26-31 August under east wind forcing. A large upwelling has occurred in the eastern region of the lake. This combined with local shoreline sources results in atypical phytoplankton associations in the eastern nearshore region. The extent of nutrient re-supply also causes somewhat atypical summer associations in most of the southern portion of the lake, and these communities intrude into Saginaw Bay, as the expected eutrophic communities are transported northward along the Michigan (western) shore. The expected offshore "oligotrophic" summer phytoplankton association is only found at a few stations in the north-central quarter.

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Taxonomy and Ecology: An Inseparable Pair

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Some examples from the diatom genera *Gyrosigma* and *Pleurosigma* are presented to illustrate the following postulates: (1) the notion that taxonomy is an “old-fashioned” activity is a relict of the pseudo-progressive Seventies; (2) faulty taxonomy results in irreproducible pseudo-science, e.g., in unverifiable ecological conclusions; (3) ecological studies on diatoms should take account of the micro-sized biotope in which diatoms live and of the time factor; (4) phenotypically identical populations in widely different habitats may constitute different “ecospecies.”

The central theme of this workshop is the synergy between taxonomy and ecology in the study of diatoms and the application of its results. To set the stage, I will try to illustrate what may happen if this synergy is disregarded with some examples from the genera *Gyrosigma* and *Pleurosigma* — not because they are particularly important in this respect, but as a result of personal interest. Call it a “travelogue” in which we travel from one taxon to another and from one issue to the next. In addition, I will offer some personal comments on the financial, political and societal context in which we have to study diatoms.

THE TAXONOMIC SITUATION

In many countries including The Netherlands, the situation for diatom taxonomy is deplorable. No specific budgets are available and expertise in the practical application of diatom taxonomy is at risk of being destroyed by budget cuts that may lead to the closure of entire departments.

This is partly due to the fact that funding for basic research is becoming difficult to secure, because research may be at the mercy of leaders who think that Science can be profit-driven. But another factor involved is the widespread image of taxonomy as an unimportant activity, and this is a serious problem we must address.

The Image of Taxonomy

In the first place, the very nature of taxonomy is often unclear, even to some diatomists. Students think that the short courses they receive in identification of the more common diatoms constitute “taxonomy.” Taxonomy, however, is the fundamental investigation of organisms aiming at a circumscription of their biological (that is, genetic) individuality.

Secondly, in some circles there is a strong aversion to what they *think* is “diatom taxonomy” because in their past experience this has resulted in long lists of names permitting no scientific conclusion whatsoever. A floristic inventory does not equate to taxonomy and it’s the diatomists’ own fault that this antipathy has arisen.

Thirdly, there is the widespread misconception that taxonomy consists of the description of

new species or varieties. The realisation that taxonomy may instead have to start with the *elimination* of established but invalid “pseudospecies” may come as a surprise to workers not specialising in the subject.

Finally, the practice of taxonomy, with its careful procedure of literature research, tracing herbarium materials, determining synonyms and formal typification is dismissed as “old-fashioned” by some. Many biologists are unaware that the only permissible taxonomic procedure for diatoms (as for other algal groups and higher plants) must follow the rules of the ICBN (International Code of Botanical Nomenclature).

In this situation we must formulate convincing reasons why diatom studies involving taxonomy are important and should be supported. Unfortunately, the principal character separating humans from other animals — the Pursuit of Knowledge — is no longer regarded as sufficient *per se* by potential funders. Therefore, our arguments should in a sense also be “politically correct,” fitting in with the societal-political issues of the moment. This may seem a mercenary attitude, but it merely recognises the reality that science is pursued in a societal — and thus political — context.

Taxonomy and Ecology: Inseparable

The examples given here relate to the diatom genera *Gyrosigma* and *Pleurosigma*. These diatoms illustrate the lack of taxonomic research very well, as evidenced by the amazing fact that of the many thousands of diatom illustrations published in the course of 85 years in Schmidt’s *Atlas* (1875–1959) *not a single one* showed a representative of these genera!

Neglect of taxonomy violates the most basic rule of science. For human communication of *any* nature to make any sense at all, the entities under discussion must be unambiguously defined. If no proper taxonomic separation were made between *Canis lupus* and *Canis domesticus*, one would conclude that the development of human society since the Neolithic has been associated with an explosive increase in the population of wolves.

Only when the identity of an organism has been unambiguously fixed does it become possible to determine its biological characteristics: its physiology, nutritional requirements, habitat and biogeography. Only when these are known, the organism can become a source of information on the Earth’s history. This is especially the case for diatoms, whose siliceous exoskeleton is both taxonomically informative and durable, permitting conclusions over many millions of years.

EXAMPLE (FIG. 1): Published studies on the Dutch Wadden have described an abundant presence of *Gyrosigma spenceri* (Quekett) Griffith et Henfrey. The type material of this diatom indicates a freshwater environment, however. This would imply that either the Dutch Wadden Sea is subject to massive freshwater influx (which is not the case) or that *Gyrosigma spenceri* has an ecology ranging from freshwater to fully marine. Taxonomic studies have shown, however, that *Gyrosigma spenceri* — for 150 years one of the most frequently recorded members of the genus — is merely a later name for *Gyrosigma acuminatum* (Kützing) Rabenhorst, a purely freshwater diatom. In addition, it became clear that at least 6 different species with different ecologies ranging from freshwater to brackish and fully marine have been called “*Gyrosigma spenceri*,” or varieties thereof. The previous studies thus presented irreproducible results because of taxonomic errors (Sterrenburg 1995, 1997; Sterrenburg and Underwood 1997).

The taxonomy of *Gyrosigma* and *Pleurosigma* species is a challenge, but their ecology is not particularly diverse. The freshwater species all avoid acidic, oligotrophic waters but do not appear to permit fine ecological distinctions. Also, especially in Holland there are major gradients in salinity from freshwater via brackish to fully marine and these show that some *Gyrosigma* and a few *Pleurosigma* species can tolerate a wide range of salinity. The genera clearly flourish best in the

marine littoral and in general they favour the presence of organic detritus, but for really sensitive ecological indicators other diatom genera offer better candidates.

EXAMPLE (FIG. 2): The most extreme case so far observed is *G. wormleyi* (Sullivan) Boyer, also on record as the illegitimate synonym *G. parkeri* (Harrison) Elmore. Its type material is definitely freshwater and I have indeed collected it in non-saline Dutch waters, but I have also found flourishing populations in the marine littoral of Cameroon, for instance. Also, Tiffany and I have verified that it grows abundantly in the Salton Sea, California, which is 30% saltier than seawater! Morphologically, the marine and the Salton Sea populations are completely identical to the freshwater type specimens so that identifications arrive at the same morphospecies. One could think of two different explanations: (1) *G. wormleyi* is very euryhaline by nature, any population being able to grow under widely different conditions of salinity; or (2) The populations from highly saline waters observed might not be genetically compatible with the type. The latter might apply to the Salton Sea populations in particular, because the Salton Sea is man-made and the result of an engineering mishap about a century ago. This caused the Colorado River to be dumped into a natural depression in the Californian desert and as the salinity of this artificial lake increased over time, an originally “freshwater population” from the Colorado River may have adapted and drifted apart genetically. One would need to verify whether these individuals can still cross with their parent line — if not, they should be considered a different “ecospecies.”

This shows that we may need to consider the species concept from the ecological as well as the traditional taxonomic perspectives (see Sterrenburg 1994; Sterrenburg, Tiffany, and Lange 2000).

Spatial and Temporal Factors

Examination of the literature of freshwater diatom surveys that include ecological data raises the question how reliable such “traditional” data really are. Typical sampling methods comprise too

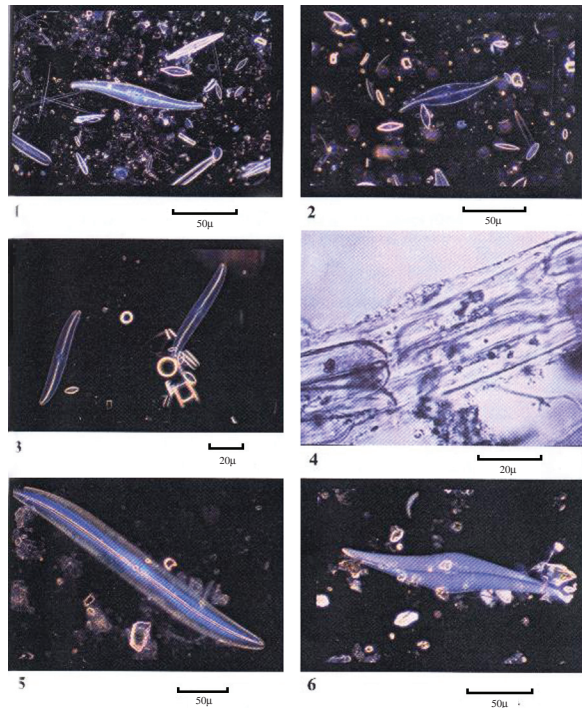


FIGURE 1. Specimen typical of “*Gyrosigma spenceri*” identifications in the literature: *G. acuminatum* from a ±freshwater ditch, North Holland. Bar = 50 μ m.

FIGURE 2. *Gyrosigma wormleyi*, Salton Sea, California, USA. Morphologically this is a complete match for the freshwater type specimens. Bar = 50 μ m.

FIGURE 3. Specimens matching the protologue of *Gyrosigma exilis* from the only population observed so far in The Netherlands (North Holland). Bar = 20 μ m.

FIGURE 4. Live specimens of *Gyrosigma obliquum* in mucus tubes, Samoa, Pacific. Bar = 20 μ m.

FIGURE 5. *Gyrosigma spectabile* from one of the “standing crops” in the Florianopolis area, Brazil. Bar = 50 μ m.

FIGURE 6. Specimen fully matching the New Zealand type specimens of *Pleurosigma sterrenburgii*, from one of the rich populations seen in the Jadebusen, North Germany. Bar = 50 μ m.

broad a scale for microscopic, rapidly dividing organisms such as diatoms, both spatially and temporally. Scaling down could reveal much more about the taxonomy and ecology of diatoms.

Suppose that physico-chemical analysis of a water column sample from a stagnant freshwater pool yields a certain pH and certain values for salinity, phosphate etc. Certainly, these values do not define the ecology of the bottom-dwelling as well as the epiphytic and planktonic species. Such a stagnant pool — because of the absence of mixing — shows a series of gradients in temperature, insolation, pH, mineral concentrations and organic compounds that may favour or inhibit the growth of certain species. When organic matter in the mud decays, this will lead to strong local physico-chemical gradients, which could lead to major changes in the diatom assemblage over very short distances. For micro-organisms we would need to scale down properly, using microsensing instead of analysing “a bulk water column sample.”

EXAMPLE: (FIG. 3): This small freshwater *Gyrosigma* matches the protologue for *G. exilis* Grunow. It had never been described for The Netherlands and the only locality where I have found it is a spot measuring only a few square meters: a sandy slope wetted by a trickle of freshwater in a reclaimed area called the Wieringermeer in the province of North Holland. In this tiny area, I have found that the species has continued to grow for about 20 years. Topological isolation is not involved, the physico-chemical conditions appear to be the same as everywhere else in the area and although some ecological factor is likely to be involved, I can offer no explanation.

For intertidal mudflats in the marine littoral, one does not expect to find major local ecological differences over short distances as intensive mixing is involved, but the time factor also needs to be considered.

EXAMPLE: (FIG. 4): When this sample was collected from an intertidal mudflat on the coast of West Samoa, the temperature of the surface mud was near 50°C and evaporation had led to the appearance of salt crusts in some places — indicating a hypersaline habitat. A few minutes later, a torrential monsoon rain submerged the site ankle-deep in cool and only mildly brackish water. The diatom flora here has to be resistant against severe osmotic shock and probably for protection, *Gyrosigma obliquum* Grunow (like several other diatoms from such habitats) can develop thick mucus tubes. An ecological “snapshot” of the habitat may therefore be insufficient, one must consider the ecological extremes to which the diatom may be exposed during its lifetime (Sterrenburg 1989).

In other words, we may have to look at diatom ecology at the proper spatial and temporal scales. Such an integration of ecology and taxonomy could certainly yield valuable data from the purely scientific point of view, but I am not sure we could convince many politicians to finance it.

The Environment

Studies on the impact of human activities on the environment are certainly regarded as “politically correct.” A previous generation of engineers and scientists was able to pursue a career studying acid rain and its effects. For this subject, diatoms have indeed contributed valuable data — provided there was a sound taxonomic basis for identification of species tolerant to low pH. But because electricity generation is now much cleaner, acid rain as a source of money has dried up in the developed countries.

Global warming was another good source of potential income for research but it may not be easy to find strong arguments for improved diatom taxonomy in support of short-term global warming studies — in contrast to long-term paleoclimatology, of course. And because of the recent political dissent over the Kyoto protocol, the immediate future for global warming studies looks somewhat chilly anyway in certain countries.

Water quality studies continue to be a modest but steady source of income for some diatomists, but it may not be easy to convince our paying customers of the necessity of further development of taxonomy here. Usually, customers want to hear simple and unambiguous answers to their questions. Customer relations would not receive a major boost if we told them that we'd have to spend lots of extra time and money to answer their question because we're not really sure our taxonomy is correct! Scientifically, this may be quite true, but we'd eliminate ourselves from the market.

BIODIVERSITY

The situation becomes different, however, if we consider taxonomy and ecology in relation to studies on biodiversity. And "biodiversity" *has* become a word even government circles have become familiar with. It is certainly politically correct to express concern about the extinction of species due to human impact. Therefore, a taxonomically impeccable record of verified distribution patterns is highly valuable. The basic shortcoming in the concern about the loss of species diversity expressed by non-scientists is that we *should first know what there is in an area before we can determine what we are losing* — and that is far from being the case.

If we take the marine littoral as an example, a survey of the literature will immediately show that data on the diatom species diversity of many areas of the globe may amount to a single publication based on one or two poorly documented samples collected in the 19th century. This is especially true for tropical coasts, and there the situation is particularly serious for three reasons:

- (1) these may be the areas where species diversity in certain diatom genera may be *particularly high*;
- (2) they may be under severe human-related ecological pressure — for instance, the large-scale destruction of coastal wetlands and mangrove forests, or pollution by industrial effluents or sewage;
- (3) but tropical and subtropical countries are often precisely the areas where funding for research is *minimal*!

EXAMPLE: (FIG. 5): The total verifiable documentation of *G. spectabile* Grunow ex Peragallo consisted of a schematic drawing of a single specimen and minimal diagnosis published in 1891. De Souza-Mosimann, Fernandes, and I have verified that this presumably "rare and obscure" species, which had not been recorded for over a century, is actually an abundant member of the standing diatom crop of the coast of South Brazil to French Guyana (see Sterrenburg, de Souza-Mosimann, and Fernandes 2002)!

But even for our own backyard, great improvement in diatom biodiversity data is possible — and necessary before we can draw useful conclusions.

EXAMPLE: (FIG. 6): Ten years ago, Stidolph described this diatom as a new species from New Zealand. I had never found it in samples from any other area, e.g., the Indian Ocean, Pacific, Caribbean, Arabian Gulf or Mediterranean until a few months ago when I found large populations in the German Jadebusen! This second, literally antipodal, record of *Pleurosigma sterrenburgii* Stidolph constitutes the greatest extension of biogeography possible, and, since then, it has been observed in large numbers in that area (Witkowski, pers. commun.; Stidolph 1993).

To illustrate the actual species diversity in *Gyrosigma* and *Pleurosigma* for The Netherlands: the Dutch flora of Van der Werff and Huls recorded about a dozen taxa for these genera. About half of these are synonyms or confused entities, so there remained only about half a dozen Dutch sigmoid diatoms whose identity was reasonably certain. So far, I have recorded about 60 species from these genera in the same area — and more continue to be found. With a Macchiavellian line of rea-

soning, it could be claimed that human activity does not harm Nature at all but can instead lead to a *ten-fold increase in species diversity*.

Although a combination of taxonomy and ecology properly scaled in space and time would be ideal, even a more modest effort to get an insight into the huge diversity of diatoms, with *verified* data on their biogeography and reliable information on their autecology, is necessary and can be argued to be compatible with the current societal-political trends. It can contribute to the challenge raised by the All Species Foundation (www.all-species.org) to catalogue all the World's living beings!

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Microalgal (Microphytobenthic) Biofilms in Shallow Coastal Waters: How Important are Species?

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Microphytobenthic biofilms, dominated by diatoms, are important components in many intertidal and shallow water marine environments. Much of our understanding of their functioning comes from studies that have not treated species composition as a significant factor. Conversely, many studies concerned with species distribution have not encompassed our understanding of the dynamic nature of biofilms. This paper presents data to show there are significant differences in the behaviour and physiology of different taxa of diatoms within the same biofilm, and that species respond differently to the external nutrient environment. These data indicate that consideration of the importance of the species-niche (both autecological and synecological) can be beneficial to both taxonomy and ecology.

In many marine and estuarine environments, large areas of shallow intertidal and subtidal habitats are dominated by microalgal assemblages. These are known by a number of terms, epipsammon, epipelon, periphyton, benthic microalgae and microphytobenthos (Round et al. 1990). Although these communities are mixed assemblages containing representatives of many algal groups, those communities found on muddy, and to some extent, sandy sediments are dominated by diatoms (Admiraal 1984; Underwood and Kromkamp 1999). Overall species richness of marine benthic diatoms is quite high, particularly over geographical scales (Witkowski et al. 2000), yet within a particular environment, it is more usual to find only a few (20+) taxa that are numerically dominant within assemblages (Admiraal and Peletier 1980; Colijn and Dijkema 1981; Underwood 1994; Thornton et al. 2002).

The ecology of these systems has been extensively studied, in particular estuarine intertidal habitats, saltmarshes and in shallow coastal seas, primarily the Baltic. From these studies we know that in ecological terms, microphytobenthic biofilms are extremely important in ecosystem functioning. The primary production of microphytobenthos can be very high, and this can contribute a significant proportion of the autochthonous carbon production in estuarine and shallow lagoon environments (Underwood and Kromkamp 1999; Cahoon 1999). Microphytobenthos also mediate a whole range of biogeochemical processes, such as nutrient exchange and nitrogen cycling and attenuation of nitrogen loads (Dong et al. 2000; Thornton et al. 2002). This is because biofilms occur at the interface between the water column and the sediment, and within the relatively narrow zone, high rates of biological activity can result in oxygen supersaturation, release of organic carbon exudates, anaerobic conditions and rapidly changing chemical gradients (Underwood and Kromkamp 1999). Microphytobenthos can sequester phosphorous, silicates and nitrogen from the water column and both enhance, and inhibit, denitrification and coupled nitrification-denitrification (Sundbäck et al. 1991; Rysgaard et al. 1994; Dong et al. 2000). As such, extensive areas of

biofilms can significantly attenuate the flux of nutrients through coastal areas (Thornton et al. 2002). Another property of biofilms is their ability to increase the stability of sediments, usually through the production of mucilage (extracellular polymeric substances, EPS) (Smith and Underwood 1998, 2000; de Brouwer and Stal 2001), which acts to increase the critical erosion stress required to initiate erosion of flocs from the sediment bed (Widdows et al. 2000; Tolhurst et al. 1999; Underwood and Paterson 2003). Thus biofilm-inhabited sediments are more difficult to erode, and biofilm-inhabited sediments more rapidly trap and hold, fine sediments (Underwood and Paterson 1993, 2003).

As this brief overview makes clear, diatom-rich biofilms play a very important role in the ecology of shallow-water systems. However, a study of the literature clearly shows that functional studies on biofilms predominantly ignore species composition, and treat the assemblage as a black box — “a biofilm.” Conversely papers dealing with species distribution tend to rely on a very descriptive approach to defining the environment, usually in terms of nutrient concentrations, salinity and temperature. These latter (state) variables tend to be taken as a valid description of the potential niche of a species, without regard to the changeable nature of these variables over short term (hours - fluxes of nutrients rather than concentrations, diel fluctuations in temperature) and medium term (days — changes in tidal exposure period, meteorological conditions) time scales.

Can knowledge about the species of diatoms in a biofilm improve on our understanding of biofilm processes? Why should functional ecologists be interested in species composition, and therefore by association, require a good and robust taxonomy? This paper aims to show that, at least in two areas, photosynthesis and response to nutrients, species-information can improve our understanding of biofilm function.

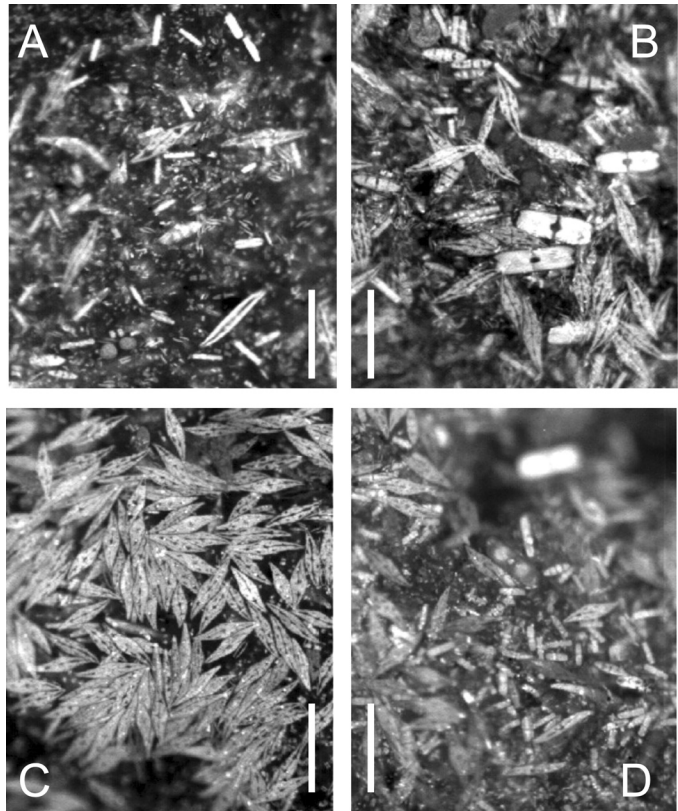
PHOTOSYNTHESIS AND DIFFERENCES BETWEEN BIOFILMS

In general, it has been shown that light intensity influences the rate of photosynthesis and overall primary production of biofilms (Underwood and Kromkamp 1999). This reasoning underlies many models that predict benthic primary production on the basis of irradiance data and biomass (Serôdio and Catarino 2000). However, this view is currently being reassessed. This is partly because some studies are based on using slurry systems for measuring photosynthesis. Using a slurry (a mixture of biofilm and sediment) removes the 3D structure of the biofilm and prevents cells from following their natural migration patterns. Placing cells in suspension means that they behave like phytoplankton and respond to light accordingly (Underwood and Kromkamp 1999). Recent developments in imaging technology have now made it possible to measure the photosynthetic performance of different cells within intact biofilms (Oxborough et al. 2000). In the natural environment, microphytobenthos show complex behaviours in response to light. In a study of microphytobenthos in the Tagus estuary, Perkins et al. (2001) showed that during tidal exposure when light levels are low, cells accumulate at the surface, but migrate away from the surface at high irradiances. This was described as a type of behavioural photoacclimation. In the Tagus estuary (Miles and Sundbäck 2000; Perkins et al. 2001), and Colne estuary (Perkins et al., unpublished data), this can result in highest rates of photosynthesis early in the morning, despite light levels increasing towards midday, as cells position themselves in an optimum light climate within the biofilm. These movements can be very rapid, and the surface community can change from a biofilm dominated by diatoms to one dominated by euglenoid algae in 10 minutes as light intensity increases (Perkins et al. 2002). Similar patterns of migration and migration responses of different microphytobenthos have been shown using low temperature electron microscopy coupled with measurements of spectral reflectance off mudflats (Paterson et al. 1998). Such micro-migrations are superimposed over

the tidal migration of cells to and from the sediments surface. Fig. 1A–D shows the change in species composition at the same point on the surface of a biofilm over a diel exposure period. Substantial changes in species composition are evident, so that measurements over a period of time will be measuring the photosynthesis of different populations of diatoms. Imaging has revealed that individual taxa can have significantly different photosynthetic efficiencies (the rate at which captured light energy is converted to electrons and used in photosynthesis). Oxborough *et al.* 2000 showed that the photosynthetic efficiency of three diatom species (*Pleurosigma angulatum* (Quekett) W. Sm., *Gyrosigma littorale* (W. Sm.) Griffith *et Henfrey* and *Plagiotropis vitrea* (W. Sm.) Kuntze differed from each other at lower light intensities, and all three species were significantly less efficient than *Euglena* sp. at higher irradiances ($> 500 \mu\text{mol m}^{-2} \text{s}^{-1}$).

Differences between species also appear during tidal exposure cycles. Fig. 2A shows the composition of a surface biofilm during a diel exposure period. Three diatom taxa dominated this particular biofilm (*P. angulatum*, *P. vitrea* and *Nitzschia dubia* W. Sm.), with small *Nitzschia* spp becoming abundant at the end of the tidal period. At the beginning of the day, the three diatom taxa had the same photosynthetic efficiency, but by midday, all three taxa showed reduced efficiencies, but also that there were significant differences in photosynthetic efficiency between species (Fig. 2B). These differences will combine to produce overall biofilm functioning, and may even be selective for particular species under different conditions. These hypotheses need to be tested, but it is evident from these data that all cells within a biofilm do not behave the same. Thus ecological function is a property that requires knowledge of species composition (including good taxonomic resolution).

This requirement to incorporate species and assemblage information with measures of community functioning is clearly shown in a study of tropical microphytobenthos. Measurements of photosynthetic efficiency, characterisation of the light climate within the sediments, algal biomass and maximum rates of relative electron transport (a proxy measure for photosynthesis) were found to be significantly different between microphytobenthos from different habitats (Underwood 2002). The conventional explanation (in the absence of any species composition information)



FIGURES 1A–D. Temporal changes in the surface composition of a microphytobenthic biofilm from the Colne estuary, UK, over a tidal exposure period taken using a microscope-based, fluorescence imaging system (Oxborough *et al.* 2000). All images are of the same area at (A) 07.30 h, (B) 11.00 h, (C) 15.30 h, (D) 18.00 h. Scale bar = 200 μm .

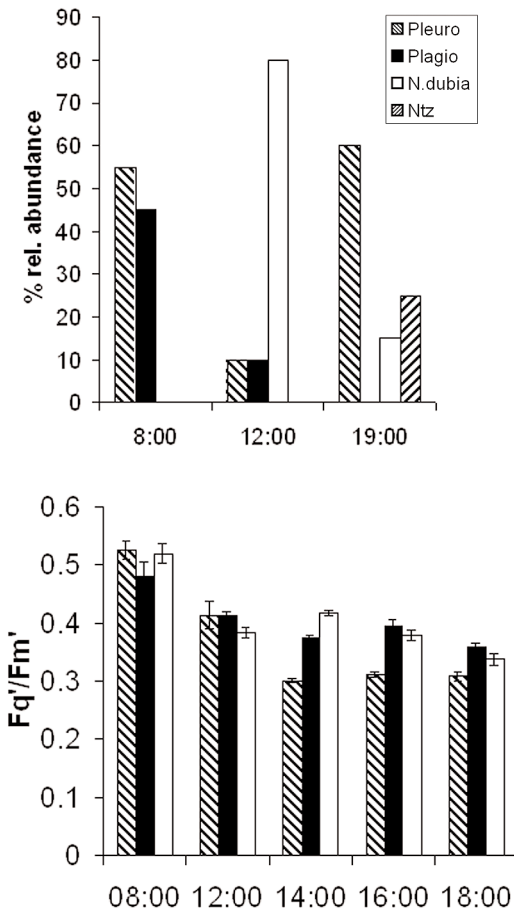


FIGURE 2. (A). Relative abundance (%) of 4 taxa of benthic diatom present at the surface of a biofilm at 3 periods over a diel cycle. (B) Measures of individual cell photosynthetic efficiency (Fq' / Fm') showing significant differences between taxa during the later part of the diel period. Values means \pm SE, n = 10 or greater.

Navicula species. The shallow subtidal biofilms in the coral sands and seagrasses had a different flora, dominated by *Diploneis*, *Amphora*, *Psammodictyon*, *Tryblionella* and *Mastogloia* and showed little evidence of vertical migration in response to light stress or tidal rhythms. Thus the differences in biofilm function can also be mapped onto differences in species composition as well as the more conventional explanations of nutrient limitation or photoacclimation.

SPECIES AS NUTRIENT INDICATORS

There are increasing data to support the hypothesis that microphytobenthos can be used as indicators of environmental conditions, particularly nutrient concentrations and salinity. This is leading to the development of trophic indices for marine and estuarine systems similar to those currently available for freshwaters. The estuarine environment is a particular challenge in this respect,

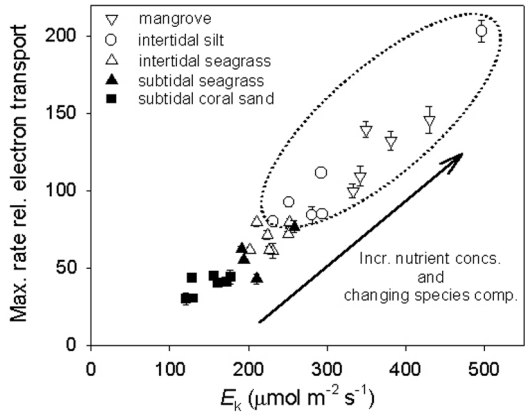


FIGURE 3. Relationships between the maximum relative electron transport rate and the light saturation parameter E_k for microphytobenthic biofilms from 5 different tropical marine habitats, showing the significant correlation with nutrients, but also changing species composition and the occurrence of vertical migration within particular biofilms (dotted ellipse). (Redrawn from Underwood 2002).

would be to explain the significant correlations between maximum rates of relative electron transport (a proxy measure for photosynthesis) and E_k (the half light saturation coefficient) with nutrient concentrations in terms of nutrient limitation causing biofilms to be less efficient. However, this significant “nutrient photosynthesis” relationship also corresponded directly with differences in species composition between biofilms (Fig. 3). Biofilms showing the highest values of photosynthetic parameters also exhibited strong vertical migration in response to light and comprised many large, motile taxa, such as *Hantzschia virgata* (Roper) Grun., *Berkeleya scopolorum* (Bréb.) Cox and

partly because of the significant human impacts on estuarine habitats, due to proximity of large centres of human habitation and industry (Hessen 1999; Nedwell et al. 1999), but also because of the wide range of conditions estuarine taxa have to tolerate. Thus estuarine microphytobenthos appear to be tolerant of a fluctuating range of conditions (Admiraal 1984). In the Baltic Sea, various diatom taxa have been shown to be sensitive to the well-defined and constant salinity gradient present in the Baltic Sea (Snoeijs 1993; Snoeijs and Vilbaste 1994; Snoeijs and Potopova 1995; Snoeijs and Kasperovièiene 1996; Snoeijs and Balashova 1998). This stable gradient may allow quite narrow species niches to be defined, but it would be incorrect to attribute the same salinity niche to one of these taxa if it was found in a meso- or macrotidal estuarine environment. However, even in the more variable environment of tidal estuaries, species shifts with nutrients can be demonstrated. A number of field studies, long-term data sets, experimental-nutrient enrichments, experimental studies in mesocosms and on isolated cultures have all indicated that some taxa (e.g., *Fallacia pygmaea*, *Navicula salinarum*) have greater tolerance to high nutrient concentrations and organic loads and may potentially be indicators (Sullivan 1976, 1981; Admiraal 1984; Peletier 1996; Underwood et al. 1998; Sullivan 1999). It is clear that broad scale patterns of species variability reflect changed environmental conditions (sediment type, water flow, salinity). However, more detailed studies are needed to demonstrate that the diatom community at a particular site will change if nutrient loads increase or decrease (Peletier 1996). In particular, experimental testing of hypotheses derived from correlative field measurements of species occurrence and environmental variables, to demonstrate causes and mechanisms for changing species composition is needed. For example, Figure 4 shows the maximum intrinsic growth rate (μd^{-1}) of cultures of *Navicula phyllepta* Kützing isolated from the Colne estuary, U.K. and grown in a range of nitrogen con-

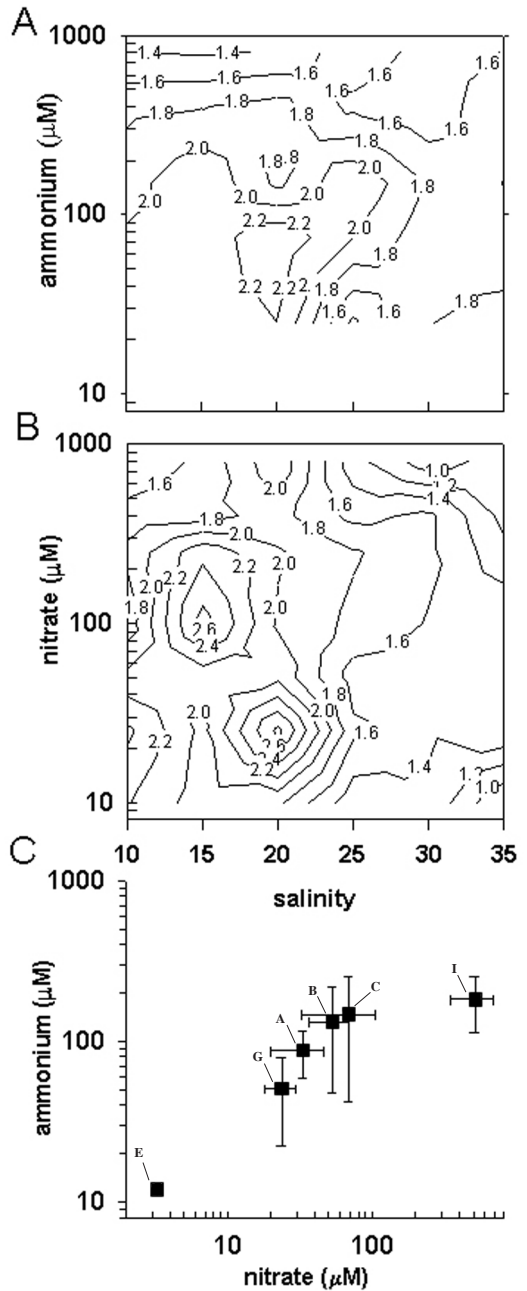


FIGURE 4. Maximum intrinsic growth rates (μd^{-1}) of *Navicula phyllepta* grown in culture in a range of ammonium and salinity (4A) or nitrate and salinity (4B) conditions. (4C) Occurrence of various diatom assemblages related to ammonium and nitrate concentrations over a 12 month period in the Colne estuary, UK. Assemblages A, B and C were dominated by *N. phyllepta*. (Redrawn from Underwood and Provot 2000 and Thornton et al. 2002.)

centrations (ammonium and nitrate) at different salinities. *Navicula phyllepta* showed maximum growth within an inorganic nitrogen range of between 50–300 μM and at salinities between 15–25 ppt (Fig 4A, 4B). These culture data agree closely with field data, where assemblages dominated by *N. phyllepta* were present in the estuary when nitrate and ammonium concentrations were within this range (Fig 4C). Underwood and Provot (2000) showed that three taxa of *Navicula* had different, but overlapping nitrogen and salinity optima, and these may be partly an explanation for field patterns. Such experimental approaches do need to consider the physiological responses of cells to changing environments, particularly the ability of cells to adapt to changing conditions.

CONCLUSIONS

There are good reasons to encourage a “marriage” of taxonomy with ecology. For the reasons outlined above, the ecological importance of biofilms has meant that substantial funding has been provided for scientific investigations of biofilm functioning in the marine environment. Such studies have been quick to embrace new technologies to increase the resolution of measurement down to the microscale and now it is possible to measure and visualise the environment at a scale comparable with that of individual diatom cells. This provides a great opportunity to link ecosystem functioning with knowledge of individual species. Up till now, much of this ecological research has tended to ignore species composition as a factor in biofilm functioning. New techniques, such as *in situ* quantitative PCR and using fluorescently-labelled markers to identify species, provide a mechanism for taxonomic expertise to interface with functional studies. This does require diatom taxonomy to broaden its view on what characteristics of diatoms are important taxonomically and a willingness to “widen” the species concept away from the rigid morphological definition of a species. The “marriage” will be harmonious when separations of species on taxonomic grounds are found to match, in some way, the functioning of those taxa in the environment. There is plenty of scope within the marine microphytobenthos to investigate the concept of the species-niche in its broadest sense (both autecological and synecological) and to use this information in both taxonomy and ecology.

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Structural, Biochemical and Molecular Investigations on Wadden Sea Diatoms: Field Studies and Laboratory Experiments

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WADDEN SEA-INHABITING DIATOMS

Wadden Sea sediments are inhabited mainly by diatoms, euglenoids and cyanobacteria. Diatoms may dominate these habitats with respect to species diversity and cell density and often exceed cell numbers of more than 10^6 per cm^2 sediment. Several sediment-inhabiting diatom species show a rhythmic vertical migration (VM) behaviour and move up onto the surface when the water drains off and down into the sediment bed with the incoming tide (Harper 1969, 1976; Happey-Wood and Jones 1988; Hopkins 1966; Palmer and Round 1965; Round and Happey 1965; Round and Eaton 1966). They, thus, have to face dramatic changes of several physical and chemical parameters in their natural habitat: tidal inundation results in reduced concentrations of gases and lowered light intensities, but gives rise to almost constant values of temperature, salinity, pH and nutrients. During tidal emersion these parameters may vary drastically: salinity and temperature may increase and lead to desiccation and temperature stresses, respectively, whereas light intensities of up to $2000 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ may cause photoinhibition (Underwood 2002). The dramatic changes will have a great impact on the community structure on a long-term scale (months and years) and, on a short time scale (minutes and hours), will result in adaptation processes within the cells. For investigating both kind of responses, temporal changes in community structure and short-term cellular adaptation processes, it is necessary to use “old-fashioned” classical methods of diatom research and “modern,” i.e., molecular, biophysical, and biochemical methods in parallel. In the following sections, we give a short summary of the methods used in our lab to study Wadden Sea diatoms. The methodological approaches have now been well established for laboratory experiments, and it is a challenge to transfer and use this repertoire of methods directly in the field or on field samples.

CLASSICAL TAXONOMY AND IDENTIFICATION OF WADDEN SEA-INHABITING DIATOMS

To study long-term changes of the diatom community the use of classical methods for diatom identification are indispensable. Usually, acid-cleaned diatom frustules are used for this purpose. Wadden Sea sediment samples collected at regular intervals over periods of several months or even

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years from the same sampling area can be easily treated with HCl and H₂O₂ as oxidative agents followed each by repetitive washing steps with water. Light microscopy and scanning electron microscopy give information on species diversity and species abundances. These data allow statements on local and temporal successions of distinct species at a given habitat. A major disadvantage of this approach is that no information on the distribution of individual cells within the sediment bed becomes available. For this, sediment cores have to be withdrawn, frozen and sectioned horizontally into slices of 200 to 500 μm width (de Brouwer and Stal 2001; Kelly et al. 2001). The slices can also be used for frustule preparations.

LABORATORY TIDAL MICRO-ECOSYSTEM AND MINI-MESOCOSMS

Vertical movement can be investigated in the laboratory under almost natural conditions. Sediment samples collected in the field and transferred to the laboratory do not show fluctuations in species abundance during the first two weeks after transfer (Defew et al. 2002). During this time period, tidal immersion and tidal emersion can be simulated in tidal micro-ecosystems (Paterson 1986). Alternatively, sediment samples can be put into mini-mesocosms, i.e., aluminium stubs (Fig. 1) or small petri dishes, which are placed in wet chambers and subjected to defined regimes of several physical and chemical parameters: light intensity, light quality, temperature, pH, salinity, or gas availability may be varied each separately while leaving the others constant (see Fig. 2). After incubation, the cell densities on the sediment surfaces are evaluated by means of epifluorescence light microscopy or low-temperature scanning electron microscopy (see below). Thus, data on the effects of these external parameters on the VM and species abundances become available.

LOW-TEMPERATURE SCANNING ELECTRON MICROSCOPY (LTSEM) AND EPIFLUORESCENCE LIGHT MICROSCOPY

LTSEM and epifluorescence light microscopy of aluminium stubs or small petri dishes filled with sediment allow the investigation of diatom migration and lead to similar results. LTSEM was first introduced for the investigation of Wadden Sea sediments by Paterson (1986) and allows the observation of sediments and diatoms living therein in an almost natural state. The fixation procedure of sediment samples during cryofixation was further improved by the development of the Cryolander device (Whiltshire et al. 1997). Using LTSEM, data on diversity and abundances of species covering the sediment surface become available (see Fig. 3A). If sampling is performed at regular intervals during a complete tidal cycle, it is even possible to deter-



FIGURE 1: Mini-mesocosms in aluminium stubs of 4 mm height and 10 mm diameter. The cavities are 3 mm in depth and 6 mm in diameter (A). Small aliquots of thoroughly homogenized sediment samples are transferred into the cavities of aluminium stubs (B). These can be placed in humid chambers under defined conditions of e.g. light, temperature and salinity. After cryofixation, the stubs are mounted onto a specimen holder (C) and transferred into cryochamber attached to a scanning electron microscope.

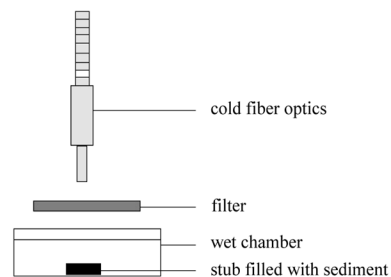


FIGURE 2: Experimental setup for investigating the effects of external factors on the VM. Small petri dishes or aluminium stubs filled with sediments are placed in a humid chamber. Light is supplied from above by using cold fiber optics. Gray or interference filters may be used to alter either light intensity or light quality. The temperature may be varied by placing the wet chambers onto a cooling/heating device. Furthermore, the chambers can be flushed with gases via inlet/outlet ports (not shown in the figure).

mine at which time distinct species show VM (Paterson 1986). The latter can also be done by epifluorescence light microscopy or by using the lens tissue technique of Eaton and Moss (1966). LTSEM, however, allows the collection of this information on natural sediments, which have been cryofixed in the field, or from those kept in mini-mesocosms

(Janssen et al. 1999; Sauer et al. 2002). When sediment samples become freeze-fractured perpendicularly to the sediment surface, LTSEM even allows investigation of the location and distribution of cells within the sediment bed (see Fig. 3B).

Sauer et al. (2002) found that the migration of diatoms onto the sediment surface was partially inhibited by darkness but strongly enhanced by light. Inhibition and enhancement were reversible. These results are in accordance with data of Palmer and Round (1967) for *Hantzschia* sp. Increasing light intensities (up to $500 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ were applied) led to rise in cell numbers on the sediment surface and resulted in variations in the composition of species migrating to the sediment surface; large species like *Gyrosigma* surfaced under low fluence rates whereas naviculoid species surfaced under higher fluence rates (Sauer et al. 2002). Changes in the composition of surfacing species have already been described by Round and Palmer (1966) and Paterson (1986). Sauer et al. (2002) found that the upward migration in the morning was most responsive to light. When the sediment samples were remixed or mixed around noon or in the afternoon, fewer cells migrated to the surface. Thus, it might be that the sensitivity to the light stimulus is highest in the early morning hours or immediately after tidal cover had drained off. A maximum upward migratory behaviour was found at 35 ppm salinity. Fewer cells surfaced when the salinity was either lowered or increased. Higher salinities might occur during hot and/or windy days and nights after prolonged exposure of the sediment surfaces whereas lower salinity values might be caused by rainfall or in inlets of estuarine waters.

Migratory speed is assumed to be an important factor responsible for the accumulation of the diatoms on the sediment surface. The migratory speed averaged over the entire diatom population was approximately $1 \mu\text{m/s}$ and remained similar during experiments in which salinity was either lowered to 5 ppm or increased to 60 ppm (Sauer et al. 2002). This value is rather low and does not necessarily reflect the migratory speed that diatoms will show when moving in natural substrates as the horizontal migration speed was measured in cuvettes. Hay et al. (1993) reported an average speed of $4.7 \mu\text{m/sec}$ for a *Gyrosigma* species over an artificial sediment surface (kaolin) but a much slower migration speed of 0.17 to $0.19 \mu\text{m/sec}$ when the diatom moved through a sediment bed.

The light quality also has a great impact on the upward directed VM. Thus, diatoms surface most when illuminated with blue light; almost no response was registered under green light, whereas illumination with red light seems to have some positive effect on the migration onto the sedi-

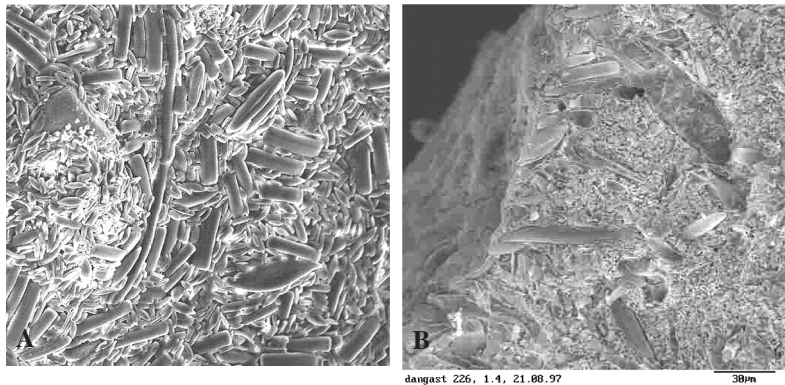


FIGURE 3: (A) Electron micrograph of a sediment surface visualized by LTSEM. Diatom cells dominate the surface. Beside, a filamentous cyanobacterium can be seen. (B) LTSEM electron micrograph of a sediment sample which has been freeze-fractured perpendicularly to the sediment surface. The location and distribution of cells within the sediment bed become visible.

ment surface (Wenderoth and Rhiel 2004). Several classes of photoreceptors with defined functions and absorbance characteristics have been described for plants, and the results indicate that most probably the cryptochromes, which absorb blue light, and the phytochromes, which absorb in the red light/far red light region, are involved.

TIME-LAPSE VIDEO MICROSCOPY

Time-lapse video microscopy is another excellent tool to study the migration behaviour, i.e., migratory speed and migration on/in natural/artificial sediments or horizontal cuvettes. Individual cells or cell assemblages can be tracked for hours and days. Although LTSEM finally results in cryofixation and death of living cells, time-lapse video microscopy allows investigations without damaging them. Single pictures and videos can be recorded using framegrabber software and hardware and stored as digitized files (pictures as TIF or JPG formatted files, video clips as MPG or AVI files) on a personal computer (Sauer et al. 2002). An example is given in Figure 4. It shows that the trails of individual large cells, most probably species of the genera *Pleurosigma* or *Gyrosigma*, were used by other, smaller diatoms, most probably *Navicula* species, for upward directed VM (Wenderoth et al. 2004). The movement of three large diatoms was monitored. One cell moved up and down the cuvette on the same trail, from the upper to the lower edge of the screen before it disappeared at the lower left corner. Its trail was used by smaller cells for upward migration. The other larger cell moved from the upper to the right edge where it disappeared. Later, a third large cell, which may or may not be the same individual as the second one, moved in from the right edge and formed a new trail moving downwards and upwards before it disappeared in the lower right corner. It was followed by smaller cells, which soon afterwards used all the trails formed by the large cells for upward VM.

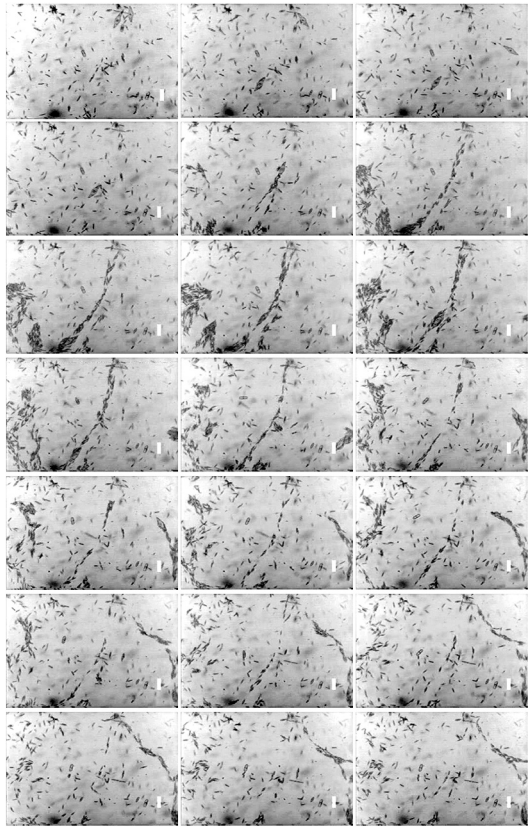


FIGURE 4: Images taken by time-lapse video microscopy showing the movement of diatoms in the vertical cuvette. For the video documentation, a small amount of sediment was placed onto the bottom of a home made cuvette which was positioned vertically in front of a horizontally fixed light microscope. The cuvette was floated with artificial seawater and illuminated from above. Near infrared light for video microscopy was provided by a projector using a 740 nm interference filter. The migratory behaviour of diatoms was documented immediately above the sediment sample in the cuvette over a time period of 24 hours using a 12.5 \times Leitz achromatic objective in combination with a Panasonic B/W CCD camera and a time lapse video cassette recorder. The video tape was digitized on a personal computer to an AVI file. Representative single pictures taken from the video clip are shown with the first one in the upper left and the last one in the lower right corner of the figure. The area size of the pictures is 700 $\mu\text{m} \times 500 \mu\text{m}$.

NUCLEIC ACID AND PROTEIN WORK

Endogeneous rhythms in gene expression as well as short-term adaptation processes on external factors such as fluctuating light intensities will result in fluctuating mRNA and polypeptide abundancies. The polypeptides, constituting the light-harvesting (LH) complexes, are an excellent starting material for studying gene expression and protein quantities of Wadden Sea-inhabiting diatoms. Both the genes encoding LH polypeptides (*lhc* genes) and the LH polypeptides and their mRNAs are highly abundant and have already been investigated in detail in higher plants and green algae: *lhc* genes exhibit an endogenous circadian rhythmic expression pattern with increasing amounts of mRNA from the onset of light towards noon and decreasing amounts in the afternoon towards night. This expression pattern results in almost concomitant enhanced amounts of newly synthesized LH polypeptides in the morning and reduced synthesis in the afternoon. *lhc* mRNA and LH polypeptide abundancies are further regulated by external factors such as light (intensity and quality), temperature, and nutrient availability. In diatoms, the counterparts to the *lhc* genes and LH polypeptides of higher plants and green algae are the *fcp* genes and their corresponding gene products, the fucoxanthin chlorophyll *a/c* binding polypeptides (*Fcp*). Data on *fcp* gene expression and *Fcp* abundancies are rare and almost restricted to laboratory studies. Eight *fcp* genes of the centric diatom, *Cyclotella cryptica*, have been cloned from a cDNA library and investigated in detail (Eppard and Rhiel 1998; Eppard and Rhiel 2000; Eppard et al. 2000). Phylogenetic analyses show that they can be grouped into three distinct clusters. Cluster I harbours the *fcp* genes *fcp1*, *fcp2*, *fcp3* and *fcp5*. They are similar to the *fcp* genes known from other diatoms and brown algae. Cluster II contains the *fcp* genes *fcp6*, *fcp7* and *fcp12*, which are more closely related to light-inducible *lhc*-related genes, which have been cloned from the green alga, *Chlamydomonas*. In cluster III, currently one *fcp* gene, *fcp4*, has been placed which shows the highest homology to the *lhc* genes cloned from the red alga, *Porphyridium cruentum*. The transcript sizes of *fcp* genes of *Cyclotella cryptica*, belonging to different *fcp* gene clusters and encoding different *Fcps*, the diurnal expression of the *fcp1/fcp2/fcp3/fcp5* gene cluster and the steady-state mRNA concentrations of all gene clusters in response to light quality and quantity were investigated by Oeltjen et al. (2002). The mRNAs of the gene cluster I are approximately 950 bases in length, whereas those of the *fcp4* and the *fcp6/fcp7/fcp12* clusters are approximately 1050 (*fcp4*), 880 (*fcp6/fcp7*) and 1150 (*fcp12*) bases in lengths. Similar to what is found for higher plants, the steady-state mRNA concentration of the *fcp1/fcp2/fcp3/fcp5* gene cluster increased with the onset of light, reached a maximum around noon and dropped in the afternoon. The steady-state mRNA concentrations of the genes belonging to cluster I and of the *fcp4* gene were higher when *C. cryptica* was grown in low light, whereas the steady-state mRNA concentration of the *fcp6/fcp7/fcp12* gene cluster increased under high light growth conditions. The steady-state mRNA concentrations of all gene clusters were highest when *C. cryptica* was grown in red light, intermediate in green light, and lowest in blue light. The *fcp* genes, especially those belonging to the gene cluster I, and a polyclonal antiserum raised against the *Fcps* of *C. cryptica* are excellent tools for studying steady-state *fcp* mRNA concentrations and *Fcp* abundancies of diatoms directly in the field. The methodological approaches were published by Hust et al. (1999) and Meyer et al. (2003); they are summarized in the flow chart of Figure 5.

Generally, the results using these techniques are in line with those obtained in laboratory experiments on unialgal cultures. Hust et al. (1999) found that repetitive extractions with sodium dodecylsulfate (SDS) containing sample loading buffer used for SDS-polyacrylamide gel electrophoresis ensured that more than 98% of the extractable protein was recovered. Subsequent Western immunoblotting with the *Fcp*-antiserum selectively immunodecorated *Fcps* and, thus, demonstrates that a taxon-specific class of polypeptides can be visualized and quantified directly

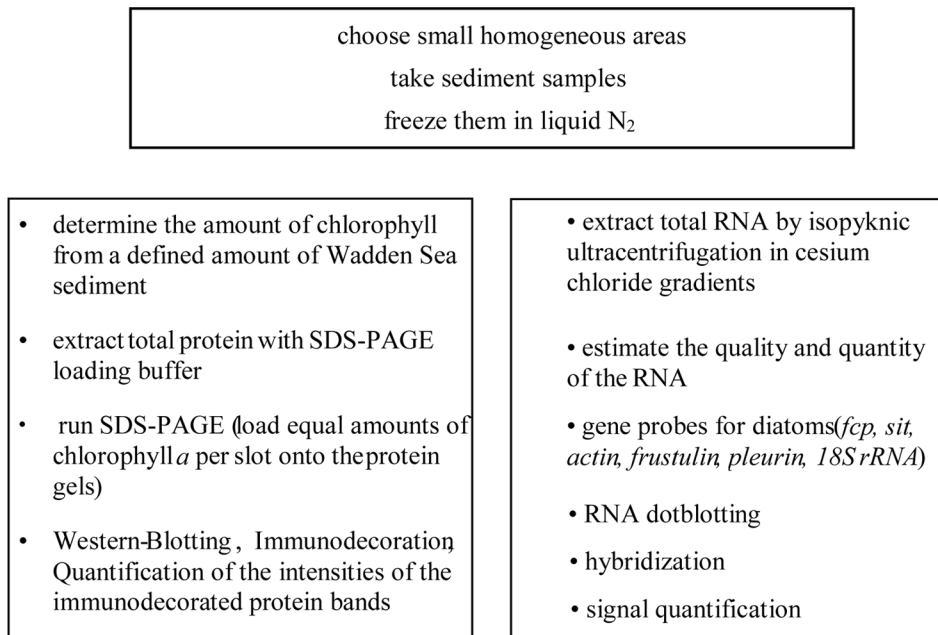


FIGURE 5: Flow chart for the isolation of total protein (left) or total RNA (right) out of Wadden Sea sediments.

in sediment samples. In shading experiments, shaded sediment areas generally revealed higher amounts of *Fcp* subunits which could be immunodecorated.

Meyer et al. (2003) established a method to investigate the steady-state levels of *fcp* mRNAs of diatoms *in situ*. Field samples were taken after tidal exposure from dawn to late afternoon at two-hour intervals and frozen in liquid nitrogen. In the laboratory, total RNA was isolated by isopycnic ultracentrifugation in cesium chloride gradients. Defined amounts of total RNA were blotted onto nylon membranes and hybridized with probes against the *fcp2* and 18S rDNA genes of *C. cryptica*. The steady-state amount of *fcp* mRNAs was estimated by normalizing the *fcp* signal intensities to the signal intensities obtained from hybridization experiments, in which the 18S rDNA gene probe was used (see flow chart, Fig. 5). In time course studies, which were performed to demonstrate the applicability of the method, the steady-state levels of *fcp* mRNA increased up to 12-fold with the onset of light. Similar to what has been found in laboratory experiments on unialgal cultures, the levels reached a maximum 6–8 h after sunrise before they decreased again. Further results using the methodological approaches described above are given in Figure 6. Here, Wadden Sea sediments were withdrawn during the morning hours up to 2 pm in the afternoon and subjected to RNA and protein isolation. For both the *Fcp* abundances and steady-state *fcp* mRNA concentrations, an increase towards the early afternoon could be demonstrated.

FUTURE PROSPECTS

At present, neither the effects of chemical gradients (O₂, CO₂, S²⁻, NO₃⁻) nor the impact of physical gradients such as temperature and pH on the VM have been investigated. The influences of excessive light (> 500 μmol photons m⁻² s⁻¹) and gravitaxis on the VM have not been elucidated either. Further experiments have to be undertaken to unravel the individual impacts of the entire set of these factors.

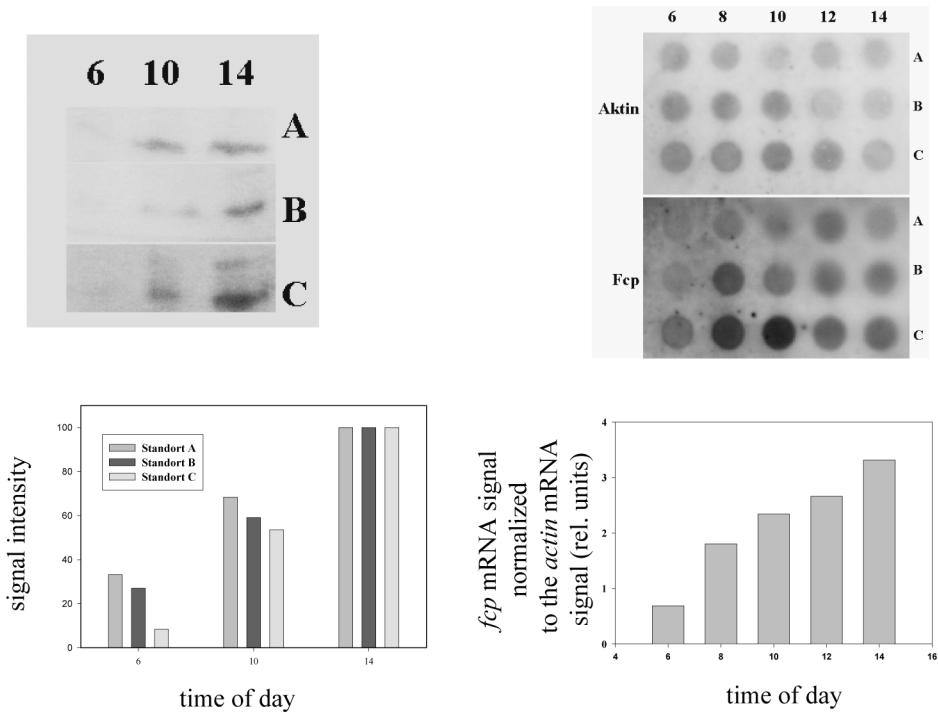


FIGURE 6: Left side, upper part: Western immunoblots of total protein extracted from three sediment sampling sites (A, B, and C). Sampling was performed at 6 am, 10 am and 2 pm, respectively. The proteins were blotted onto nitrocellulose after electrophoresis and immunolabeled with an antiserum directed against the Fcp subunits of the diatom *C. cryptica*.

Left side, lower part: The signal intensities obtained from quantitative analysis of the immunodecorized bands are presented as bars and plotted against the time of day; the highest signal intensity is set to 100 %.

Right side, upper part: Representative dot blots of 10 μ g RNA isolated from three Wadden Sea sediment sampling sites (A, B, and C) and hybridized with either the *fcp2* gene probe or the actin gene probe. The values above the dots show the local time of sample withdrawal. The gene probes are indicated on the left.

Right side, lower part: Bar graph showing the steady state level of Wadden Sea sediment *fcp* mRNA, which was estimated by normalizing the *fcp* signal intensities to the corresponding actin mRNA signal intensities. Abscissa: time of day, ordinate: normalized steady state *fcp* mRNA levels.

Additional molecular techniques have to be adjusted and applied: total DNA and RNA can be isolated from sediment samples which is suited for polymerase chain reaction (PCR-) mediated amplification of diatom-specific 18S rDNA or mRNA after being reverse-transcribed. The PCR products could be used for standard molecular techniques such as Single Stranded DNA Conformation Polymorphism (SSCP), Denaturing Gradient Gel Electrophoresis (DGGE), or Differential Display. The PCR products can be subjected to routine DNA sequencing protocols to yield information on the species from which they were derived as well as on species diversity. *In-vivo* cell labelling, in combination with confocal light microscopy, will allow tracing of individual species within their natural habitat by using species-specific gene probes derived from the sequencing data and carrying a fluorescence label. Antisera directed against proteins that play major roles in main enzymatic pathways (e.g., uptake of nitrate, phosphate, silicate, synthesis and excretion of polymers) will allow a closer look at protein abundancies, whereas the corresponding gene probes will allow conclusions on gene expression.

Diatoms are fascinating microorganisms. It is no matter of debate that they have attracted the

attention of “observing and describing” scientists first: microscopists and taxonomists. As new methods, i.e., molecular, biochemical, and biophysical, have become available, it is — also no matter of debate — a challenge and chance to use these on diatoms in their natural habitats as well. In the future, modern methods will allow testing of species concepts and will surely yield information on how diatoms live and survive in their natural habitats.

ACKNOWLEDGEMENTS

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The Sino-Siberian Distribution of *Eunotia clevei* and its Relatives, from Lake Baikal to the Mekong Delta: The Union of Taxonomy, Biogeography, and Ecology

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In discussions of the interface between taxonomy and ecology one area emerges of prime importance: Biogeography. Whereas taxonomy deals with the grouping and naming of organisms and ecology deals with the parameters required for an organism to exist, biogeography explores the reasons why different biota come into being. In this paper we first review the status of taxonomic descriptions, in an attempt to quantify the information already available for use in biogeographic analyses. Second, we briefly describe two distinct patterns of distribution relative to the Lake Baikal diatom flora based on species in the *Eunotia clevei* species group.

In a recent issue of *Diatom Research*, Kociolek and Stoermer (2001) presented some thoughts concerning the integration of diatom taxonomy and ecology, two subjects that have different and possibly diverging objectives. Kociolek and Stoermer spoke of a ‘marriage of necessity’, a desire to unite the two subjects with a common purpose or, at the very least, to identify areas that might be thought of as contributing to a common aim. One might meaningfully ask a more general question, addressing the purpose of both disciplines but that would lead into largely philosophical discussions, having limited practical value in driving forward these two branches of science in diatom biology. The purpose of this collection of papers is to identify areas that might be understood as ways forward, rather than outlining differences of opinion over the relevance or otherwise of ecology and taxonomy to each other.

Our remarks below will address the issues as we see it and, although no doubt less than comprehensive, we happen to believe that there is one very practical way to pursue common goals, of benefit to a wide variety of disciplines including evolutionary studies as well as taxonomy and ecology.

Kociolek and Stoermer included five possibilities under their suggestions for areas in which ‘correct’ taxonomy might impact ecology:

- Alien species
- Comparative autecology
- Comparison across space
- Comparison across time
- Biogeography

Here we are concerned with the last three, which are interrelated. The third topic above, ‘Comparison across space’ and the fourth, ‘Comparison across time,’ may dovetail nicely into the fifth, ‘Biogeography,’ which in our view is where the future union of taxonomy and ecology lies (Kociolek and Spaulding 2000).

‘COMPARISONS ACROSS SPACE’

Kociolek and Stoermer subdivided ‘Comparisons across space’ into three parts:

Floras
Monographs
Specimens

In diatom taxonomy (and probably throughout comparative botany), there are fewer monographs than floras, simply because, whereas the scope is narrow, detail is not. Both enterprises, monographs and floras, produce a wealth of data, primarily in the form of illustrations of specimens, secondarily in the form of associated data. Below we present a few figures that might help with some focus.

Floras

First, how might one understand the content of floras? A general view is difficult, in that they can vary in content and execution. Some might take many years to complete and, when published, are composed of many volumes. The *Seaweeds of the British Isles*, for example, will probably be complete in 2005, the first volume being published in 1977, with six further volumes each devoted to a particular algal ‘group’ (sadly, lacking a diatom volume) (Dixon and Irvine 1977, 1995); Irvine 1983; Christensen 1987 (1995); Fletcher 1987; Burrows, 1991; Maggs and Hommersand 1993; Irvine and Chamberlain 1994; Brodie and Irvine 2003). Such comprehensive works are usually undertaken by a number of people, some of whom may end up devoting most of their working lives to completing their particular taxonomic treatment.

The most comprehensive European diatom flora appears in the *Süßwasserflora von Mitteleuropa* series, primarily undertaken by two diatomists, Horst Lange-Bertalot and Kurt Krammer. It is principally composed of four volumes spanning a 5-year publishing period (1986–1991), with a 5th volume providing taxonomic keys in French and English and a 6th volume, a revised edition of 2(3), both published in 2000 (Krammer and Lange-Bertalot 1986, 1988, 1991a and b, 2000a and b). The first four volumes include roughly 650 plates, each plate having, on average, 20 illustrations, giving a rough total of 13000 images in all.

In contrast, most diatom floras are usually less broadly conceived, containing detailed accounts of taxa found in a particular area, accompanied by notes (where necessary), descriptions of new taxa (if any), an illustration or two and maybe some reference to the herbarium (or other collection) where the specimens can be found. On average, floras of this kind have between 30 and 50 plates, each plate having 10–20 separate pictures, giving a total of between 300 and 1000 illustrations per flora.

If five floras of this kind were published per year, then over a 5-year period, the 25 floras would contribute some 25000 illustrations — an impressive amount of data.

Monographs

Half a century ago Robert Ross wrote a little on the subject of diatom monographs. He noted that “Very little monographic work has been done on the Diatoms during this century and only a few small genera have been dealt with. Almost the whole group is in need of taxonomic revision...” (Ross 1951:142). Up until the mid-1980s there were few works that could be called monographic. Since that time things have changed. For example, of the 46 volumes in the *Bibliotheca Diatomologica* series, eight are monographs, devoted to a particular genus or a section within a

large genus. The series has a publishing history from 1983 to the present, roughly 20 years. By definition monographs will vary and it might be futile to generalise about the number of illustrations. Nevertheless, as an example, consider Krammer's monograph on Cymbelloid genera (Krammer 1997a, b). Published in two volumes, this work presents a total of roughly 950 printed pages, of which more than 300 are illustrations. At an average of 15 pictures per page, there is something in the region of 4500 pictures.

Specimens

The calculations given above for published illustrations are very approximate but give some indication of the volume of data available for taxonomists, even with the meagre amount of time diatomists have to devote to this kind of work.

The one factor common to both enterprises, floras and monographs alike, is that no matter how well (or poorly) documented the taxa are in the final publication, all these data must have been based on specimens of one kind or another. So where are those specimens now? Again, it might be easy to peruse the publications and trace the herbarium or collection to which the samples were eventually deposited (in a certain number of cases that might not be possible).

The storage and retrieval of these data to one side, what is again inescapable is their abundance. But what of its relevance, which might seem opaque, other than simply documenting either one group of diatoms or one particular area or region? Usually, at least for diatomists, these works (floras in particular) are seen as aids to further scientific study, as guides to the organisms that inhabit an area — perhaps a starting point for generalisations to be made concerning issues of their ecology. How might these data be brought to bear on any particular problem, any particular biological problem?

One purpose of this meeting was to detect or suggest ways in which two potentially 'symbiotic' disciplines of taxonomy and ecology might contribute to something bigger than each on its own. That might be biogeography, the study of the distribution of organisms and their relation to Earth history. And biogeography is where the data of monographs and floras intermingle and gain meaning — irrespective of how poor the ecological data might be, every organism occurs somewhere and that information is almost always recorded.

LAKE BAIKAL: AN EXAMPLE OF FLORISTIC NECESSITY VERSUS MONOGRAPHIC REQUIREMENT

Lake Baikal in western Siberia is a well-defined area and, conceivably, might yield more of general relevance via floristic studies than other less well-defined areas, such as New Zealand, or more precise than Northumberland, in the UK, as two extreme examples — both of which have published floras (Donkin 1858, 1861, 1869; Cassie 1989). The latter two areas may simply indicate political boundaries rather than biological regions. That suggests another significant problem. What are biological regions? This question is relevant to comparative biology as a whole and one we do not address further here (but see Williams and Ebach 2004).

Lake Baikal does not really have a comprehensive flora, in spite of many papers published over a period of nearly 100 years. Nevertheless, the available data do provide a kind of snapshot. From the floristic point of view, a snapshot is about the best we can do.

Consider the contributions of Boris Skvortzov. He published two large papers on the diatoms of Lake Baikal. The first paper, published in 1928, was a preliminary survey (Skvortzov and Meyer 1928). That survey was based upon just 36 samples (Williams 2004). His second paper, published

10 years later, was a more detailed examination of just one of those 36 samples (Skvortzov 1937a). From Skvortzov's study, one might hazard an estimate of Lake Baikal's benthic diatom diversity. By his estimate there are roughly 450 taxa present (452 in Skvortzov 1937a). Of those, Skvortzov's figures suggest, by inference, that 304 are cosmopolitan and 148 endemic (the endemics were described by Skvortzov). By cosmopolitan, we mean simply that some taxa were described prior to Skvortzov's work and hence are known from some other locality. If these figures mean anything, they suggest that roughly one third of the flora is endemic to Lake Baikal (Williams and Reid 2003). But Skvortzov did not see the 304 non-endemic taxa as truly cosmopolitan, in the sense they occurred everywhere else on the globe. He adopted a particular way of understanding the flora by dividing the species he recognised into five groups:

- (A) Siberian and sub-alpine elements
- (B) Tertiary freshwater remains and tropical origin
- (C) Marine elements or marine relicts
- (D) Brackish-water species
- (E) Elements of indistinct origin

At first sight Skvortzov's groupings are a little puzzling, as they appear to be a mix of geography, history and ecology. For instance, it is quite possible for a taxon to be a marine relict (C) as well as of tropical origin (B). One might adjust Skvortzov's groups to align them with just one parameter, even if that parameter is broadly construed. One might assume that category (A), although defined geographically, may be equated with species present only (and always) in 'cold' freshwater habitats. Category (B) might be construed to refer to species once believed to have been tropical (warm water species) but are not so now. Categories (C) and (D) might be construed to refer to a previous existence, where the species in question once dwelt in either a marine (C) or brackish (D) environment and now do not. Category (E) may be safely ignored as of no real meaning. Surprisingly, Skvortzov wrote of this last category that it "is represented by a large series of Baikal endemics to which I have not yet found relationships" (Skvortov 1937a:298). In other words, many of the Lake Baikal endemics could not be easily related to the five groups. Skvortzov simply did not know what to do with them.

This might be a fair summary of Skvortzov's divisions. But it is also instructive to know that he based them upon a previous scheme, drawn up by Vereshagin in the early 1900s based, in part, on work undertaken by Lev Berg, a talented, but now almost forgotten, Russian ichthyologist and evolutionary biologist (see Skvortzov 1937a:295; Berg 1926). How useful are Skvortzov's divisions today? Probably not much — one has to work quite hard to derive any real meaning from them. Perhaps also, his ideas belong to a bygone era, one in which ecology was not particularly uppermost in peoples' minds, or at least not particularly well-defined (Flower, this volume).

These comments are not intended as critical of Skvortzov, Vereshagin or Berg. We simply wish to draw attention to one aspect of possible misunderstanding between diatom ecologists and taxonomists, one that remains today. Skvortzov had a purpose. His reasons for the sub-divisions were an attempt to explain the *origin* of Lake Baikal's diatom flora; *origin* in terms of where the present day taxa may have come from. It is worth quoting Skvortzov at length, as his own words explain his purpose:

"The present study shows a certain similarity of the Baikal diatoms to those of Tanganyika Lake, Africa; to Neogene freshwater floras of Nippon [Japan]; to Tertiary diatom floras of Hungary; to the recent flora of Demerara River, Paraguay [*sic*], South America; and to some forms widely represented in oceans. All this can be explained only by the help of Prof. G.I. Wereschtschagin's theory of the origin of the Baikal fauna and flora" (Skvortzov 1937a:298).

We may abstract from this statement (along with the five categories above) two kinds of information: geography and, broadly speaking, ecology. Skvortzov's ecology might be thought of as simple; he is really talking about four broad 'categories': (A) cold-water, (B) tropical water, (C) marine, and (D) brackish. His geography is somewhat more puzzling, as it includes Europe, Africa, Japan, South America and the world's Oceans. Taken together, they lack precision: Lake Baikal diatoms are related to organisms somewhere in the rest of the world, be that Hungarian fossil deposits or Lake Tanganyika in Africa. But the general message is interesting and has been little exploited in recent years. What other areas of the world are the diatoms of Lake Baikal related to? And what can be said of the environments that make up those areas? Buried in Skvortzov's prose is the essence of comparative biology. What relationships can be specified, first by the organisms themselves, second by where those organisms live. So where did Lake Baikal's diatom flora come from? Here we see the problem illuminated via individual taxa, or more precisely, via individual groups of taxa.

Previously, we examined species in the genus *Tetracyclus* (Williams et al. 2002) and its patterns of distribution in Lake Baikal (Williams 2004). Here we deal briefly with species from the genus *Eunotia* Ehrenb. We chose this genus for a number reasons. First, it is large and diverse with perhaps over 1200 species, distributed globally. Second, within that 1200 species, a fair number are endemic to different parts of the world. Third, the genus is well defined, with the arrangement of raphe and rimoportulae quite unique among diatoms (Kocielek 2000). Fourth, it has a well-defined ecological niche, rarely if ever, does it occur in habitats that are not acidic.

THE GENUS *EUNOTIA* IN THE SINO-SIBERIAN REGION

Skvortzov believed that there were 30 cosmopolitan taxa belonging to *Eunotia* in Lake Baikal, of which 12 have a fossil record. There are 11 endemic taxa belonging to *Eunotia*, of which four have a fossil record, roughly one third being endemic, similar to the entire flora, with half of those having a fossil record. Skvortzov listed just two taxa from *Eunotia* (*E. praerupta* and *E. praerupta* var. *inflata*) as a 'Siberian and Subalpine element,' and three species (*E. mondon*, *E. clevei* and *E. lacusbaikalii*) of 'Tertiary freshwater remains and tropical origin' but placed no species in the group of 'Marine Elements or Marine Relicts.' In a general sense, the last two categories are of interest: the possibilities of tropical relatives and the possibilities of marine environments.

Among the species of *Eunotia*, *E. clevei* and its morphologically similar relatives have recently been revised (Williams and Reid 2005). This species complex is of some significance, from the perspective of ecology as well as taxonomy. First, it is structurally different from other species of *Eunotia* (Vyverman et al. 1998; Edlund et al. 2000; Reid and Williams 2001) and second, it is never found in acidic waters. In fact, both ecologically and morphologically it is quite atypical. We have described a new genus to accommodate this species complex. The revised taxonomic views do not affect the general argument presented here (Williams and Reid 2005).

Skvortzov placed *Eunotia clevei* in the 'Tertiary freshwater remains and tropical origin' category. It is useful to sub-divide Skvortzov's category (B) 'Tertiary freshwater remains and tropical origin' into "tertiary relicts" and "tropical origins." Skvortzov suggested the 'Tertiary freshwater remains and tropical origin' group for *E. clevei*, as it is found in Sweden, Finland, Russia, and Mongolia, and known as a fossil from the USA, Japan, and China. With knowledge of these distributions there is the suggestion that *E. clevei* is indeed a relict, Tertiary or otherwise, *but* its presence in China suggests a tropical component as well as a marine environment (see below).

"TERTIARY RELICTS."— In Lake Baikal there are several 'kinds' of *Eunotia clevei*. There is the typical species, known from elsewhere in the Northern hemisphere (Reid and Williams 2001;

Edlund et al. 2000). In addition, Skvortzov identified and described two new varieties, *baicalensis* and *hispidia* and one new species, *Eunotia lacusbaikalii*, similar in morphology to *E. clevei*. *E. clevei* var. *baicalensis* and *E. lacusbaikalii* seem to be both truly endemic to Lake Baikal and therefore ‘Siberian and Sub-alpine’. *Eunotia hispidia* has been considered a Lake Baikal endemic but appears to be present in Lake Onega and, as a fossil, Lake Ladoga in Finland, and seems also to be a ‘Tertiary relict’ (Reid and Williams 2001).

Elsewhere in Russia, Moisseeva described another variety, *E. clevei* var. *aculeata* Moisseeva (Moisseeva 1971) and, in another publication, Lupikina and Dolmatova (1982) described two species, *Eunotia maculata* Lupikina and Dolmatova and *Actinella penzhica* Lupikina and Dolmatova, both having morphological similarities to *E. clevei*, suggesting a close relationship. Therefore, in the Boreal (cold-water) parts of the Northern Hemisphere there are several entities that appear to belong to one complex, related directly to *E. clevei* (Table 1). What is of significance is that if the ecology is separated from the geography, then some greater precision is possible in specifying the taxa and the places they live.

“TROPICAL ORIGINS.”—What of other specimens possibly related to *E. clevei* but described from elsewhere? Skvortzov named and described another variety of *E. clevei*, *E. clevei* var. *sinica*, from China (Skvortzov 1929). A little later he changed his mind and declared his new variety a synonym of *E. clevei*, a hasty judgement in our view (Skvortzov 1937b; Reid and Williams 2001; Williams and Reid 2005). Since that time six further species have been named, all with morphological features that suggests a close relationship to *E. clevei*; and all occur in marine or brackish waters (Voigt 1969; Qi et al. 1986; Shi 1991, 1997; Wang 1998) (Table 2).

So what we have is a diverse assemblage of *Eunotia clevei*-like specimens in Lake Baikal — Northern Hemisphere relicts — and a second group of *Eunotia clevei*-like specimens in and around the tropical parts of China and possibly South-east Asia.

The details of all the species from these areas are not yet well known but separating their geography from their ecology helps a little with identifying the complex factors required to explain their origin relative to the entire Lake Baikal diatom flora, and possible its entire fauna and flora.

TABLE 1. Species of ‘*Eunotia clevei* associated with Skvortzov’s ‘Tertiary freshwater remains...’, the first pattern. All species belong to a new genus, to be described (Williams and Reid 2005).

Northern Hemisphere: ‘Tertiary freshwater remains	
<i>Eunotia clevei</i> Grunow	“Northern Hemisphere”
<i>Eunotia hispidia</i> (Skvortzov) Reid & Williams	Lake Baikal (and elsewhere)
<i>Eunotia clevei</i> var. <i>baicalensis</i> Skvortzov	Lake Baikal
<i>Eunotia lacusbaikalii</i> Skvortzov	Lake Baikal
<i>Eunotia clevei</i> var. <i>aculeata</i> Skvortzov	“Primorskii Krai”
<i>Eunotia maculata</i> Moiseeva	Kamchatka
<i>Actinella penzhica</i> Lupikina & Dolmatova	Kamchatka

TABLE 2. Species of ‘*Eunotia clevei* associated with Skvortzov’s ‘tropical origin...’, the second pattern. All species belong to a new genus, to be described (Williams and Reid 2005).

Northern Hemisphere?? (‘...tropical origin’)	
<i>E. americana</i> var. <i>asiatica</i> Voigt	Canto and Shanghai
<i>E. reimerii</i> Williams & Reid	West River
<i>Eunotia botuliformis</i> Wang (non <i>E. botuliformis</i> Nörpel-Schempp & Lange-Bertalot)	Pearl River, South China
<i>Eunotia pseudoclevei</i> Wang	Pearl River, South China
<i>E. clevei</i> var. <i>obliquestriata</i> Qi, Lin et Hi	Hubei Province
<i>E. clevei</i> var. <i>sinica</i> Skvortzov	Foochow, South China
<i>Actinella miocenica</i> Li	Jiling Province

SUMMARY

First, none of the *E. clevei* group of species occurs in acid waters, so they are very different from the usual species in *Eunotia*. Second, the ‘tropical’ specimens are, more or less, marine or brackish. Third, two patterns of distribution seem to be emerging: One in the Northern hemisphere, the other extending towards the tropics. Although data on their distribution are sparse, the pattern of extinction and survival is not too opaque to be lost forever.

If the unique elements of taxonomy, ecology and geography are separated out and dealt with in their own terms, then their marriage, or reunion, is likely to be more harmonious. Given the abundance of taxonomic data already available it is possible to select genera for investigation in the geographical dimension — and thereby identifying problematic taxa. Only by knowing exactly what each discipline can contribute to a particular problem — in this case biogeography and the origins of the Lake Baikal diatom flora — can progress be made on the understanding of how and why diatoms species became so diverse, occupy so many different niches and continue to flourish.

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