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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 5$^{th}$ volume providing taxonomic keys in French and English and a 6$^{th}$ 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 occured 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 (Kociolek 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 *hispida* and one new species, *Eunotia lacusbaikalii*, similar in morphology to *E. clevei*. *E. clevei* var. *baicalensis* and *E. lacusbaikali* seem to be both truly endemic to Lake Baikal and therefore 'Siberian and Sub-alpine'. *Eunotia hispida* 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 | |
|---|---|
| *Eunotia clevei* Grunow | "Northern Hemisphere" |
| *Eunotia hispida* (Skvortzov) Reid & Williams | Lake Baikal (and elsewhere) |
| *Eunotia clevei* var. *baicalensis* Skvortzov | Lake Baikal |
| *Eunotia lacusbaikali* Skvortzov | Lake Baikal |
| *Eunotia clevei* var. *aculeata* Skvortzov | "Primorskii Krai" |
| *Eunotia maculata* Moiseeva | Kamchatka |
| *Actinella penzhica* 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') | |
|---|---|
| *E. americana* var. *asiatica* Voigt | Canto and Shanghai |
| *E. reimerii* Williams & Reid | West River |
| *Eunotia botuliformis* Wang (non *E. botuliformis* Nörpel-Schempp & Lange-Bertalot) | Pearl River, South China |
| *Eunotia pseudoclevei* Wang | Pearl River, South China |
| *E. clevei* var. *obliquestriata* Qi, Lin et Hi | Hubei Province |
| *E. clevei* var. *sinica* Skvortzov | Foochow, South China |
| *Actinella miocenica* 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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