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Diatoms, salt lakes and climate change: inter-regional datasets and transfer functions for global application

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Diatoms, salt lakes and climate change: inter-regional datasets and transfer functions for global application

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DETAILED REPORT

1. Project Objectives

Concern about global warming has highlighted the need, not only to improve General Circulation Models (GCMs) in order to accurately predict future climate, but also to validate GCM predictions against reliably reconstructed past changes in climate. Diatom remains in the sediments of closed-basin, saline lakes can provide a proxy record of past water chemistry, especially palaeosalinity, and an indirect measure of climate change in arid and semi-arid regions (Fritz *et al.*, 1991). Consequently, there is a great demand for diatom-based salinity reconstructions for saline lakes world-wide.

Over the past decade the development of transfer functions has revolutionised palaeoecological interpretation by providing quantitative reconstructions of key hydrochemical parameters, such as salinity. Transfer functions are calibrated from a modern dataset of diatoms and associated water chemistry. In East Africa, transfer functions for pH have already been developed for bicarbonate-carbonate waters and applied to fossil sequences (Gasse & Tekaia, 1983). For other regions in Africa and in the Northern Great Plains of North America calibration datasets and salinity transfer functions have been developed (Gasse, 1987; Fritz *et al.*, 1991; Fritz *et al.*, 1993). Elsewhere diatomists are rapidly extending sampling networks to create new regional datasets which will be used to generate independent transfer functions (e.g. British Columbia, Wilson *et al.* (1994); Mexico, Metcalfe (1988); Turkey, Kashima (1995); Spain, Reed (1995); Australia, Gell & Gasse (1994)).

In 1991 several people involved in the collection of these modern datasets established the Climate and Salinity Project (CASPIA) to compare saline lake diatom floras, with the eventual aim to merge regional datasets into a single database of diatom and environmental data, in order to generate inter-regional transfer functions (Juggins *et al.* 1994). This is desirable for two reasons. First it will provide a better understanding of species optima and tolerances in relation to range of hydrochemical chemical gradients, and may allow more accurate and sophisticated chemical reconstructions, not just for total salinity, but also for brine type. Secondly, the increased biological diversity of combined datasets will help in the search for modern analogues of fossil assemblages. Unfortunately these do not always exist within the same geographical region, and transfer functions are likely to be most accurate when analogues can be identified, even if these are geographically distant.

Vital prerequisites to merging datasets are correct identification and nomenclatural consistency between palaeolimnologists. Detailed systematic studies can provide an insight as to whether biogeography limits the application of regional and global transfer functions.

The project had the following original objectives:

i. Production of a diatom iconograph and taxonomic quality control (TQC)
ii. Merging diatom/water chemistry datasets, specifically those from the North American Great Plains and Africa
iii. Development of inter-regional transfer functions
iv. Workshops and inter-group communication
v. Identification of sites for model validation
vi. Computing and database developments - taxonomic database, stored images and image analysis

As less than half the grant money applied for was received, in the absence of clear guidelines from NERC, the work was restructured on the basis of the referees comments. Work focused on objectives i-iv.

2. Development of Methods and Techniques

Collaboration between taxonomists (NHM), palaeolimnologists and statisticians (UCL & Newcastle) has led to the development of a new diatom database linking hardcopy iconograph images and corresponding taxonomic information to ecological (distribution, habitat, chemistry) data for application to problems of diatom palaeoecology and biodiversity in saline lakes.

As a result a new training set that combines diatom assemblages from the North American Northern Great Plains and Africa has been produced that allows more robust reconstruction of past salinity, water level and climate from saline lake sediment cores in both continents.

3. Progress

The revised objectives were successfully achieved:

i. The production of a diatom iconograph has been completed and will form part of a saline diatom flora to be published in the near future (Carvalho *et al.* in prep.). As no such flora has previously been published, this will be of considerable interest to the general diatom research community in addition to those specifically investigating palaeoclimate.
ii. TQC focused on detailed studies of several important species of *Cyclotella*, *Campylodiscus*, *Craticula*, *Navicula* and *Nitzschia*. The results have begun to be published (Carvalho *et al.*, 1995; Carvalho *et al.*, 1996; Cox, in prep.).
iii. Diatom/water chemistry datasets from NGP, N. Africa, E. Africa and Niger have been merged into a single database with consistent identification and nomenclature. This has allowed the development of an inter-regional transfer function that can be applied to fossil sequences that had taxa which were absent from the individual regional datasets (Gasse *et al.* 1995; Juggins *et al.*, in prep.).
iv. Evaluation of different numerical approaches to diatom-based environmental reconstructions (Chalié *et al.* in prep.).
v. Comparison of the datasets, development of the flora and manuscript writing has taken place at four workshops held in Paris and London and attended by diatomists working in saline lake regions throughout the world (N. America, Africa, Spain, Turkey, Mexico, Australia). In addition a workshop was held for the wider diatom community at the 13th International Diatom Symposium in Italy (Carvalho & Fritz, 1995) and a paper was presented at the British Phycological Society annual winter meeting (Carvalho, Cox & Sims, 1995).

4. Summary of Results

i. Diatom iconograph and TQC.

TQC relies upon correct identification and a clearer understanding of taxa boundaries. This has been approached in two ways: (1) The production of an iconograph and associated saline diatom flora covering a diversity of habitat and brine types, and (2) detailed taxonomic studies of problematic taxa.

The diatom iconograph, covering over 160 taxa, has been completed along with elements of the text for the flora. This includes species descriptions, identification guidelines and detailed ecological and distributional data (an example element from the flora is provided along with the publications).

Detailed systematic studies of important or problematical taxa were carried out using light microscopy (LM) and scanning electron microscopy (SEM). Type material was examined, alongside material from the datasets, to ensure decisions were based on clear taxonomic criteria.

The first completed study investigated material recorded as *Cyclotella caspia* Grunow (Carvalho *et al.*, 1995). The identity of this species was of particular interest as it is present in Holocene sub-fossil assemblages from S. Algeria, S. Tunisia and N. Niger, yet it appears to be absent from the modern flora of East and North Africa. It occurs abundantly in saline lakes in North America, although uncertainties about its correct identification have prevented material in the North American dataset from being used as an analogue for the fossil African assemblages.

Our analysis showed that the species occurring in saline lakes is quite different from *C. caspia* and corresponds with the type material of *C. choctawhatcheeana* Prasad. Misidentification had occurred because the identity of *C. caspia* was, until recently, not fully investigated and the two species are similar in terms of valve diameter and stria density. The study also confirmed that the American and African material contain the same species and that the salinity optimum, calculated from the North American saline lake water chemistry data, could be used in the salinity transfer function at Adrar Bous. This permitted salinity and climate reconstructions at this site for time periods previously poorly reconstructed (Juggins *et al.*, in prep.).

The second detailed study examined *Campylodiscus clypeus* (Ehrenb.) Ehrenb. This is abundant in the North American and North African datasets but is rare in East Africa. Previous analyses of distribution patterns of *C. clypeus* in the NGP dataset (Fritz *et al.*, 1993) suggested that this species is more characteristic of sodium carbonate lakes, than sulphate-dominated lakes.

The study of type material alongside saline lake material showed that populations in North America, Africa, and Europe should be regarded as the same species. The enlarged dataset also shows that it occurs in carbonate-, sulphate- and chloride-dominated waters and so cannot be used as a clear indicator of a particular brine type.

The third detailed study carried out was on four species of *Craticula*: *C. elkab* (Müller) nov. comb., *C. halophila* (Grun.) D.G. Mann, *C. ambigua* (Ehrenb.) D.G. Mann and *C. cuspidata* (Kütz.) D.G. Mann. *C. elkab* is recorded throughout East Africa and Niger, yet was absent from the Northern Great Plains dataset. Material closely resembling *C. elkab* from saline lakes in Central Mexico was also examined. The African and Mexican lakes are characterised by carbonate / bicarbonate waters. This preference may explain its absence from the sulphate- and chloride- dominated saline lakes of the NGP and North Africa, and from brackish estuarine and coastal waters. Its presence in core material may be used to indicate water quality when carbonate ions were significant.

Two morphologically distinguishable taxa have been recognised within *C. cuspidata sensu lato*, matching the modern concepts of the species *C. cuspidata* and *C. ambigua* (Cox, in prep.). A few NGP records of *C. cuspidata* should be recorded as *C. ambigua*. Of the *C. halophila* records, many of the African valves also matched the concept of *C. ambigua* whilst many of the NGP valves belonged to the genus *Navicula sensu stricto*.

The fact that *C. choctawhatcheeana*, *C. clypeus*, *C. halophila*, *C. ambigua* and *C. cuspidata* are cosmopolitan species found in inland saline lakes and brackish environments, together with many other species, indicates that global, or inter-regional datasets are valid in palaeoclimate studies and can improve reconstructions as they allow more accurate estimation of ecological optima and tolerances. The study of material recorded as *C. halophila* and *C. cuspidata*, however, demonstrates the underlying importance of TQC in merging regional datasets.

The saline diatom flora with its detailed species descriptions and taxonomic notes, together with iconograph images, will promote TQC by providing a tool for accurate identification and consistent taxonomy amongst the palaeolimnological community. Both the flora and the detailed taxonomic work is of wide application to diatomists and ecologists worldwide.

ii. Merging regional diatom/water chemistry databases

Taxonomic workshop discussions and initial statistical comparison of the NGP and African material showed there to be a number of differences in species' concepts and nomenclatural use between these datasets and highlighted problem taxa that required further clarification and/or detailed TQC before the datasets could be successfully merged. Inital work therefore focused on merging the existing regional datasets from Niger, East Africa and North Africa, as these had been generated in a single laboratory and used a consistent taxonomy and nomenclature. This work led to the the development of a new African dataset of 282 samples and 389 taxa that has been documented in Gasse *et al.* (1995).

Once taxonomic and nomeclatural inconsistencies between the African and NGP datasets had been resolved these were merged into a single database containing a total of 363 samples and 455 taxa identifed to species level or lower. Figure 1 illustrates the increased chemical diversity of the combined dataset, with lakes of predominately carbonate/bicarbonate (E. Africa), chloride (N. Africa) and sulphate (NGP) waters now included. The increase in biological diversity is also significant, with 66 new taxa added to the original merged African dataset, and the distribution of many of the original 389 taxa are now better described in terms of the expanded hydrochemical gradients.

iii. Development and application of inter-regional transfer functions

Statistical analysis of the both the combined African and the new African + NGP datasets show that in addition to salinity (or conductivity) chemical variables reflecting water pH, and cation and anion composition also account for significant and independent components of the total variation in the diatom data. This indicates that transfer functions for these variables may be developed that are independent of salinity, and greatly enlarges the domain for reconstruction of past hydrochemistry from fossil diatoms preserved in lake sediments. For the African dataset transfer functions for conductivity, pH, and ratios between alkali and alkaline earth metals, and carbonate-bicarbonate and sulphate+chloride ions have been derived using the method of weighted averaging and published in Gasse *et al.* (1995). New transfer functions have also been derived for the combined African and NGP dataset and have similar prediction errors to the African TFs (Juggins *et al.* in prep.). This is important as it indicates that the increased chemical and biological diversity, and hence applicability, of the new TFs has not compromised their accuracy.

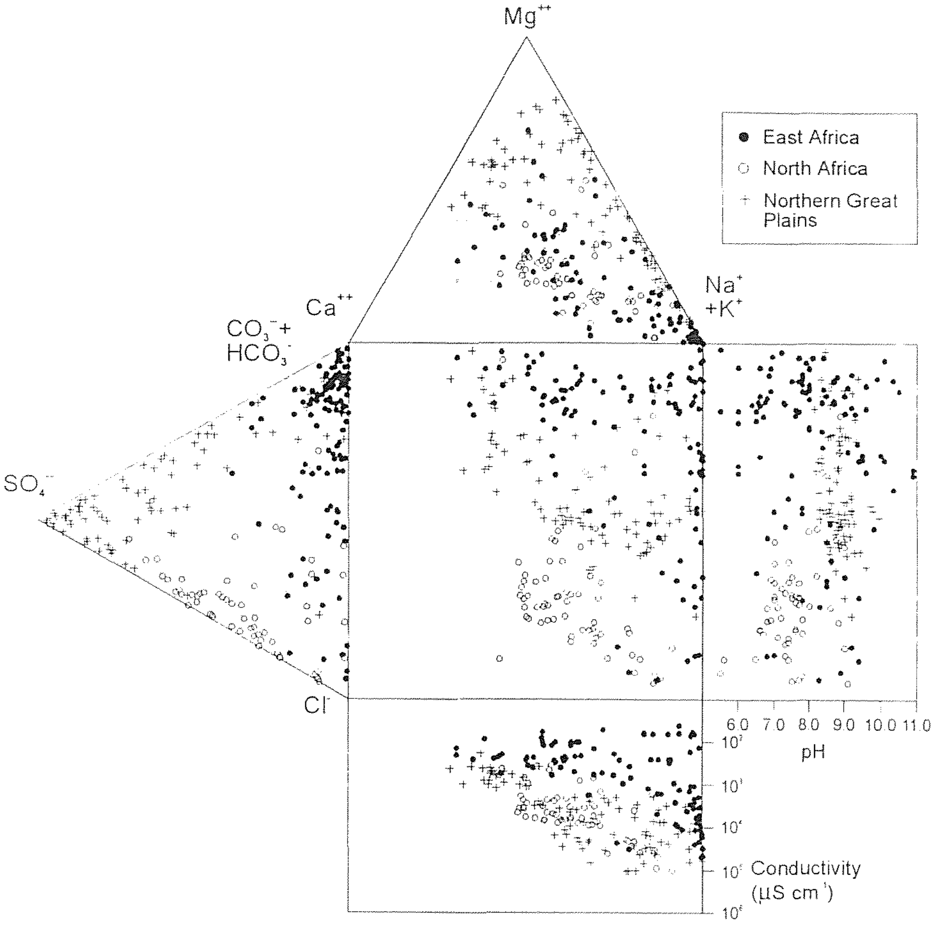

Figure 1 Chemical composition of the combined African and NGP datasets

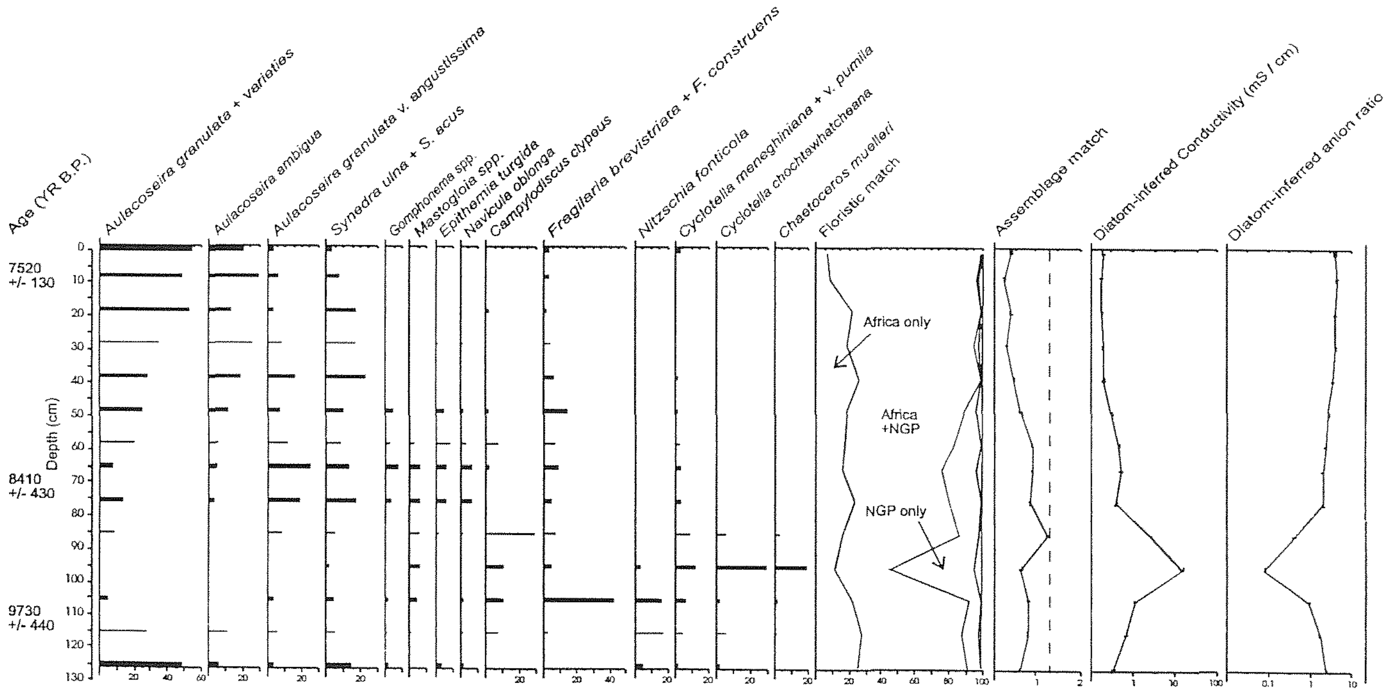

Figure 2 Adrar Bous, northern Niger: Diatom stratigraphy and environmental reconstructions

In addition to developing the new weighted averaging (WA) transfer functions we have also compared the performance and applicability of different numerical approaches to diatom-based environmental reconstruction, in particular comparing the WA to the Best Analogues (BA) approach used by palynologists (Chalié *et al.* in prep.). Results indicate that both methods perform well when tested on the training sets using cross-validation methods, and give similar results when applied to un-mixed or ecological coherent fossil assemblages. However, where the fossil material consists of mixed assemblages of taxa with very different ecological requirements the methods yield rather different reconstructions: WA gives a reconstruction that tends towards the mean of the mixed assemblage, whereas BA tends towards one of the extemes or end-members. Since mixed assemblages are not always easy to identify from inspection of taxon lists, these results suggests a method for their identification, and an additional check on the validity of the reconstructions.

To illustrate these points we have applied the new transfer functions to two fossil sequences from Africa (Juggins *et al.* in prep.). The early Holocene sequence from one of these sites, Adrar Bous, northern Niger is shown in Figure 2. Below 110cm and above 50cm *Aulacoseira*, *Synedra* and *Fragilaria* taxa dominate. The distribution of these taxa in the modern datasets is illustrated by the floristic match, which shows the percentage of the individuals in each of the fossil assemblages that are present in the different modern datasets. Results of these comparisons show that 90-95% of the *Aulacoseira - Synedra - Fragilaria* assemblages are composed of individuals that present in either the modern Afican alone, or Africa and NGP datasets. In addition, the assemblage match, which is defined as the squared chi-squared distance between the fossil and modern samples, is also low for these levels, indicating the the modern and fossil samples are also similar in the *relative proportions* of their constituent taxa.

Between 50 and 110cm taxa which are either rare (*Chaetoceros muelleri*, *Epithemia* spp., *Navicula oblonga*) or absent (*Cyclotella chochtawhatcheana*) in the modern African material, but which are present in the NGP dataset, comprise ca. 20-50% of the assemblages. Analogues for these levels are not present in the African dataset and although values for the assemblage match for these levels are higher they are still below the cut-off, showing that good analogues for these can now be found in the NGP samples.

Diatom-based hydrochemical reconstructions for this sequence are shown on the right of Figure 2, and agree with inferences made from other proxies. Below 110cm the reconstructions indicate deposition in carbonate-rich freshwater, a conclusion supported by the lithology and oxygen isotope data (not shown) indicating a carbonate-rich water body supplied by surface runoff. Above 110cm the diatom flora changes and indicates a rapid rise in conductivity to a maximum of ca. 10 mS cm^{-1} coupled with a transition from carbonate dominated to chloride- rich waters. These floristic changes are coincident with an increase in carbonate deposition and maximum $\delta^{18}O$ values, indicating a minimum ratio of freshwater input versus evaporation. Diatom reconstructions indicate that freshwater conditions are then progressively re-established towards the top of the section, an inference supported by a marked decrease in $\delta^{18}O$ values suggesting a rise in aquifer supplying dilute water to the basin.

In summary, these results improve on previous attempts to derive diatom-based environmental reconstructions in several ways. First, the conductivity and pH TFs includes a greater chemical range and more taxa (455) than those previously published, and so are more widely applicable. Second the new anion and cation TFs allow more detailed palaeohydrological and palaeoenvironmental interpretations by reconstructing the pathways of brine evolution accompanying climatically-mediated evaporation and dilution of inland waters. Finally, the greater biological diversity of the combined dataset increases the possibility of finding good modern analogues of fossil assemblages, in terms of either floristic matches or assemblage composition.

5. Conclusions

i. Inter-regional datasets are valid as many species appear truly cosmopolitan.
ii. TQC is essential prior to merging regional diatom datasets.
iii. Merging of datasets has allowed the reconstruction of past anion and cation proportions, providing more detailed palaeohydrological and palaeoenvironmental interpretations.
iv. The new transfer functions have allowed palaeoenvironmental reconstructions of salinity and other climatically-controlled hydrochemical variables to be made for time periods previously poorly reconstructed.
v. Problem areas remain in species delimitation, particularly within the genus *Nitzschia* (section *Lanceolatae*)

6. Future Research Arising from the Project

Related NERC-funded research is continuing at UCL via a small grant to Professor R.W. Battarbee and Dr David Ryves (GR9/02033). This small grant builds on the combined results of Dr Ryves' NERC funded PhD (Ryves 1994) on diatom dissolution and on the taxonomic component of the grant reported here.

Further work is planned as follows:

i. application to crater lakes in Ethiopia (in collaboration with Dr Francoise Gasse) and to lakes in the Northern Great Plains, especially a re-examination of Medicine Lake, North Dakota (in collaboration with Dr Sheri Fritz);
ii. further systematic studies using more novel taxonomic approaches e.g. ultrastructure features, image analysis, experimental culture and molecular biology;
iii. examination of inter-regional datasets to assess the importance of biogeography and brine type on species distributions and forms, using experimental culture techniques to test hypotheses.

7. Publications Arising from the Project

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SUMMARY OF RESEARCH

Diatoms, salt lakes and climate change: inter-regional datasets and transfer functions for global application

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Keywords: Climate change, saline lakes, diatoms

Concern about global warming has highlighted the need to develop models to predict future climate. To test the validity of these models, they are run to see if they accurately hindcast past climate change. As historical climate records only exist for the last few hundred years, and then largely only for Europe, methods are required to reconstruct past climates, particularly in hot, dry regions, where even minimal warming is a serious threat to agriculture. In these regions, diatoms, a group of algae that have silica cell walls, can be used to reconstruct past climates.

Saline lakes, found in dry regions, respond to changes in climate. As temperature increases and rainfall decreases more water is lost from the lake through evaporation, concentrating the salts present in the water, therefore, raising salinity. The biological community in the lake, including diatoms, respond to the changes in salinity that occur as climate changes. Species more tolerant of higher salinities increase in warm, dry years and those preferring lower salinities decrease. On dying, diatoms sink to the bottom sediment of the lake. Their silica remains, accumulating year after year, provide a record of past salinity and a measure of climate. To calculate past salinities, the relationship of each diatom species present in the sediment to salinity must be known. This is obtained from a data set of modern lake sites where salinity and diatom species abundances have been recorded. Each species relationship to salinity can then be applied to the past diatom communities in the sediment. To apply all this, diatom species must be identifiable from their silica remains and their tolerances to salinity must be accurately known.

This study, therefore, had two main aims that were successfully achieved:
1) To produce a detailed guide to diatom species by providing a catalogue of photographic images of their silica remains and associated species descriptions. This will be published as a book to aid other workers in this field identify species accurately and consistently.

2) To merge diatom and chemistry data sets from Africa (East, North, and North-west (Niger)) and North America. This is beneficial because if the same species are present in more than one region, a single large data set should provide a fuller understanding of species relationships to salinity.

Additionally, detailed studies of important species, or those difficult to identify, was carried out. One species examined in detail was a small circular-shaped diatom named *Cyclotella caspia*. The identity of this was particularly important as it is present in sediment assemblages in Niger, Africa, yet it appears to be absent from the modern flora of Africa. It occurs abundantly in saline lakes in North America, but uncertainties about its correct identification prevented the salinity relationship calculated from the American dataset from being used in climate reconstructions in Africa. Our study confirmed that the African and American material were of the same species, permitting salinity reconstruction at the African site and identifying past periods of warmer climate.

PUBLICATIONS ARISING FROM PROJECT

Diatom Research (1995), Volume 10 (2), 229-240

STANDARDIZING THE TAXONOMY OF SALINE LAKE *CYCLOTELLA* SPP.

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To obtain more accurate reconstructions of past salinities and climate it is necessary to merge regional datasets of saline lake diatoms and water chemistry; a prerequisite of which is to standardize taxonomic practice. To illustrate this process, an investigation of the identity of a small *Cyclotella* species, frequently observed in the diatom community of saline lakes, is described. This taxon, which has been referred to in earlier literature as *Cyclotella caspia*, is of interest because it is present in fossil African assemblages, yet is absent from the modern flora of this region. Uncertainties over its correct identification prevented material in a North American dataset from being used as an analogue in salinity reconstructions. LM and SEM investigations reveal that there are no significant differences between Recent North American and Holocene sub-fossil North American and African material which suggests that the salinity optimum calculated from the North American water chemistry data can be used for salinity reconstructions in Africa. The species occurring in saline lakes is clearly different from *C. caspia* Grunow, but conforms with the description of *Cyclotella choctawhatcheeana* Prasad.

INTRODUCTION

In arid and semi-arid regions, the chemistry of closed-basin saline lakes responds directly to changes in the hydrological budget, through dilution or evaporative concentration of dissolved salts. Using a transfer function calibrated by a contemporary dataset of diatoms and water chemistry, diatom remains in the sediments can provide a record of past water chemistry, especially palaeosalinity, and a measure of water level and climate change. Calibration datasets and salinity transfer functions have been developed, or are being developed, for East and North Africa (Gasse 1987), the diagramatically suggests measuring costa density along a tangent with the valve margin. As pointed out by Kiss *et al.* (1988), the latter method is particularly inappropriate for small species of the Thalassiosiraceae.

RESULTS

Recent North American material

The diameter of the valves ranges between 6.9 and 10.6 µm. The marginal zone is well-defined, with 19–25 costae in 10 µm (Figs 1–3). The central area has a colliculate surface (*sensu* Håkansson 1982) with two to six puncta visible on some valves.

The SEM pictures show details of both the external and internal features of the valve. The puncta of the central area, seen with the light microscope, are revealed as the external openings of the central area fultoportulae and are situated on the elevated section of the central area (Fig. 4). Internally the central area is smooth, except for the projections of the central area fultoportulae which each have three satellite pores (Figs 5–6). Externally the marginal fultoportulae are visible as circular openings on every second to fourth interstria (Fig. 4); internally two satellite pores flank each one and are orientated radially (towards the valve face and the valve edge) (Fig. 5). There is one rimoportula which, viewed internally, is radially orientated and aligned with the ring of marginal fultoportulae. It is situated opposite the central area fultoportulae (Figs 5–6). Externally the rimoportula is visible, on an interstria, as a small slit-like opening situated slightly above the openings of the marginal fultoportulae (Fig. 7). No spines are visible on the valve surface, but granulae are found on the marginal zone.

Sub-fossil North American material

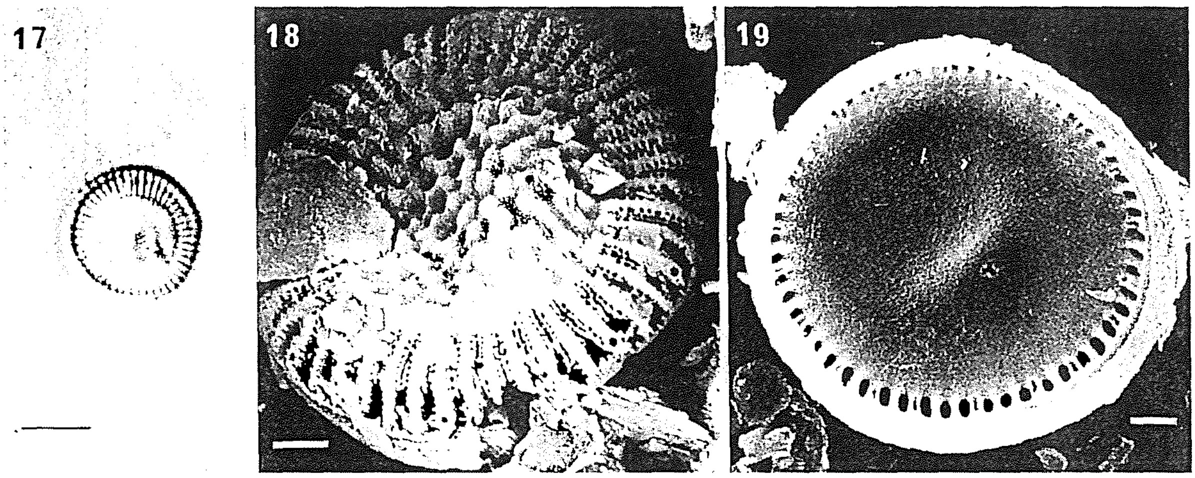
The diameter of the valves ranges between 6.9 and 11.9 µm. The marginal zone has 16–24 costae in 10 µm (Figs 8–11). The marginal fultoportulae are situated on every second to fifth interstria (Figs 12–16) and there are one to five fultoportulae on the elevation of the central area (Figs 8–11 & 13–15). Medicine Lake core material appeared to contain two distinct forms; form A (Fig. 8) which has a smaller diameter (7.5–7.9 µm), fewer central area fultoportulae (2) and a higher marginal fultoportula:costa ratio (1:3–4) than form B (Fig. 9) (10.0–11.9 µm diameter, 2–5 central area fultoportulae, 1:2–4 marginal fultoportula:costa ratio). In all other respects this material is identical to the Recent material (Figs 12 & 16), although, because of dissolution, the number of satellite pores surrounding the marginal fultoportulae could not be assessed for form A in Medicine Lake; neither could the form and position of the rimoportulae on the Medicine Lake form A and Devil's Lake specimens be established.

Sub-fossil African material (Adrar Bous)

The diameter of the valves range between 8.1 and 9.4 µm. The marginal zone has 16–20 costae in 10 µm (Fig. 17). One to two central area fultoportulae are found on the elevation of the central area (Fig. 18) and there are marginal fultoportulae on every second to third interstria (Figs 18–19). Because of dissolution the number of satellite pores surrounding the marginal fultoportulae could not be assessed, neither could the form and position of the rimoportula. In all other respects the sub-fossil African material was identical to the Recent and sub-fossil North American material. Two valves were seen which had a larger diameter and lower costa density (form B).

Table 1. Morphological and ecological features of material recorded as *Cyclotella caspia* from N. American and African saline lake basins.

Site	Basin Lake	Waldsea Lake	Deadmoose Lake	Devil's Lake	Medicine Lake (form A)	Medicine Lake (form B)	Moon Lake	Adrar Bous	Adrar Bous (form B)
(No. of valves viewed)	(25)	(8)	(25)	(20)	(17)	(9)	(25)	(25)	(2)
Diameter in µm	6.9–8.1	8.8–10.0	7.5–10.6	6.9–10.0	7.5–7.9	10.0–11.9	6.9–9.4	8.1–9.4	12.5–13.1
(mean)	(7.7)	(9.2)	(9.3)	(8.9)	(7.7)	(10.8)	(8.2)	(8.7)	(12.9)
Costae/10 µm	22–24	19–23	22–25	19–24	16–20	16–20	18–21	16–20	13–14
(mean)	(23)	(21)	(24)	(21)	(18)	(18)	(19)	(18)	(14)
Marginal fultoportula:costa ratio.	1:2–4	1:2–4	1:3–4	1:3–5	1:3–4	1:2–4	1:2–3	1:2–3	1:2–3
No. of satellite pores	2	2	2	2	2?	2	2	?	?
Central fultoportula no.	2–4	2–3	2–6	1–5	2	2–5	1–4	1–2	?
No. of satellite pores	3	?	3	3	3	3	3	3	?
No. of rimoportulae and location	1 radially orientated	1 radially orientated	1 radially orientated	?	?	1 radially orientated	1 radially orientated	?	?
Sample type	surface sediment	surface sediment	surface sediment	core	core	core	core	core	core



Figs 17–19. Specimens from sub-fossil African material, Adrar Bous, North Niger. Fig. 17. Light micrograph, scale bars = 5 µm. Figs 18–19. Scanning electron micrographs, scale bars = 1 µm. Fig. 18. External view of partly dissolved valve with one (visible) central fultoportula and marginal fultoportulae on every third interstria. Fig. 19. Internal view of partly dissolved valve with one central fultoportula flanked by three satellite pores and marginal fultoportulae every second to third costa.

from Basin Lake and Medicine lake (form A) did not overlap with those of Waldsea Lake and Adrar Bous. The ranges of valve diameter for material from Deadmoose Lake and Devil's Lake overlapped with all samples (excluding Adrar Bous form B). With respect to costa density, valves from Basin lake and Deadmoose Lake showed no overlap with valves from Medicine Lake, Moon Lake & Adrar Bous. However, the ranges of costa density for material from Waldsea Lake and Devil's lake overlapped with all samples (excluding Adrar Bous form B). The central area fultoportula number also varied between samples; the only clearly observable difference was that, except for a single valve which had two, only one fultoportula was observed on valves in the sub-fossil African sample. The variation in numbers of central area fultoportulae and marginal fultoportula:costa ratio may be related to the size of the valve, as it is known that they are involved in the secretion of β-chitin fibrils (Herth 1978) and may be involved in colony formation; presumably a greater number being required on larger cells. More are present in the larger form B from Medicine Lake than form A, giving support to this hypothesis.

The three sites from which Recent material was obtained had very similar salinities, close to the estimated salinity "optimum" of 21 g l^{-1} (Fig. 20). This figure was calculated by weighted averaging of relative abundance (%) from the North American sites where *C. caspia* was recorded (Table 2, modified from Fritz *et al.* 1993). Ion dominance, or brine type, was also similar for these three sites (Table 2). Salinity and brine type differences, therefore, do not appear to offer an explanation for the variations in valve morphology seen within these sites. This does not discount the possibility that they affect morphology, as has been shown for *C. cryptica* Reimann, Lewin & Guillard which has a *C. meneghiniana* Kützing valve pattern at low salinities (<4.3 g l^{-1}) (Schultz 1971). The fact that the variations in valve morphology cannot be explained in terms of salinity, brine type, or geography suggests that the American and African material should be considered as the same species and that the salinity "optimum", calculated from the North American saline lake water chemistry data, can be used in the salinity transfer function at Adrar Bous.

From our studies it is quite clear that the species occurring in saline lakes is quite different from *C caspia* for which see Håkansson *et al.* (1993). Apart from Adrar Bous form B, our material

Table 2. Water chemistry data for the North American saline lake sites where *Cyclotella caspia* has been recorded. The abundance of this taxon at each site is also given. (Taken from Fritz *et al.* (1993).

Site	State	% Abundance	Ion Dominance	Salinity (g l^{-1})
Basin Lake	Saskatchewan	15.6	$Mg(Na)SO_4$	21.2
Big Quill Lake	Saskatchewan	7.6	$Mg(Na)SO_4$	37.9
Deadmoose Lake	Saskatchewan	13.0	$Na(Mg)SO_4(Cl)$	21.5
East Devil's Lake	N. Dakota	7.0	$Na(Mg)SO_4$	9.9
Free People Lake	N. Dakota	1.4	$NaSO_4(CO_3)$	8.9
Lake George	N. Dakota	37.9	$NaSO_4$	21.2
Medicine Lake	S. Dakota	9.4	$MgSO_4$	38.6
Rabbit Lake	Saskatchewan	2.6	$Mg(Na)SO_4$	7.7
Rederry Lake	Saskatchewan	7.1	$Mg(Na)SO_4$	18.9
Sayer Lake	Saskatchewan	3.6	$MgSO_4$	18.8
Stink Lake, Stutsman Co.	N. Dakota	13.2	$Na(Mg)SO_4$	26.7
Waldsea Lake	Saskatchewan	14.4	$Mg(Na)SO_4(Cl)$	20.5

extend over part of the striated zone in the African material. More valves would have to be viewed to confirm its identity.

Inferences for environmental reconstructions

From Table 2 it appears that *C. choctawhatcheeana* is generally characteristic of sodium/ magnesium sulphate-dominated saline lakes, although it was abundant in two sites where chloride is also an important anion. Its general scarcity in carbonate-dominated saline lakes most probably reflects the lack of these sites within the NGP dataset. Other published sites of *C. choctawhatcheeana* are all chloride-dominated brackish environments, such as the type locality (Choctawhatchee Bay), the Baltic Sea (Snoeijs 1994, Håkansson *et al.* 1993), Chesapeake Bay (Cooper, in press), and the Schlei estuary (as *C. hakanssoniae* Wendker) (Wendker 1991). Its occurrence over this range of waters suggests that its presence cannot be used as a clear indicator of brine type.

In the NGP saline lake sites, *C.choctawhatcheeana* was most abundant at salinities around 21 g l^{-1} (Fig. 1) (Fritz *et al.* 1993). In Choctawhatchee Bay it was present throughout the year, but was most abundant in early summer, when salinities ranged from 15–20 g l^{-1}, being succeeded at higher salinities by *C. striata* (Kütz.) Grunow (Prasad *et al.* 1990) and in the Baltic Sea it was most common at salinities ranging from 8–10 g l^{-1} (Håkansson *et al.* 1993). It may be that the apparent lower salinity "optima" in chloride-dominated sites is because competition, or other factors in the environment, generate different optima in the different brine types, or it may reflect the fact that the surface sediment samples from saline lakes contain an assemblage which was growing earlier in the year when the salinity may have been lower. It is also possible that the discrepancy is a result of the salinity optimum in saline lakes being calculated from relative (%) abundance, rather than density. The latter could not be calculated as valve counts were made on the uppermost 3 cm of sediment at each site, not the phytoplankton. Alternatively, the range of salinities at which *C. choctawhatcheeana*

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CASPIA update on saline lake diatoms: report on a workshop

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CASPIA workshop

The workshop began with an outline of the history of the CASPIA project and its present state. What follows is a summary of this, accompanied by a brief outline of some of the points raised.

Diatom remains in the sediments of saline lakes can provide a direct record of past salinity and an indirect measure of water level and climate change (Fritz *et al.* 1991; Gasse 1987). Quantitative reconstructions of salinity require the development of a transfer function calibrated from a modern data set of diatoms and water chemistry. The CASPIA project (Climate and Salinity Project) was set up in 1991 by a group involved in the collection of these modern data sets from various saline lake regions around the world (Juggins *et al.* 1994). The aim of the project was to merge the different regional data sets into a single data base of diatom and environmental data.

Merging of regional data sets is desirable as it can provide a fuller understanding of species optima and tolerances. It also improves salinity transfer functions where modern analogues of fossil taxa do not occur within the same geographical region. Consistent sampling methodology and taxonomy is a prerequisite before merging the data sets, particularly if weighted-averaging based transfer functions are to be applied, as these rely on precisely quantified, species-rich assemblages (ter Braak & Looman 1986).

Taxonomic consistency is being achieved using methods of taxonomic quality control (TQC) developed during the SWAP (Munro *et al.* 1990) and PIRLA (Kingston *et al.* 1992) projects on lake acidification. Initially this involved the comparison of

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Table 1: Initial taxa to be investigated from African and North American data sets

Amphora:	*acutiuscula* Kütz.
	coffeaformis (Ag.) Kütz.
	ovalis var. *pediculus* (Kütz.) Van Heurck
	perpusilla (Grun. *in* Van Heurck) Grun. *in* Van Heurck
Campylodiscus:	*bicostatus* Wm Smith
	clypeus (Ehrenb.) Ehrenb.
Cyclotella:	*choctawhatcheeana* Prasad (misidentified as *C. caspia* Grun.)
	meneghiniana Kütz.
	quillensis Bailey
Navicula:	*bulnheimii* Grun. *in* Van Heurck
	capitata Ehrenb.
	cincta (Ehrenb.) Ralfs *in* Pritchard
	cryptocephala Kütz.
	cuspidata (Kütz.) Kütz.
	digitoradiata (Gregory) Ralfs *in* Pritchard
	elkab Otto Müller
	halophila (Grun. *in* Van Heurck) Cleve
	oblonga (Kütz.) Kütz
	pseudohalophila Cholnoky
	radiosa Kütz.
	veneta Kütz.
Nitzschia:	*constricta* (Kütz.) Ralfs *in* Pritchard
	hungarica Grun.
	punctata Wm Smith (Grun.)/*compressa* f. *minor* A. Cleve-Euler
	elegantula Grun. *in* Van Heurck
	fonticola Grun. *in* Cleve *et* Möller
	inconspicua Grun. (*frustulum* var. *subsalina* Hustedt)
	lacuum Lange-Bertalot
	microcephala Grun. *in* Cleve *et* Möller
	palea (Kütz.) Wm Smith
	subacicularis Hustedt
Surirella:	*brightwelli* Wm Smith
	crumena Bréb *in* Kütz.
	peisonis Pantocsek

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PALAEO

A 135,000-year record of vegetational and climatic change from the Bandung area, West-Java, Indonesia

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Abstract

Sedimentological and palynological analyses of sediment cores from the intramontane Bandung basin (West-Java, Indonesia) provide a first palaeoclimatic record for the Indonesian region covering continuously the last 135,000 years. Our data on palaeosol development indicate anomalously dry conditions for the final part of the penultimate glacial period, around 135,000 yr B.P., and very warm and humid interglacial conditions from 126,000 to 81,000 yr B.P. During the transition to the last glacial period, around 81,000 yr B.P., freshwater swamp forest of the Bandung plain was replaced by an open swamp vegetation dominated by grasses and sedges, indicating a change to considerably drier conditions, possibly related to reduced moisture uptake by the NW monsoon as a consequence of lower sea levels at the onset of glacial conditions. A strong reduction in *Asplenium* ferns from 81,000 to 74,000 yr B.P. suggests that drier conditions may also have occurred in the mountains of the Bandung area, while increased numbers indicate that from 74,000 to 47,000 yr B.P. it was slightly wetter again. Inferred depression of montane vegetation zones and reduced fern percentages suggests distinctly cooler and possibly drier climatic conditions prevailed in the Bandung area from 47,000 to approximately 20,000 yr B.P. For the Last Glacial Maximum 4–7°C lower temperatures are recorded.

1. Introduction

Earlier Quaternary palynological research in the Malay Archipelago included studies of highland, coastal and marine sites, but with the exception of a pollen record from the New Guinea believed to cover the last 60,000 years (Hope and Tulip, 1994) not one of these records reaches beyond 40,000 yr B.P. (Anderson and Muller, 1975: Borneo; Hope, 1976: New Guinea; Haseldonckx, 1977: Malaysia; Walker and Flenley, 1979: New Guinea; Maloney, 1980: Sumatra; Morley, 1981: Kalimantan, 1982: Sumatra; Hillen, 1984: Malaysia; Newsome and Flenley, 1988: Sumatra; Gremmen, 1990: Sulawesi; Van der Kaars, 1991: marine records; Barmawidjaja et al., 1993: Halmahera; Stuijts, 1993: Java). These studies suggest that in the last glacial period montane vegetation zones were depressed, indicating lower temperatures. But clear evidence for significantly drier conditions, as in other tropical regions i.e. northern Australia, South America or Africa (Flenley, 1979; Kershaw, 1986, 1994; Van der Kaars, 1991; Kuhry et al., 1993; Vincens et al., 1993) has so far not been found. In these regions sclerophyll and open dry vegetation types expanded during the last glacial period, indicating increased aridity. Only from some of the marine records indications for drier conditions during the last glacial period have been reported (Van der Kaars, 1991; Barmawidjaja et al., 1993). In these marine records fern spores percentages reduced strongly during the last glacial period, suggesting overall drier conditons in the Indonesian region.

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PALAEO

Diatom-based transfer functions for inferring past hydrochemical characteristics of African lakes

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Abstract

A new dataset of 282 modern diatom samples and associated environmental information has been created by merging existing regional datasets from North and East Africa and Niger. The relationships between diatom species distributions and hydrochemistry are examined using canonical correspondence analysis (CCA) and partial CCA. Variables reflecting water conductivity, pH, and cation and anion composition account for significant and independent components of the total variation in the diatom data. Predictive models (transfer functions) are developed using the method of weighted averaging for conductivity ($r^2 = 0.87$), pH ($r^2 = 0.77$), and ratios between alkali and alkaline earth metals ($r^2 = 0.81$), and carbonate–bicarbonate and sulphate + chloride ions ($r^2 = 0.82$). Prediction errors are estimated using the computer-intensive method of jackknifing. These transfer functions enlarge the potential domain for reconstruction of past hydrochemistry from fossil diatoms preserved in lake sediments.

1. Introduction

The development of General Circulation Models (GCMs) to predict future changes in the global environment has focussed the need for comparison of model results with proxy data for key periods of the past (COHMAP Members, 1988). Such comparisons require accurate, quantitative reconstruction of hydrological and climatic variables. Pollen records have been used successfully to infer past precipitation and temperature for temperate and tropical regions (e.g. Guiot et al., 1989; Bonnefille et al., 1990). Independent methods can be used to complement pollen-based reconstructions, and to provide cross-disciplinary control of the interpretation of vegetation changes.

In arid and semi-arid regions there is a direct link between climate and surface water hydrology, and closed lakes may fluctuate in both water level and water chemistry in response to seasonal, interannual or longer-term climatic fluctuations. Past lake-level fluctuations may be recorded in former high shorelines or other lithostratigraphic evidence and provide a powerful tool for palaeoclimatic reconstruction at large spatial and temporal scales (e.g. Street-Perrott et al., 1989). The chemistry of closed basins also responds to the hydrological budget through the concentration or dilution of dissolved salts. Where hydrochemistry is not driven by local hydrological factors, the reconstruction of past water chemistry from proxy indicators therefore provides an independent method for estimating changes in the precipitation–evaporation balance of the lake catchment area.

Inferring changes in water chemistry from a palaeolake record is a two-step process. First, the

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response of environmental indicators to water chemistry is modelled from their relationships in a suite of modern reference samples. Second, the modelled responses, or transfer functions, are applied to the palaeolimnological record. A large variety of palaeochemistry indicators is found in salt lake sediments. The list includes authigenic mineral species (e.g. Teller and Last, 1990), trace element and stable isotope content of authigenic minerals of biogenic or inorganic origin (Chivas et al., 1986; Gasse et al., 1987; Talbot, 1990, among others), and biological remains, primarily molluscs, ostracods (e.g. De Deckker, 1982), and diatoms. Among the latter category, diatoms emerge as an unrivalled tool for quantitative reconstruction, because (1) they are extremely sensitive indicators of lake-water chemistry, (2) they commonly occur in high numbers in both modern environments and sedimentary sections, allowing quantitative numerical analysis, and (3) the great majority of diatom taxa are cosmopolitan or have a widespread geographical distribution. Modern reference, or calibration datasets established for different regions can thus be combined to reinforce the relationships between diatoms and chemical variables observed at a regional scale.

Over the past decade enormous progress has been made in diatom palaeoecological interpretation by the development of transfer functions which provide quantitative reconstructions of key hydrochemical parameters. For example, statistical analysis of 156 modern diatom samples from East Africa showed that diatoms respond primarily to total salinity or conductivity, and to the ionic ratios which define the chemical facies of the waters (Gasse et al., 1983). This dataset, which consisted primarily of samples of the carbonate–bicarbonate type, was used to develop transfer functions for pH (Gasse and Tekaia, 1983) and conductivity (Gasse, unpublished), and to provide quantitative reconstructions of these variables for a 26 kyr diatom record from Djibouti (Gasse, 1986a), and for several post-glacial sequences from East Africa (Barker, 1990) and the Sahel (Gasse et al., 1990). Using similar methodology, investigations of saline lakes in the northern Great Plains of North America, where most waterbodies are of the sodium-magnesium sulphate type, also demonstrated that water chemistry is the major factor explaining the composition of diatom communities (Fritz et al., 1993). For this region a transfer function was developed from 55 modern samples and used to reconstruct late-glacial and Holocene salinity fluctuations at two sites (Fritz et al., 1991; Juggins et al., submitted).

The consistency between diatom records and other independent evidence for reconstructing past hydrology and climate are promising (Gasse et al., 1987; Fritz, 1990). However, the different categories of brines in the individual regional datasets are not equally represented, making it difficult to quantify diatom response to brine type. For example, the East African modern dataset could not predict well changes from carbonate- to chloride-dominant brines when total salinity increased, because of the relatively low numbers of reference samples of the chloride type.

This paper is based on a considerably enlarged African dataset of 282 samples from 164 sites. It includes 125 new modern samples from Niger and the Maghreb, where most of the waterbodies are of the chloride or chloride-sulphate type. Despite the large geographical area investigated it is clear from initial comparison of datasets that samples with similar water chemistry also exhibit marked similarities in the diatom flora. For example, taxa such as *Thalassiosira faurii* and *Navicula elkab*, which are regarded as characteristic of hyperalkaline water in East Africa, were also found in natron ponds in southern Niger. The transfer function for pH based on the initial East African dataset was also tested with success on modern samples from Niger (Gasse, 1987). Similarly, species considered characteristic of the rare chloride-type waters investigated in East Africa, e.g. *Amphora coffeaeformis*, *Synedra hartii*, and *Stauroneis wislouchii* are widespread in North Africa. The merging of individual regional datasets therefore offers the potential to increase the coverage of particular chemical gradients and to allow diatom response along these gradients to be modelled.

We present here new transfer functions established using the method of weighted averaging regression (ter Braak and Looman, 1986; Birks et al., 1990). Conductivity and pH transfer functions refine previous investigations of these parameters. For the first time, transfer functions are developed for alkali/alkaline earth metals, and (carbonate + bicarbonate)/(chloride + sulphate) ratios. These new transfer functions enlarge the potential domain for predictions of water chemistry evolution. They will allow the reconstruction of changes in cation and anion dominance which may accompany salt precipitation and brine evolution as waters follow particular geochemical pathways in response to evaporative concentration of a primary solution (Hardie and Eugster, 1970).

2. The calibration dataset

The African diatom dataset currently available results from 25 years of published and unpublished work, conducted by F. Gasse and collaborators in different regions of the continent. A wide variety of modern waterbodies (lakes, swamps, peat-bogs, springs, stagnant sections of wadis) lying under diverse climatic and hydrological conditions have been investigated. Where possible a range of sample-types has been collected from each site, including phytoplankton, epiphyton and benthos. The geographic distribution of samples is shown in Fig. 1. The regional datasets are briefly described below.

2.1. *East African dataset (167 samples)*

The sites investigated (98) are situated between 19°N and 14°S in latitude, 27°E and 43°E in longitude. They range from afro-alpine bogs at

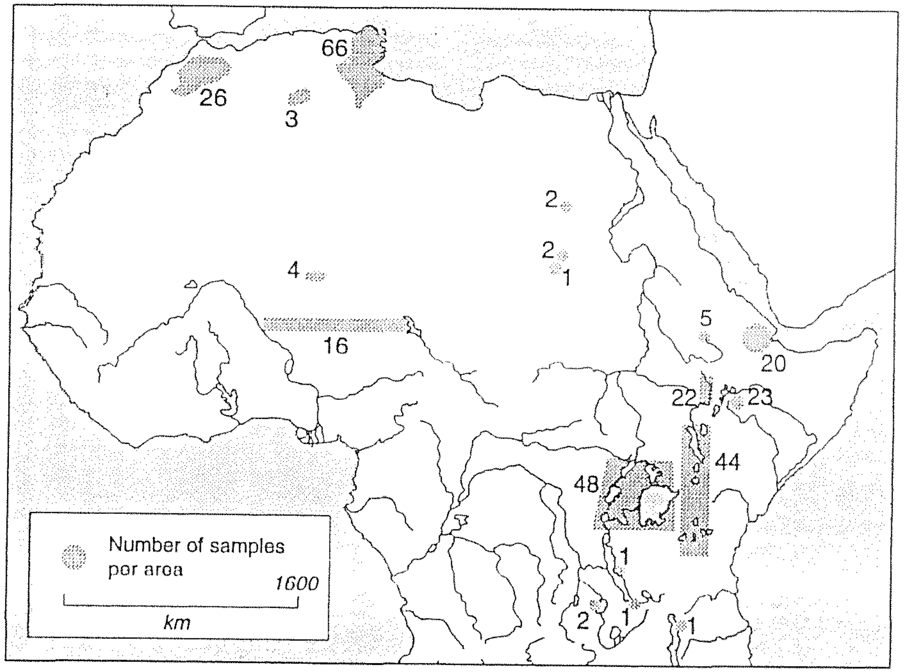

Fig. 1. Location of sampling areas for the combined modern diatom/chemistry dataset, showing numbers of samples from each area.

altitudes of up to 4000 m to hypersaline lakes lying below sea-level. The pH ranges from 5 to 10.9, and the conductivity from about 40 to 50,000 µS cm^{-1}. Detailed descriptions of the 167 diatom samples and chemical analyses were published by Gasse et al. (1983). This paper also provides a numerical classification of the diatom assemblages, and shows that these are clearly linked to the total water-salinity and major ion composition. Despite the large climatic gradients sampled there was no clear correlation between temperature and diatom communities. A total of 579 taxa was identified in the dataset, the taxonomy and autecology of which are discussed and illustrated by Gasse (1986b).

2.2. *Northwest Africa dataset (125 samples)*

The northwest African dataset consists of 66 samples from Tunisia, 3 samples from Algeria, and 26 samples from Morocco. The Tunisian samples were collected from the Mediterranean northern regions to the margins of the Sahara southwards. In the Chott el Jerid area samples were collected from small permanent waterbodies (gueltas) supplied by ground water, temporary salt lakes (sebkhas) or salt marshes, and small artificial ponds developed around boreholes. Numerous samples were collected from Wadi el Akarit, near Gabès, a permanent river supplied by several springs, which contains a chain of mini reservoir lakes or swamps. Samples from hydrothermal springs have also been collected throughout the country and, together with freshwater samples from the Mejerda channel in northern Tunisia, provide a large range of hydrochemical conditions. Waters range from fresh to metasaline. Most samples are of the sodium-chloride, or calcium–magnesium/chloride–sulphate type. The dataset contains a total of 457 taxa. Details of diatom and hydrochemical analyses are given in Ben Khelifa (1989).

Sites from southern Algeria supplied by groundwater show clear similarities with the waterbodies of southern Tunisia in both water chemistry and diatom flora (Gasse, unpublished) and complement information from the northern margin of the Sahara.

The 26 samples from Morocco were collected by F. Gasse in 1989 from 17 localities situated between 30°30′–34°30′N and 5°–7°30′E. Sites are distributed in the western plains close to Casablanca, the Middle Atlas mountains, and the more arid southeast margins of the Atlas ranges. Localities range in altitude from 300 to 2050 m. In the Atlas, phytoplankton, bottom mud, littoral epiphytic and epipelic flora were sampled from several permanent (e.g. Aguelmane Sidi Ali, A. Azigza, Dayet Aoua) and temporary (e.g. Dayet Iffrah) karstic lakes. In southern Morocco (Marrakech and Ouarzazate regions) samples were collected from man-made lakes and wadis. Conductivities range from 195 µS cm^{-1} for the most dilute waters from the Middle Atlas (Aguelmane Taanzoult), to 3900 µS cm^{-1} for small swamps supplied by the overflow of the southern wadis, which are subjected to evaporative concentration. Chemical analyses have been conducted at the Centre des Faibles Radioactivités, Gif-sur-Yvette, under the supervision of L. Labeyrie (by atomic absorption and colorimetry). Lakes from the Middle Atlas belong to the calcium–sodium/bicarbonate type, while oligosaline waters from southern Morocco are of the sodium-chloride type. One of the most characteristic features of this Moroccan dataset is the abundance and the diversity of planktonic *Cyclotella* species, including taxa close to *C. comensis*, and *C. azigzensis* described as a new species by Flower et al. (1990) and found in several lakes from the Middle Atlas.

2.3. *Niger dataset (20 samples)*

In southern Niger, modern samples were collected from the Niger River, the Bara salt pond near Niamey, and from interdunal depressions on the Manga plateau, west of Lake Chad. Several of the latter are occupied by small permanent or seasonal waterbodies supplied by the regional aquifer and vary from freshwater, circumneutral swamps (e.g. Falki Karama, Guidimouni lake) to hyperalkaline ponds (Guidimouni salt pond), or playas. The main characteristics of the water chemistry and diatom communities of these samples are presented in Gasse (1987). A few samples from northern Niger (Air) have also been collected from groundwater-supplied gueltas (Timia). Most water-bodies are of the sodium/carbonate–bicarbonate type. Chemical analyses were carried out at the Laboratoire des Eaux de la Ville de Paris by atomic absorption and colorimetry.

3. Materials and methods

3.1. *Diatom analysis and taxonomy*

For each sample, the percentage of each taxon was evaluated by counting 300 to 1000 valves distributed on four slides. All diatom analyses have been conducted by F. Gasse, except those from Tunisia (Ben Khelifa, 1989) and 3 samples from Kenya (Ben Khelifa, unpublished).

Diatom taxonomy has considerably evolved during the last decades. Diatom data obtained over several years have thus been harmonised, primarily by following the taxonomy and nomenclature proposed by Krammer and Lange-Bertalot (1986–1991). Synonyms proposed by these authors were adopted, unless individual taxa grouped by these authors appear to have ecological significance in our material. For example, we separated *Navicula halophila* (Grun.) Cl., most commonly found in sodium-chloride oligosaline waters, from *N. simplex*, observed in much more dilute environments. *Navicula elkab* O. Müller was maintained as an entity because it is an excellent indicator of hyperalkaline waters, although it fits within the Krammer and Lange-Bertalot's description of *N. halophila*, and it is likely to be conspecific with one of the specimens illustrated by these authors (Krammer and Lange-Bertalot, 1986, pl. 44, fig. 11) and called *N. halophila*.

3.2. *Hydrochemical variables*

The hydrochemical variables used in this study were chosen to reflect the major gradients influencing diatom distribution identified in previous studies. Specifically, we included conductivity, pH, major cations (Na^+, K^+, Ca^{2+}, Mg^{2+}) expressed as a proportion of total cations, major anions ($CO_3^{2-}+HCO_3^-$, Cl^-, and SO_4^{2-}) expressed as a proportion of total anions, cation ratio (the ratio of alkali to alkaline earth metals (($Na^+ + K^+$)/($Ca^{2+} + Mg^{2+}$)), and anion ratio (($CO_3^{2-} + HCO_3^-$)/($Cl^- + SO_4^{2-}$)). Ionic proportions and ratios were based on ions expressed in meq l^{-1}. Conductivity and pH measurements are available for all 282 samples. Anion and cation data are available for 237 samples. Summary statistics for the hydrochemical variables are given in Table 1.

Table 1
Summary statistics (minimum, maximum and median) for the variables used in the multivariate analyses

Variable	Minimum	Maximum	Median
Conductivity (µS cm^{-1})	40	99,060	925
pH	5.5	10.9	7.8
Na + K (%)	11.2	99.5	67.1
Mg (%)	0	69.3	15.3
Ca (%)	0	56.3	13.8
Cation ratio	0.13	1966.1	2.04
Carbonate – bicarbonate (%)	0	98.1	65.2
Sulphate (%)	0	70.6	7.2
Chloride (%)	0.7	94.0	28.9
Anion ratio	0.001	51.9	1.9

3.3. *Data analysis*

After harmonisation the combined African dataset of 282 samples contained a total of 665 taxa. To reduce the number of rare taxa we have grouped varieties to the nominate when they appear to have the same ecological distribution, or when the level of identification was different in individual datasets. This resulted in a dataset of 604 taxa. For the multivariate analyses and development of transfer functions we further reduced the dataset by deleting species that were present in only one sample, or had a maximum relative abundance of less that 1%. This resulted in a final dataset of 389 taxa.

The relationship between diatom distribution and the hydrochemical environment was explored by detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA) (Ter Braak, 1986) of the 237-sample dataset for which full anion and cation data were available. For a transfer function to be developed for a particular environmental variable we require that the variable should explain a significant part of the total variation in the diatom data, independent of any additional variables. The independence and relative strength of the major hydrochemical gradients was estimated by using a series of partial CCAs to partition the total variation in the diatom data into components representing (1) the unique contribution of individual chemical variables, (2) the contribution of interactions between pairs of variables, and (3) unexplained variance (Borcard et al., 1992). The statistical significance of CCA and partial CCA ordination axes was determined using a Monte Carlo permutation test. All ordinations were performed using the program CANOCO version 3.10 (Ter Braak, 1988, 1990).

Weighted-averaging (WA) and tolerance-downweighted WA transfer functions were developed using the program CALIBRATE (Juggins and Ter Braak, 1992). The WA regression coefficients for each species are abundance-weighted means and abundance-weighted standard deviations and give estimates of species' ecological optima and tolerances along the chemical gradient of interest. Full details of the method and a palaeoecological example are given in Birks et al. (1990). Transfer functions were developed using both classical and inverse deshrinking.

The performance of the various transfer functions is reported in terms of the root mean square of the error (RMSE) (observed–inferred), the squared correlation (r^2) between observed and inferred values, and the maximum bias. For estimation of the latter the gradient was subdivided into 10 equal intervals, the bias per interval calculated and the (signed) maximum of the 10 values calculated (Ter Braak and Juggins, 1993). The first two measures indicate the overall performance of the model; the RMSE indicates prediction errors while r^2 measures the strength of the relationship between observed and inferred values and allows comparison between transfer functions for different chemical variables. The maximum bias is a measure of the tendency to over- or underestimate along particular parts of the gradient. These three parameters are calculated as both "apparent" measures in which whole dataset is used to both generate the transfer function and assess its predictive ability, and jackknifed or "leave-one-out" measures. The former measures allow comparison with other published transfer functions, but the latter are more reliable indicators of the true predictive ability of the transfer functions as they are less biased by sample resubstitution (Dixon, 1993).

A large heterogeneous dataset such as this will inevitably contain some samples that show a poor statistical relationship to one or more of the environmental variables of interest. Such outliers can decrease the predictive ability of the estimated transfer function coefficients (Martens and Naes, 1989). They should therefore be identified and removed from the dataset. After derivation of initial transfer functions for each environmental variable the data were screened and samples that had a difference between the observed and jackknife-inferred environmental value of greater that one-quarter of the total range of the variable were deleted.

4. Results and discussion

4.1. Ordination analyses

CCA axes 1 ($_1$= 0.50) and 2 ($_2$= 0.27) explain 6.8% of the total variance in the diatom data. The low percentage variance explained is typical of datasets with a large number of samples and species and with many zero values (e.g. Dixit et al., 1993). However, ordination axes which account for only a low percentage may be informative and their significance is better judged using a permutation test (Ter Braak, 1988), the results of which indicate that CCA axes 1 and 2 are both highly significant (p= 0.01, 99 random permutations). In addition, the eigenvalues for CCA are similar to those for DCA ($_1$= 0.59, $_2$= 0.35), and the similar configuration of taxa and samples in both ordinations indicates that the gradients of conductivity, pH, and brine type included in the CCA account for the major patterns of floristic composition in the diatom data.

The CCA species- and sample-environment biplots are shown in Fig. 2. In the biplot the length of environmental arrows approximate their relative importance in explaining the variance in the diatom data, and their orientation shows their

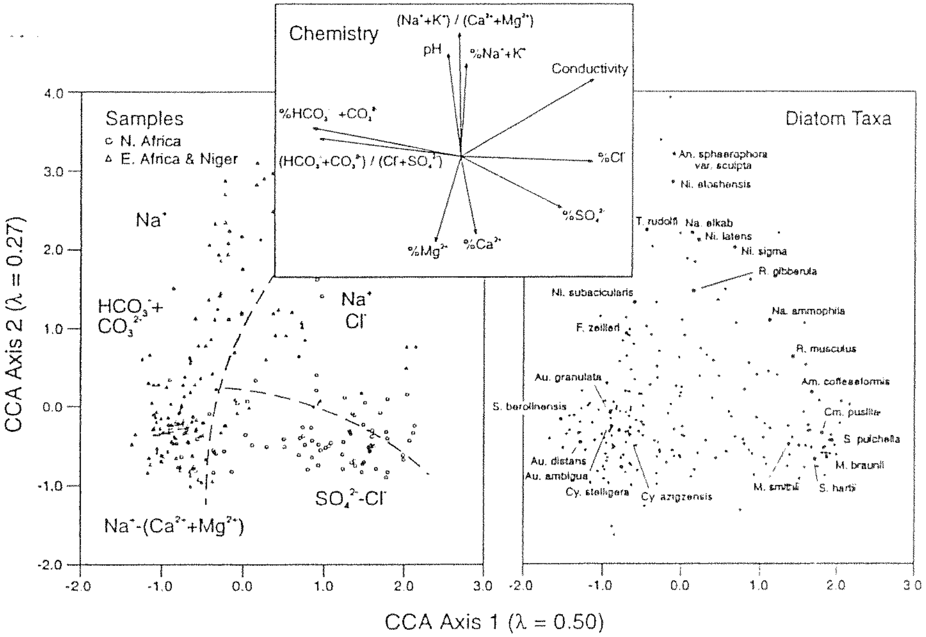

Fig. 2. CCA sample- and species-environmental biplot. The ordination is based on 237 samples with conductivity, pH and full cation and anion data, and 354 taxa, although the positions of only 219 taxa with maximum relative abundance greater than 5.0% are marked, and only selected taxa indicative of particular brine-types are labelled.

approximate correlations to ordination axes and other environmental variables. Intra-set correlations of environmental variables with axes 1 and 2 show that conductivity and variables representing anion type, are highly correlated with axis 1, and that pH, conductivity, and variables representing cation type are highly correlated to axis 2. Axis one therefore reflects the major gradient from the predominantly East African carbonate-bicarbonate waters plotted on the left of the diagram to the chloride/sulphate waters of North Africa plotted on the right. Axis two reflects the cation and to some extent conductivity gradients, from (1) the more dilute East and North African calcium–sodium–magnesium/carbonate–bicarbonate waters plotted bottom left, to the East Africa sodium-dominated hyperalkaline waters plotted top left, and (2) from the North African calcium–magnesium/chloride–sulphate waters plotted bottom right to the hypersaline North African sodium chloride waters plotted top right.

On the species-environment biplot the position of taxa projected perpendicularly onto environmental arrows approximate their weighted average optima along each environmental variable. In this way taxa characteristic of particular brine types may be identified; e.g. *Thalassiosira rudolfi* and *Navicula elkab* (hyperalkaline sodium carbonate), *Aulacoseira* spp. and *Cyclotella stelligera* (dilute calcium–sodium/bicarbonate), and *Rhoplodia musculus* and *Navicula ammophila* (sodium chloride).

The ten environmental variables used in the ordination analyses account for a total of 11.6% of the variance in the diatom weighted-averages.

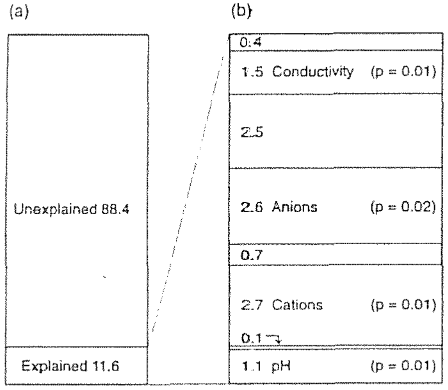

Fig. 3. Results of partial CCAs partitioning the total variance in the diatom data into (a) explained and unexplained portions, and (b) components representing the unique contributions of variables representing the conductivity, pH, cation and anion gradients (open), and correlations between gradients (shaded). Significance (*p*) values are based on 99 random Monte Carlo permutations.

Fig. 3 summarises the results of the partial CCAs in which this total explained variance is partitioned into components representing the four major hydrochemical gradients, ie. conductivity, pH, and cation and anion dominance. In the analysis these gradients were represented by single variables (in the case of conductivity and pH), and groups of variables (in the case of cation and anion dominance). Fig. 3 shows (1) the unique contribution of individual gradients, ie. the variance explained after the effects of the three other gradients has been partialled out, and (2) the variance explained by interactions between pairs of gradients. The results indicate that the total explained variance of 11.6% is made up of unique contributions of 1.5, 2.6, 2.7 and 1.1% for variables representing the conductivity, anions, cation and pH gradients, respectively. The associated Monte Carlo permutation tests (99 random permutations) indicate that these components are highly significant. Thus each of these gradients accounts for an independent and significant portion of the total variance in the diatom data.

In addition, relatively little of the explained variance is accounted for by inter-correlations between the pH and cation variables (0.1%), or between these gradients and the conductivity and anion gradients (c. 1.0%). The pH and cation gradients therefore represent largely independent directions of variation in the diatom data. However, 2.5% of the total explained variance is accounted for by correlations between conductivity and anion variables, reflecting the trend towards higher conductivities along the gradient from carbonate–bicarbonate to sulphate–chloride dominated waters in this dataset. This is in part due to the lack of samples from low-conductivity sulphate and chloride waters, and to the dominance of chloride in high conductivity waters, the latter reflecting this ion's conservative behaviour during brine evolution through evaporative concentration and salt precipitation. Transfer function coefficients (ie. species optima and tolerances) for conductivity are therefore partially influenced by anion type, and vice-versa. These results indicate that statistically significant and independent transfer functions can be developed for variables reflecting the four major hydrochemical gradients of interest, but that transfer functions for conductivity and anion type cannot be considered to be completely independent.

4.2. *Hydrochemical transfer functions*

Data screening for conductivity, pH, cation ratio and anion ratio transfer functions produced 8, 33, 13 and 2 samples respectively with a jackknife residual of greater that one-quarter of the total gradient length. These were deleted and weighted-averaging transfer functions developed using the remaining samples. The number of taxa and samples used for each transfer function and their inverse- and classical-deshrinking regression coefficients are given in Table 2. Summary statistics describing the predictive ability of the transfer functions are given in Table 3 and relationships between measured and diatom-inferred hydrochemistry are shown in Fig. 4.

Squared correlations between observed and inferred values show that conductivity is the strongest variable, followed by anion ratio, cation ratio and pH. Tolerance-downweighted WA appears to perform better that ordinary WA when apparent errors are considered, but gives larger RMSEs and lower r^2 for all variables under cross-validation (jackknifing) (Table 3). Thus we recommend ordinary WA as the most appropriate method and report deshrinking regression coefficients for this method only. Jackknife estimates of the prediction error (RMSE) for ordinary WA are between 18 and 32% higher that the corresponding apparent errors, highlighting the importance of using a method of cross-validation to estimate likely error when the transfer functions are applied to unknown samples.

The performance of the conductivity transfer function established here ($r^2 = 0.87$) is very similar to that of WA salinity transfer functions developed

Table 2
Summary statistics after screening for the datasets used to develop transfer functions for conductivity, pH, cation ratio, and anion ratio (numbers of samples and numbers of taxa), and deshrinking regression coefficients (b_0, and b_1) for the resulting transfer functions. See text for an explanation of these coefficients

Variable	Number of samples	Number of taxa	Regression coefficients			
			Inverse		Classical	
			b0	b1	b0	b1
Conductivity	274	389	−1.123	1.367	1.105	0.639
pH	249	388	−5.536	1.689	4.358	0.458
Cation ratio	224	367	−0.229	1.474	0.217	0.551
Anion ratio	235	370	0.024	1.334	−0.028	0.612

Table 3
Statistics summarising the performance of ordinary weighted averaging (WA), and tolerance-downweighted WA (Tol-WA) transfer functions for conductivity, pH, cation ratio and anion ratio using inverse (I) and classical (C) deshrinking. See text for explanation of the performance statistics

Method	Deshrinking type	Apparent			Jackknife		
		RMSE	r^2	Max. bias	RMSE	r^2	Max bias
Conductivity							
WA	I	0.32	0.87	0.40	0.39	0.81	0.52
Tol-WA	I	0.26	0.92	0.32	0.41	0.80	0.48
WA	C	0.34	0.87	0.35	0.40	0.81	0.46
Tol-WA	C	0.27	0.92	0.28	0.42	0.80	0.39
pH							
WA	I	0.48	0.77	0.72	0.61	0.63	0.86
Tol-WA	I	0.42	0.82	0.63	0.67	0.55	0.98
WA	C	0.54	0.77	0.58	0.65	0.63	0.68
Tol-WA	C	0.47	0.82	0.47	0.70	0.55	0.87
Cation ratio							
WA	I	0.34	0.81	0.44	0.45	0.68	0.70
Tol-WA	I	0.29	0.87	0.38	0.49	0.63	0.73
WA	C	0.38	0.81	0.37	0.48	0.68	0.69
Tol-WA	C	0.31	0.87	0.32	0.51	0.63	0.73
Anion ratio							
WA	I	0.43	0.82	0.51	0.54	0.72	0.68
Tol-WA	I	0.36	0.88	0.52	0.53	0.73	0.63
WA	C	0.48	0.82	0.37	0.58	0.72	0.54
Tol-WA	C	0.38	0.88	0.43	0.54	0.73	0.57

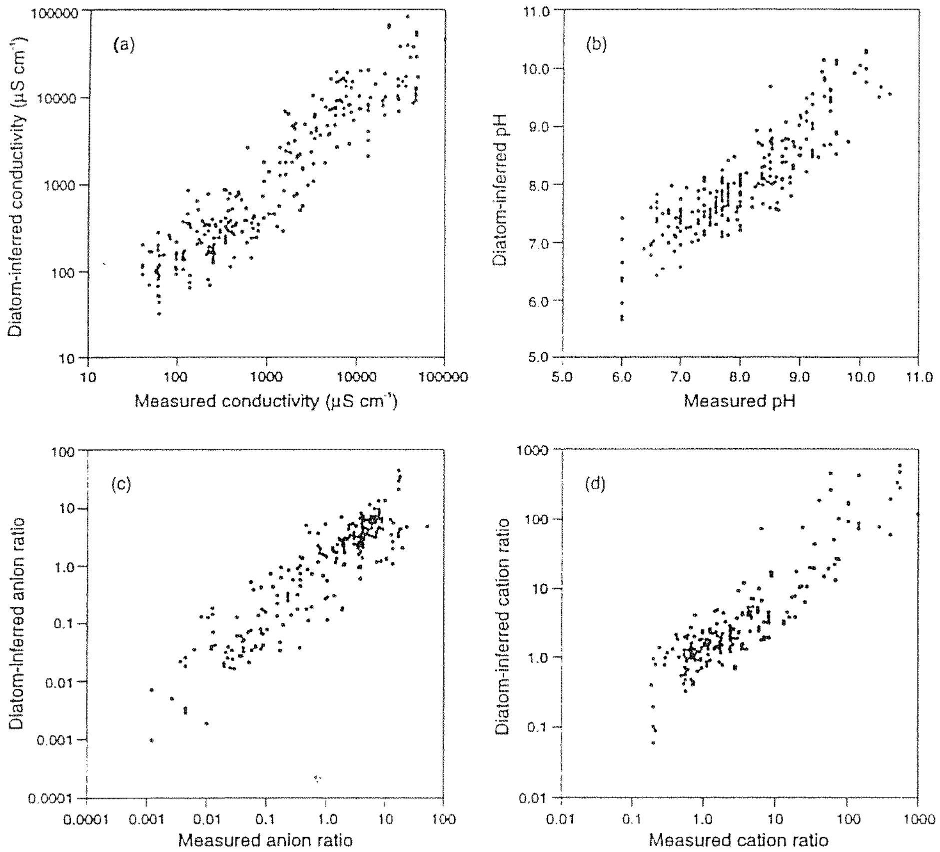

Fig. 4. Relationships between measured and diatom-inferred conductivity (a), pH (b), anion ratio (c), and cation ratio (d).

for the northern Great Plains (apparent $r^2 = 0.83$, Fritz et al., 1991) and British Columbia (apparent $r^2 = 0.89$, Cumming and Smol, 1993). Similarly, the performance of the pH transfer function for the combined African dataset ($r^2 = 0.77$) is comparable to that for a transfer function developed for the East African dataset alone (apparent $r^2 = 0.73$, Gasse and Tekaia, 1983), or for an alkalinity transfer function developed for Bolivian lakes (apparent $r^2 = 0.70$; Roux et al., 1991). Combining regional datasets thus extends the coverage of brine types and allows the development of new transfer functions for novel hydrochemical variables without compromising the ability of the dataset to predict conductivity or pH. The effect of increasing the diversity of hydrochemical-types by combining datasets, which could act to reduce predictive ability by introducing unmodelled or "nuisance" variables into the WA regression (cf. Ter Braak and Juggins, 1993), is apparently offset

by the larger number of samples which presumably result in more accurate estimates of species' parameters.

Weighted-average optima and tolerances are listed in Table 4. For each transfer function the number of occurrences of each taxon (*N*), its maximum relative abundance (*Max*), and Hill's N_2, the number of effective occurrences (Hill, 1973; Ter Braak, 1990) are also listed. The latter gives an indication of the number of samples contributing to the calculation of a taxon's WA optima. Optima estimated for taxa with a low number of occurrences or a low N_2 should be interpreted with caution.

These optima can now be used to infer the hydrochemical variables from fossil diatom assemblages using the WA calibration formula:

$$\text{initial } x_i = \sum_{k=1}^{m} y_{ik} u_k \Big/ \sum_{k=1}^{m} y_{ik}$$

where y_{ik} is the abundance of taxon k in fossil sample i, u_k is the WA optimum for taxon k ($k = 1....m$ diatom taxa), and initial x_i is the initial inferred value of the hydrochemical variable for fossil sample i.

In weighted averaging regression and calibration averages are taken twice, and the range of the estimated environmental variable (initial x) is shrunken. Deshrinking regressions were therefore performed using both classical (initial x on observed x), and inverse regressions (observed x on initial x). The latter has the advantage of minimising the root mean squared error in the training set, but at the cost of introducing bias at the endpoints (Ter Braak and Juggins, 1993; Martens and Naes, 1989). The choice of deshrinking method thus depends on the part of the gradient of interest; if greatest accuracy is required at high or low environmental values then classical deshrinking is preferable. If the focus is on mid-range environmental values then inverse deshrinking should be used.

The regression coefficients listed in Table 2 should be used to deshrink to the initial values to give final estimates of the diatom-inferred hydrochemical variables using either classical deshrinking:

$$\text{Final } x_i = (\text{initial } x_i - b_0)\ b_1$$

or inverse deshrinking:

$$\text{Final } x_i = b_0 + b_1 * \text{initial } x_i$$

Reconstructed values for conductivity and ionic ratios will be in $\log_{10}$ units and should be back-transformed if conductivities in S cm^{-1} or ionic ratios based on meq l^{-1} are required.

5. Conclusions

Our results show strong and highly significant relationships between modern diatom assemblages and major hydrochemical variables. Transfer functions quantifying these relationships can now be used to reconstruct conductivity, pH, and alkali/alkaline earth metals and (carbonate + bicarbonate)/(chloride + sulphate) ratios from fossil diatom assemblages. These transfer functions will be applied to well-dated sedimentary sequences from Africa for which diatom records are already available in harmony with the taxonomic concepts used in our modern dataset.

However, application of the transfer functions should proceed with caution as several factors may affect the accuracy of hydrochemical reconstructions and their palaeoclimatic interpretation. First, water bodies in arid and semi-arid zones commonly experience large fluctuations in water chemistry which influence diatom productivity and community composition during a single hydrological cycle. The taphocenoses may thus contain a mixed assemblage of diatoms derived from different source communities which reflect a range of water qualities. Second, taphonomic problems related to diatom dissolution are critical in saline waters. Dissolution of diatoms can bias the assemblage by selective dissolution of weakly silicified forms. This process depends on both ionic composition and concentration and is thus site specific (Barker et al., 1994).

In addition, palaeochemistry may vary in response to non-climatic factors. For example, lake chemistry may be influenced by the weathering of salt crusts or seepage of saline brines through

Table 4

The total number of occurrences (N), effective number of occurrences (Hill's N_2), maximum percent abundance (Max), and optima and tolerances for WA transer functions for conductivity, pH, cation ratio and anion ratio. Optima and tolerances for conductivity are in $\log_{10}(x)$ units where x is measured in S cm^{-1}. For cation and anion ratios optima and tolerances are in $\log_{10}(x)$, where x is the ionic ratio calculated from concentrations expressed as meq l^{-1}. Tolerances are adjusted for number of occurrences (Ter Braak, 1990). Blanks in the table represent zero abundance

Taxon name	Authority	Conductivity					pH					Cation ratio					Anion ratio				
		N	*Max*	N_2	Optimum	Tolerance	*N*	*Max*	N_2	Optimum	Tolerance	*N*	*Max*	N_2	Optimum	Tolerance	*N*	*Max*	N_2	Optimum	Tolerance
Achnanthes brevipes var. *intermedia*	(Kütz) Cleve	11	55.7	1.8	3.79	0.34	11	55.7	1.5	7.39	0.30	10	55.7	1.8	0.07	0.15	10	55.7	1.8	−1.61	0.32
Achnanthes clevei	Grun.	5	3.7	1.9	1.93	1.04						5	3.7	1.9	0.87	0.72	5	3.7	1.9	0.47	0.34
Achnanthes *exigua*	Grun.	25	8.9	10.1	3.21	0.99	23	8.9	9.1	8.62	0.96	20	6.2	8.1	1.00	0.93	20	6.2	8.1	0.46	0.27
Achnantes *exigua* var. *heterovalvata*	Krasske	4	2.2	3.2	2.47	0.25	3	2.2	2.2	7.94	0.07	2	2.2	2.0	−0.24	0.41	3	2.2	2.3	1.00	0.14
Achnanthes *grimmei*	Krasske	16	63.5	4.4	3.89	0.26	15	63.5	4.3	6.88	0.43	16	63.5	4.4	0.15	0.26	15	63.5	4.4	−1.33	0.29
Achnanthes *hungarica*	(Grun.) Grun.	10	18.1	1.9	2.31	0.70	8	2.2	4.7	7.86	1.07	6	2.2	3.5	−0.33	0.23	7	18.1	1.6	1.49	0.77
Achnanthes *lanceolata*	(Bréb.) Grun.	25	18.4	4.3	1.82	0.53	20	4.6	9.4	7.24	1.21	23	18.4	3.5	0.77	0.52	25	18.4	3.8	0.52	0.49
+ var. *elliptica*	Cleve																				
+ var. *rostrata*	Hust																				
Achnanthes *linearis*	(W. Sm.) Grun.	3	13.7	1.9	2.84	0.03	3	13.7	1.9	8.83	0.64	3	13.7	1.9	0.09	0.04	3	13.7	1.9	−0.75	0.08
Achnanthes *minutissima*	Kütz	62	83.8	18.7	2.42	0.55	54	83.1	16.5	7.93	0.84	51	83.8	15.4	0.52	0.61	53	83.8	15.5	0.40	0.71
+ var. *cryptocephala*	Grun																				
+ A. *microcephala*	(Kütz) Grun																				
Achnanthes *minutissima* var. *affinis*	(Grun.) Lange-Bertalot	43	73.1	15.3	3.43	0.35	43	73.1	16.1	7.62	0.62	41	73.1	15.4	0.03	0.22	42	73.1	15.5	0.76	0.72
Achnanthes *ploenensis*	Hust.	9	8.5	2.4	3.61	0.56	9	8.5	2.4	7.17	0.44	8	8.5	2.3	0.06	0.39	8	8.5	2.3	−1.21	0.49
Achnanthes *subhudsonis*	Hust.	2	2.9	1.9	1.79	0.33	2	2.9	1.9	6.54	0.07	2	2.9	1.9	0.45	0.79	2	2.9	1.9	0.59	0.02
Amphipleura *rutilans*	(Trentepohl) Cleve	2	3.1	1.2	3.75	0.09	2	3.1	1.2	7.53	0.42	2	3.1	1.2	0.13	0.31	2	3.1	1.2	1.37	0.13
Amphora *acutiuscula*	Kütz	24	32.9	9.5	3.90	0.39	26	32.9	9.5	7.54	0.77	26	32.9	9.5	0.24	0.27	25	32.9	9.5	1.08	0.55
Amphora *angusta*	Greg.	5	1.8	3.1	3.64	0.81	6	1.8	3.6	7.67	0.14	5	1.8	2.8	0.30	0.10	5	1.8	2.8	1.13	0.61
Amphora *arcus*	Greg.	7	5.4	1.8	3.85	0.46	8	5.4	2.0	7.36	0.19	7	5.4	1.7	0.22	0.18	7	5.4	1.7	−1.47	0.28
+ var. *sulcata*	Schmidt																				
Amphora *castellata*	Giffen	17	49.8	2.5	3.93	0.30	18	49.8	2.4	7.53	0.50	19	49.8	2.6	0.01	0.29	18	49.8	2.5	−1.63	0.30
Amphora *coffeaeformis*	Ag.	68	69.9	25.4	4.06	0.53	65	51.8	25.8	7.69	0.68	61	69.9	20.3	0.41	0.48	60	69.9	20.3	−1.32	0.79
+ var. *borealis*	(Kütz.) Cleve																				
+ aff. *coffeaeformis*	Ag. [Ben Khelifa 1989]																				
Amphora *cognata*	Cholnoky	5	6.0	2.3	4.57	0.33	4	6.0	2.2	7.61	0.15	4	1.6	2.9	0.55	0.30	4	1.6	2.9	−1.92	0.47
Amphora commutata	Grun.	3	1.6	2.2	3.68	0.23	3	1.6	2.2	6.99	0.34	3	1.6	2.2	−0.10	0.27	3	1.6	2.2	−1.25	0.15
Amphora *delicatissima*	Krasske	27	6.6	11.3	4.12	0.38	25	6.0	10.1	7.59	0.42	27	6.6	11.5	0.45	0.43	26	6.6	11.3	−1.40	0.56
Amphora *exigua*	Greg	8	46.9	3.8	3.51	0.43	7	46.9	3.7	8.12	1.08	7	46.9	3.7	0.30	0.33	7	46.9	3.7	−0.47	1.47
Amphora aff. *holsatica*	Hust [Ben Khelifa 1989]	4	5.3	1.3	4.84	0.79	4	5.3	1.3	8.77	1.20	4	5.3	1.3	0.65	0.53	4	5.3	1.3	−2.43	0.72
Amphora *inarriensis*	Krammer	2	1.0	1.6	3.22	0.41	2	1.0	16.7	7.00	0.78	2	1.0	1.6	−0.07	0.09	2	1.0	1.6	−0.88	0.29
Amphora *micrometra*	Giffen	7	9.4	2.5	4.62	0.37	5	9.4	1.9	7.56	0.31	6	2.8	3.6	0.49	0.21	6	2.8	3.6	−1.92	0.56
Amphora aff. *micrometra*	Giffen [Ben Khelifa 1989]	2	3.3	2.0	4.93	1.29	2	3.3	2.0	7.72	0.35	2	3.3	2.0	0.62	1.13	2	3.3	2.0	−2.35	1.44
Amphora *montana*	Krasske	19	4.7	8.1	2.86	0.70	16	4.7	6.0	7.44	0.58	18	4.7	7.1	0.27	0.43	17	4.7	6.1	−0.45	0.75
Amphora *normanii*	Rab.	2	4.3	1.2	4.56	1.00	2	4.3	1.2	7.57	0.28										
Amphora *ovalis*	Kütz.	49	19.1	9.1	3.25	0.73	49	19.1	9.1	7.74	0.59	44	19.1	8.3	0.14	0.34	47	19.1	8.7	−0.61	0.95
+ var. *affinis*	Kütz.																				
+ *A. libyca*	Ehr.																				
Amphora *ovalis* var. *tallingii*	Gasse	6	16.8	2.6	2.52	0.29	5	7.3	2.7	7.68	0.48	6	16.8	2.6	−0.39	0.23	6	16.8	2.6	1.12	0.59
Amphora *pediculus*	(Kütz.) Grun.	33	26.2	9.3	2.73	0.37	29	9.0	12.3	8.39	0.83	25	11.5	10.1	−0.06	0.48	30	26.2	8.2	0.71	0.71
Amphora *perpusilla*	Grun.	13	14.6	3.9	1.97	0.41	10	6.6	3.3	6.70	1.36	11	14.6	3.7	0.28	0.51	13	14.6	3.9	0.45	0.31
Amphora *proteus*	Greg.	4	2.9	2.4	4.67	1.19	4	2.9	2.4	7.60	0.78										
+ var. *oculata*	Peragallo																				
Amphora *somalica*	Frenguelli	9	8.3	3.2	3.89	0.43	8	8.3	2.9	9.28	0.59	9	8.3	3.2	1.76	0.87	9	8.3	3.2	0.06	0.69
Amphora *strigosa*	Hust	3	6.1	2.6	3.64	1.25	3	6.1	2.6	7.75	0.53	3	6.1	2.6	0.31	0.39	3	6.1	2.6	−1.41	1.23
Amphora *submontana*	Hust.	5	2.2	3.4	3.00	0.73	4	2.2	2.7	7.21	0.91	5	2.2	3.4	0.58	0.28	5	2.2	3.4	0.12	0.35
Amphora *subturgida*	Hust	7	9.5	1.9	4.13	0.61	6	9.5	1.5	7.49	1.91	7	9.5	1.9	1.70	0.65	7	9.5	1.9	1.06	0.96
Amphora *tenerrima*	Aleem and Hust.	14	70.3	3.3	4.38	0.22	13	70.3	2.5	9.05	0.64	14	70.3	3.3	0.39	0.26	14	70.3	3.3	−1.10	0.82
Amphora *veneta*	Kütz	46	25.2	12.7	3.06	0.64	43	25.2	12.2	8.14	0.72	41	25.2	11.8	0.43	0.49	42	25.2	11.8	−0.29	1.06
+ var. *capitata*	Haworth																				
Anomoeoneis *sphaerophora*	(Kütz.) Pfitzer	66	41.2	11.6	3.88	0.59	63	41.2	11.3	9.23	0.85	53	41.2	8.3	1.96	0.90	56	41.2	8.9	0.27	0.70
Anomoeoneis *sphaerophora* var. *guentheri*	O. Müller	10	2.9	6.1	4.26	0.56	10	2.9	6.1	9.51	0.74	7	2.9	3.3	2.19	0.69	8	2.9	4.1	0.05	0.48
Anomoeoneis *sphaerophora* fo. *costata*	(Kütz.) Schmidt	8	1.6	5.2	4.09	0.57	8	1.6	5.2	9.34	0.70	6	1.4	3.5	1.62	1.10	8	1.6	5.2	0.23	0.52
Anomoeoneis *sphaerophora* var. *sculpta*	(Ehr.) O. Müller	12	24.1	3.4	4.23	0.43	13	24.1	4.3	9.87	0.71	12	24.1	3.4	2.19	0.56	14	24.1	5.0	0.41	0.41
Anomoeoneis *vitrea*	(Grün.) Ross	9	10.5	4.1	3.34	0.12	9	10.5	4.1	8.14	0.42	5	10.5	1.6	0.64	0.95	4	10.5	1.6	−0.70	1.23
Aulacoseira *agassizii*	(Ostrup) Simonsen	41	24.4	11.5	2.20	0.43	38	24.4	10.8	7.77	0.84	36	24.4	11.0	0.01	0.55	39	24.4	11.9	0.73	0.42
+ var. *malayensis*	(Hust.) Simonsen																				
Aulacoseira *ambigua*	(Grun.) Simonsen	60	84.9	21.2	2.32	0.40	54	84.9	19.9	7.50	0.68	47	84.9	18.4	0.26	0.45	48	84.9	18.4	0.67	0.27
Aulacoseira *distans*	(Ehr.) Simonsen	13	60.2	2.3	2.13	0.18	13	60.2	2.3	7.95	0.94	6	60.2	1.7	−0.61	0.30	7	60.2	1.9	1.12	0.37
+ var. *alpigena*	(Grun.) Simonsen																				
Aulacoseira *distans* var. *africana*	(O. Müller) Simonsen	4	24.0	2.1	2.47	0.24	2	1.0	1.4	8.55	0.64	3	24.0	1.1	0.10	0.82	3	24.0	1.1	0.89	0.05
+ var. *humilis*	(A. Cleve) Simonsen																				
Aulacoseira *goetzeana*	(O. Müller) Simonsen	8	1.6	6.4	2.36	0.82	8	1.6	6.4	7.82	0.90	7	1.6	5.5	0.05	0.53	7	1.6	5.5	0.66	0.64
Aulacoseira *granulata*	(Ehr.) Simonsen	65	90.2	14.0	2.14	0.46	60	90.2	13.6	7.10	0.68	48	90.2	10.8	−0.10	0.30	52	90.2	11.2	0.56	0.36
+ var. *jonensis*	Grun.) Simonsen																				
+ var. *muzzanensis*	(Meister) Simonsen																				
Aulacoseira *granulata* var. *angustissima*	(O. Müller) Simonsen	71	81.5	15.7	2.56	0.47	68	81.5	14.4	7.66	0.75	59	81.5	13.8	0.23	0.65	59	81.5	13.8	0.52	0.60
Aulacoseira *granulata* var. *angustissima* fo. *curvata*	(Grun.) Simonsen	15	87.6	3.6	2.00	0.48	15	87.6	3.6	8.39	0.29	14	87.6	3.3	0.93	0.55	14	87.6	3.3	0.65	0.15
Aulacoseira *granulata* var. *tubulosa*	(Manguin) Simonsen	6	17.0	1.6	2.32	1.00	6	17.0	1.6	7.18	1.06	2	3.0	1.6	1.34	1.26	2	3.0	1.6	0.61	0.06
Aulacoseira *granulata* fo. *valida*	(Hust.) Simonsen	7	19.0	1.8	2.94	1.31						4	19.0	1.5	0.36	1.78	5	19.0	1.6	0.52	0.27
Aulacoseira *italica*	(Ehr.) Simonsen	6	3.9	2.5	2.72	0.47	5	3.9	1.9	8.13	0.73	6	3.9	2.5	0.27	0.31	6	3.9	2.5	0.43	0.25
+ var. *tenuissima*	(Grun.) Simonsen																				
Aulacoseira *italica* var. *bacilligera*	(O. Müller) Simonsen	6	97.3	2.5	2.14	0.05	6	97.3	2.5	8.30	0.39	4	97.3	2.4	0.70	0.00	5	97.3	2.4	1.23	0.56
Aulacoseira *magnusii*	(O. Müller) Simonsen	9	5.0	3.1	2.08	0.26	9	5.0	3.1	7.53	0.68	6	5.0	1.7	0.09	0.06	6	5.0	1.7	0.88	0.07
Aulacoseira *nyassensis*	(O. Müller) Simonsen	9	81.4	3.3	2.14	0.25	9	81.4	3.3	8.01	0.14	9	81.4	3.3	0.05	0.32	9	81.4	3.3	0.86	0.16
+ var. *peregrina*	(O. Müller) Simonsen																				
Aulacoseira *nyassensis* var. *victoriae*	(O. Müller) Simonsen	9	41.3	2.7	2.06	0.030	8	41.3	2.7	7.76	0.39	9	41.3	2.7	0.17	0.26	9	41.3	2.7	0.74	0.41
Aulacoseira aff. *perglabra*	(Ostrup) Haworth [Ben Khelifa unpubl.]	2	50.0	1.3	2.36	0.22															
Bacillaria *paradoxa*	Gmelin	4	1.0	2.8	4.13	0.40	4	1.0	2.8	7.46	0.29	3	1.0	2.3	0.20	0.37	3	1.0	2.3	−1.71	0.38
Brachysira *aponina*	Kütz.	14	21.4	5.4	3.65	1.04	12	21.4	4.6	8.10	0.77	15	21.4	6.2	0.35	0.24	15	21.4	6.2	−1.06	1.47
Caloneis *aequatoralis*	Hust	10	13.0	4.6	3.41	0.35	8	5.6	4.9	7.80	0.74	8	13.0	3.6	1.01	0.57	9	13.0	3.7	−0.14	0.24
+ var. *turgidae*	Cholnoky																				
Caloneis *bacillum*	(Grun.) Mereschkowsky	35	8.0	15.2	2.90	0.72	30	8.0	13.5	7.67	1.18	28	8.0	12.6	0.47	0.72	28	8.0	12.3	0.08	0.72
+ var. *lancettula*	(Grun.) Cleve																				

Table 4 (*continued*)

Taxon name	Authority	Conductivity					pH					Cation ratio					Anion ratio				
		N	*Max*	N_2	Optimum	Tolerance	*N*	*Max*	N_2	Optimum	Tolerance	*N*	*Max*	N_2	Optimum	Tolerance	*N*	*Max*	N_2	Optimum	Tolerance
Caloneis *silicula*	(Ehr.) Cleve	6	1.2	4.7	2.48	0.66	6	1.2	4.7	7.63	0.85	5	1.2	3.9	−0.09	0.26	5	1.2	3.9	0.17	0.99
+ var. *truncata*	Grun.																				
Campylodiscus *clypeus*	Ehr.	9	6.5	2.8	3.75	0.14	10	6.5	3.0	7.32	0.63	9	6.5	2.5	0.03	0.70	9	6.5	2.5	−1.59	0.68
Campylodiscus *clypeus* var. *bicostatus*	W. Sm.	4	4.2	1.5	3.71	0.29	4	4.2	1.5	8.34	0.81	3	4.2	1.4	0.77	0.68	4	4.2	1.5	−1.03	0.86
Chaetoceros *muelleri*	Lemmerman	5	2.0	3.2	3.85	0.70	5	2.0	3.2	9.17	1.49	3	2.0	2.1	1.20	0.43	4	2.0	2.8	−0.27	0.44
Chaetoceros sp. 1	[Gasse 1986]	2	1.0	1.6	4.26	0.62	2	1.0	1.6	9.80	0.88	2	1.0	1.6	2.13	1.76	2	1.0	1.6	0.27	0.00
Cocconeis *bardawilensis*	Ehrlich	2	7.7	1.5	4.02	0.58	3	7.7	1.5	7.70	0.09										
Cocconeis *costata*	Greg.	5	15.5	3.3	4.67	1.08	6	15.5	4.3	7.60	0.78										
Cocconeis *diminuta*	Pant.	4	2.3	3.0	2.47	0.89	3	2.3	2.1	9.06	0.48	3	2.3	2.9	0.25	0.65	4	2.3	3.0	0.16	0.43
Cocconeis *microscopica*	Cholnoky	2	1.0	1.9	4.01	0.62	2	1.0	1.9	8.36	1.48	2	1.0	1.9	0.18	0.42	2	1.11	1.9	−0.86	0.17
Cocconeis *pediculus*	Ehr.	11	6.2	4.7	2.94	0.72	10	6.2	3.9	8.44	0.47	9	6.2	4.4	−0.06	0.26	9	6.2	4.4	−0.76	0.65
Cocconeis *placentula*	Ehr.	74	99.1	15.1	2.67	0.76	70	99.1	16.2	8.31	0.93	62	99.1	13.3	−0.12	0.57	63	99.1	13.4	0.08	1.16
+ var. *euglypta*	(Ehr.) Cleve																				
+ var. *lineata*	(Ehr.) Cleve																				
Cocconeis *scutellum*	Ehr.	5	14.0	1.7	4.67	1.41	6	14.0	2.4	7.60	0.78										
+ var. *ampliata*	Grun.																				
+ var. *stauroneiformis*	Rab.																				
+ fo. *parva*	Grun.																				
Cocconeis *thumensis*	Mayer	8	13.2	2.2	1.84	0.60	5	1.9	3.3	7.49	1.75	7	13.2	1.8	0.74	0.58	8	13.2	2.2	0.55	0.41
Cyclostephanos *dubius*	(Fricke) Round	3	1.2	2.2	3.69	1.74	4	1.2	2.8	7.78	0.36										
Cyclotella *[illegible]*	Flower, Håk. and Gasse	7	88.1	2.3	2.62	0.19	7	88.1	2.3	8.02	0.16	7	88.1	2.3	−0.64	0.27	7	88.1	2.3	1.21	0.35
Cyclotella *comensis*	Grun.	10	24.1	3.3	2.71	0.47	11	24.1	4.2	8.96	0.43	10	24.1	3.3	0.06	0.40	11	24.1	4.2	0.07	0.46
Cyclotella *iris*	Brun and Héribaud	5	1.5	3.1	4.01	0.50	6	2.0	3.7	9.55	0.43	4	1.5	2.7	2.57	0.59	6	2.0	3.7	0.61	0.39
Cyclotella *kutzingiana*	Thwaites	22	88.1	3.4	2.66	0.19	24	88.1	3.6	8.57	0.36	15	3.9	7.9	0.16	0.86	18	5.7	7.8	0.62	0.63
+ var. *planetophora*	Fricke																				
+ var. *radiosa*	Fricke																				
Cyclotella *kutzingiana* var. *parva*	Fricke	2	26.8	1.1	2.66	0.12						2	26.8	1.1	−0.11	0.27	2	26.8	1.1	−0.28	0.67
Cyclotella *meneghiniana*	Kütz.	71	78.3	10.0	3.78	0.62	68	78.3	9.8	8.85	0.94	48	53.7	6.2	0.67	0.97	53	53.7	7.5	−0.45	0.86
+ var. *pumila*	Grun.																				
Cyclotella *ocellata*	Pant.	29	8.3	6.8	3.18	0.70	29	8.3	7.4	8.53	0.91	18	8.3	3.8	0.01	1.17	21	8.3	5.1	0.54	1.02
Cyclotella *pseudostelligera*	Hust.	15	14.0	8.5	2.33	0.44	14	10.2	8.2	7.62	1.08	9	14.0	4.5	0.10	0.39	10	14.0	4.7	0.57	0.18
Cyclotella aff. *meduanae*	Germain [Ben Khelifa 1989]	4	13.7	3.7	1.79	0.60	4	13.7	3.7	8.36	1.17	4	13.7	3.7	0.66	0.02	4	13.7	3.7	0.51	0.09
Cyclotella *stelligera*	Cleve and Grun.	22	37.7	5.4	2.41	0.32	18	37.7	3.8	7.82	0.92	15	31.2	4.9	−0.10	0.14	15	31.2	4.9	0.60	0.29
+ var. *tenuis*	Hust.																				
Cylindrotheca *gracilis*	(Bréb.) Grun.	9	11.3	2.4	3.97	0.31	7	11.3	1.8	7.70	0.42	9	11.3	2.4	0.10	0.28	9	11.3	2.4	−1.57	0.54
Cymatopleura *nyansae*	G.S. West	3	2.0	1.5	2.21	0.20	3	2.0	1.5	7.46	0.21	3	2.0	1.5	0.31	0.20	3	2.0	1.5	0.18	0.63
Cymbella *affinis*	Kütz.	33	55.2	5.0	2.41	0.73	31	55.2	4.5	7.20	1.39	28	55.2	4.4	0.14	0.40	28	55.2	4.6	−0.05	0.51
Cymbella *affinis* var. *afarensis*	Gasse	7	8.0	4.9	2.67	0.76	6	8.0	4.1	6.63	0.51	7	8.0	4.9	0.50	0.38	7	8.0	4.9	0.21	0.33
Cymbella *amphicephala*	Naegeli	9	13.9	3.1	3.20	0.48	8	13.9	3.0	8.38	0.29	7	13.9	2.0	−0.16	0.18	7	13.9	2.0	0.03	0.42
+ var. *hercynica*	Schmidt																				
Cymbella *cesatii*	(Rab.) Grun.	5	16.2	1.3	1.85	0.63	4	16.2	1.2	6.06	0.57	5	16.2	1.3	0.85	0.52	5	16.2	1.3	0.53	0.62
Cymbella aff. *fonticola*	Hust	2	2.8	1.2	2.00	1.46	2	2.8	1.2	6.18	1.20	2	2.8	1.2	0.31	0.34	2	2.8	1.2	−0.07	1.21
Cymbellla *helvetica*	Kütz.	6	3.0	2.3	2.64	0.52	6	3.0	2.3	8.31	1.39	6	3.0	2.3	0.24	0.42	6	3.0	2.3	−0.40	0.76
Cymbella *leptoceros*	(Ehr.) Grun.	3	2.6	2.1	2.53	0.15						3	2.6	2.1	−0.51	0.13	3	2.6	2.1	0.85	0.82
Cymbella *microcephala*	Grun.	59	41.8	18.0	3.21	0.44	55	41.8	16.8	8.00	0.61	52	37.0	15.4	0.04	0.41	51	37.0	14.5	−0.44	0.93
+ *C. hustedtii*	Krasske																				
Cymbella *muelleri*	O. Müller	24	6.6	10.6	2.81	0.52	20	4.4	11.1	8.58	0.94	24	6.6	10.6	0.35	0.92	25	6.6	11.4	0.77	0.39
Cymbella *naviculiformis*	Auers.	5	2.1	3.3	2.77	0.69	5	2.1	3.3	8.17	1.08	3	2.1	2.6	−0.11	0.18	3	2.1	2.6	−0.34	0.11
Cymbella *perpusilla*	A. Cleve	3	2.2	1.4	1.78	0.60	3	2.2	1.4	6.00	1.81										
Cymbella *prostrata*	(Berkeley) Cleve	4	4.6	2.3	2.85	0.04	3	4.6	2.0	8.85	0.07	4	4.6	2.3	0.03	0.18	4	4.6	2.3	−0.70	0.28
Cymbella *pusilla*	Grun.	52	64.6	14.8	3.96	0.43	52	64.6	14.0	7.78	0.88	49	64.6	13.1	0.31	0.69	48	64.6	12.2	−1.47	0.59
Cymbella *tumida*	(Bréb.) Van Heurck	3	1.8	2.3	2.22	0.22	3	1.8	2.3	7.42	0.73						3	1.8	2.3	0.89	0.53
Cymbella *turgida*	Gregory	45	10.4	15.2	2.53	0.60	42	10.4	14.5	8.04	1.08	31	10.4	9.3	0.58	0.88	35	10.4	10.5	0.47	0.37
Cymbella *ventricosa*	Ag.	49	24.1	10.9	2.33	0.37	44	24.1	9.6	7.88	1.06	34	24.1	5.0	0.30	0.37	36	24.1	5.5	0.39	0.51
Denticula *elegans*	Kütz.	7	31.0	5.1	3.67	0.50	7	31.0	5.6	7.30	0.30	9	31.0	7.1	0.17	0.33	8	31.0	6.3	−1.61	0.38
+ var. *africana*	Hust.																				
Diatoma *elongatum*	(Lyngbye) Ag.	8	19.1	3.1	3.26	0.24	8	19.1	3.1	8.18	0.27	4	3.1	2.6	−0.10	0.18	4	3.1	2.6	−0.55	0.21
Diatoma *vulgaris*	Bory	6	7.4	2.1	2.67	0.26	6	7.4	2.1	8.62	0.25	5	7.4	2.0	−0.11	0.16	5	7.4	2.0	−0.63	0.17
+ var. *brevis*	Grun.																				
+ var. *ehrenbergii*	Kütz.																				
+ var. *linearis*	Grun.																				
Diploneis *ovalis*	(Hilse) Cleve	30	11.5	6.7	3.57	0.80	28	11.5	6.2	8.00	0.54	27	11.5	4.7	0.59	0.74	26	11.5	4.6	−1.17	0.94
+ var. *oblongella*	Naegeli																				
Diploneis *smithii*	(Bréb.) Cleve	2	2.3	4.4	3.39	0.92	8	2.3	5.3	8.17	1.46	5	2.3	3.2	1.54	1.18	6	2.3	4.1	0.20	0.76
Diploneis *subovalis*	Cleve	8	10.7	3.5	3.73	0.31	8	10.7	3.5	7.93	0.48	6	10.7	2.5	1.62	0.41	6	10.7	2.5	−0.04	0.40
Entomoeoneis *alata*	(Ehr.) Ehr.	9	3.5	4.8	4.20	0.71	9	3.5	4.8	7.90	0.59	8	3.5	4.6	0.38	0.32	8	3.5	4.6	−1.69	0.82
Entomoeoneis *paludosa*	(W. Sm.) Reimer	2	2.4	2.0	4.47	0.20						2	2.4	2.0	0.99	1.21	2	2.4	2.0	−1.95	0.67
Entomoeoneis *paludosa* var. *subsalina*	(Cleve) Krammer	4	2.3	2.5	4.80	0.46	4	2.3	2.5	7.69	0.32	4	2.3	2.5	0.57	0.17	4	2.3	2.5	−2.25	0.35
Entomoeoneis sp. 1	[Ben Khelifa 1989]	2	1.0	1.7	3.97	0.60	2	1.0	1.7	7.33	0.07	2	1.0	1.7	0.30	0.17	2	1.0	1.7	−1.72	0.64
Epithemia *adnata*	(Kütz) Bréb	25	77.0	2.6	2.42	0.26	22	77.0	2.6	8.27	0.52	22	77.0	2.0	−0.18	0.35	24	77.0	2.0	0.70	0.35
+ var. *porcellus*	(Kütz.) Grun.																				
+ var. *saxonica*	(Kütz.) Grun.																				
Epithemia *argus*	(Ehr.) Kütz.	4	1.6	2.0	4.05	1.17	5	1.6	3.0	8.28	1.23	3	1.6	1.5	0.66	0.89	4	1.6	2.4	−0.97	1.93
Epithemia *sorex*	Kütz.	13	14.2	3.2	3.00	0.65	11	14.2	2.7	8.07	1.25	11	14.2	3.1	0.50	0.77	13	14.2	3.2	0.10	0.35
+ var. *gracilis*	Hust.																				
Epithemia *turgida*	(Ehr.) Kütz.	5	1.0	3.1	2.66	0.29	5	1.0	3.1	8.01	0.28	4	1.0	2.4	0.23	0.56	4	1.0	2.4	0.28	0.31
Eunotia *bidentula*	W. Sm.	2	5.0	1.9	2.79	0.17															
Eunotia *bilunaris*	Kütz.	11	9.0	4.3	2.20	0.54	8	9.0	2.8	6.45	0.53	7	9.0	2.0	0.89	0.88	8	9.0	3.0	0.86	0.31
Eunotia *flexuosa*	(Bréb.) Kütz.	6	4.5	2.8	2.34	0.65	5	4.1	1.9	6.64	0.66	5	4.1	1.9	0.92	0.85	6	4.5	2.8	0.82	0.50
+ *E. pseudopectinalis*	Hust																				
Eunotia aff. *incisa*	Greg.	2	4.5	1.1	2.34	0.15						2	4.5	1.1	0.03	0.21	2	4.5	1.1	0.83	0.93
Eunotia *monodon*	Ehr.	13	3.3	6.8	2.35	0.65	12	3.3	6.3	7.29	0.61	12	3.3	6.1	0.04	0.82	13	3.3	6.8	0.64	0.50
+ var. *constricta*	Cleve-Euler																				
+ var. *major*	(W. Sm.) Hust.																				
+ var. *tropica*	Hust.																				
Eunotia *naegelii*	Migula	2	2.0	1.3	2.75	0.78															
Eunotia *pectinalis*	(Dillw.) Rab.	17	29.0	3.1	2.26	0.28	17	29.0	3.1	6.99	0.57	9	1.2	6.1	0.31	0.73	9	1.2	6.1	0.46	0.57
+ var. *undulata*	(Ralfs) Rab.																				
+ var. *ventralis*	(Ehr.) Hust.																				
Eunotia *pectinalis* var. *minor*	(Kütz.) Rab.	21	17.7	4.0	2.02	0.43	19	17.7	2.8	6.96	1.10	16	17.7	2.7	1.00	0.70	17	17.7	3.0	0.68	0.29
+ var. *ventricosa*	Grun.																				
+ fo. *impressa*	(Ehr.) Hust.																				
Eunotia *praerupta*	Ehr.	2	10.7	1.1	1.78	2.74	2	10.7	1.1	6.00	0.78										
+ var. *bidens*	(Ehr.) Grun																				
Eunotia *tenella*	(Grun.) Hust.	2	1.0	1.7	1.78	0.60	2	1.0	1.7	6.00	1.54										
Fragilaria *africana*	Hust.	5	4.0	3.9	2.01	0.36	5	4.0	3.9	7.21	0.61	5	4.0	3.9	0.03	0.39	5	4.0	3.9	0.57	0.72
Fragilaria *brevistriata*	Grun.	57	70.4	7.3	2.76	0.80	48	70.4	5.4	7.82	1.02	51	70.4	6.7	0.10	0.67	55	70.4	7.2	−0.14	0.89
+ var. *elliptica*	Hust.																				
Fragilaria *capucina*	Desmazières	34	24.0	9.3	2.53	0.34	32	24.0	8.8	8.42	0.58	28	24.0	8.3	−0.00	0.50	30	24.0	8.7	0.33	0.67
+ var. *lanceolata*	Grun.																				
+ var. *vaucheriae*	(Kütz.) Lange-Bertalot																				

Table 4 (*continued*)

Taxon name	Authority	Conductivity					pH					Cation ratio					Anion ratio				
		N	*Max*	N_2	Optimum	Tolerance	*N*	*Max*	N_2	Optimum	Tolerance	*N*	*Max*	N_2	Optimum	Tolerance	*N*	*Max*	N_2	Optimum	Tolerance
Fragilaria *construens* fo. *exigua*	(W. Sm). Hust.	6	3.6	4.5	1.99	0.30	6	3.6	4.5	7.86	0.55	6	3.6	4.5	0.09	0.14	6	3.6	4.5	0.82	0.06
Fragilaria *construens*	(Ehr.) Grun.	49	59.7	13.3	2.71	0.72	42	59.7	11.2	8.39	0.92	47	59.7	13.1	0.36	0.58	50	59.7	13.4	0.41	0.56
+ var. *binodis*	(Ehr.) Grun.																				
+ var. *venter*	(Ehr.) Grun.																				
Fragilaria *crotonensis*	Kitton	5	81.0	2.8	2.54	0.60	4	81.0	2.8	8.76	1.25	5	81.0	2.8	−0.25	0.54	5	81.0	2.8	−0.43	1.20
Fragilaria *fasciculata*	(Ag.) Lange-Bertalot	2	2.9	1.8	4.66	0.02															
Fragilaria *hungarica*	Pant.	3	2.9	2.1	2.77	1.12	3	2.9	2.1	8.11	1.33	2	2.9	1.8	0.99	1.26	2	2.9	1.8	0.10	0.23
Fragilaria *lapponica*	Grun.	9	1.5	6.7	2.86	1.01	6	1.5	5.3	8.58	1.20	9	1.5	6.7	0.70	1.28	9	1.5	6.7	0.56	0.45
Fragilaria *leptostauron*	(Ehr.) Hust.	25	9.9	10.4	2.14	0.41	21	9.9	9.2	7.97	0.63	23	9.9	9.7	0.06	0.40	24	9.9	0.9	0.49	0.61
Fragilaria *pinnata*	Ehr.	26	5.7	11.2	2.16	0.46	24	5.7	10.0	8.17	0.83	23	5.7	10.3	0.16	0.57	25	5.7	11.7	0.47	0.56
Fragilaria *pinnata* var. *trigona*	(Brun and Héribaud) Hust.	7	6.9	5.5	2.33	0.67	6	6.9	4.7	8.30	0.61	7	6.9	5.5	0.26	0.71	7	6.9	5.5	0.79	0.15
Fragilaria *zeilleri*	Héribaud	8	6.6	2.2	3.03	0.70	7	6.6	2.1	9.07	0.90	6	6.6	1.8	−0.09	0.52	8	6.6	2.2	−0.03	0.32
+ var. *africana*	Gasse																				
+ var. *elliptica*	Gasse																				
Gomphocymbella *beccari*	(Grun.) Forti	4	2.0	2.5	2.74	0.46	3	1.6	1.6	8.87	1.53	3	1.6	1.6	0.49	0.93	4	2.0	2.5	0.86	0.34
Gomphonema *acuminatum*	Ehr.	2	3.3	1.4	4.13	1.67	2	3.3	1.4	9.20	1.85										
Gomphonema *angustatum*	(Kütz.) Rab.	5	1.2	3.8	2.75	1.36	5	1.2	3.8	7.60	1.61	3	1.0	2.6	0.77	0.80	3	1.0	2.6	0.51	0.21
+ var. *productum*	Grun.																				
Gomphonema *clavatum*	Ehr.	12	11.9	3.5	2.67	0.37	11	11.9	3.0	8.63	0.60	11	11.9	3.0	0.31	0.43	11	11.9	3.0	0.13	0.74
+ *G. exiguum*	Kütz.																				
Gomphonema *clevei*	Fricke	16	4.4	11.5	1.87	0.37	13	4.4	8.9	6.43	0.84	15	4.4	11.2	0.64	0.41	15	4.4	11.2	0.48	0.19
Gomphonema *clevei* var. *javanica*	Hust.	14	13.3	3.1	2.65	0.56	11	13.3	2.6	7.01	1.25	13	13.3	2.9	0.14	0.91	13	13.3	2.9	0.45	0.42
Gomphonema *gracile*	Ehr.	64	43.3	12.1	2.71	0.59	51	43.3	9.6	7.76	0.96	42	43.3	5.3	0.54	0.46	48	43.3	6.8	0.22	0.69
Gomphonema *intricatum*	Kütz.	17	7.9	7.5	2.84	0.87	15	7.9	6.8	8.33	1.04	14	7.9	5.2	0.32	0.63	14	7.9	5.2	−0.08	0.83
+ var. *pulvinatum*	(Braun) Grun.																				
+ var. *vibrio*	(Ehr.) Cleve																				
Gomphonema *intricatum* var. *pumila*	Grun.	21	19.9	7.6	2.95	0.41	18	19.9	6.1	7.79	0.74	14	19.9	5.3	−0.07	0.25	15	19.9	6.3	−0.64	0.18
+ var. *pusilla*	Mayer																				
Gomphonema *javanicum*	Hust.	3	26.2	1.7	1.77	0.04	3	26.2	1.7	6.98	0.79	2	26.2	1.2	1.35	0.06	2	26.2	1.2	0.66	0.03
Gomphonema *olivaceum*	(Lyngbye) Kütz.	19	17.3	9.3	2.10	0.60	16	13.3	7.5	7.37	1.43	19	17.3	9.3	0.56	0.46	19	17.3	9.3	0.10	0.61
Gomphonema *parvulum*	(Kütz.) Grun.	90	58.6	23.3	2.42	0.58	82	58.6	19.7	7.63	0.81	62	25.4	19.3	0.52	0.64	67	58.6	15.1	0.54	0.74
Grammatophora *marina*	(Lyngbye) Kütz.	2	5.2	1.5	4.67	1.57	3	5.2	1.8	7.60	1.51										
Grammatophora *oceanica*	Ehr.	3	1.8	1.8	4.68	0.01	4	1.8	2.8	7.61	0.04										
+ var. *adriatica*	Grun.																				
+ var. *macilenta*	(Ehr.) W. Sm.																				
+ fo. *minuscula*	Peragallo																				
Gyrosigma *scalproides*	(Rab.) Cleve	4	1.0	3.2	2.83	1.36						4	1.0	3.2	0.28	0.68	4	1.0	3.2	−0.71	1.26
+ var. *eximium*	(Thwaites) Cleve																				
Hantzschia *amphioxys*	(Ehr.) Grun.	60	6.0	21.6	2.68	0.80	51	6.0	18.3	7.57	1.34	43	5.1	16.8	0.72	0.97	46	6.0	17.5	0.34	0.54
+ var. *capitata*	Pant.																				
Hantzschia *virgata*	(Roper) Grun.	3	1.0	2.5	3.46	1.17	3	1.0	2.5	7.86	0.28	3	1.0	2.5	0.33	0.35	3	1.0	2.5	−0.46	1.49
+ var. *capitellata*	Hust.																				
+ var. *gemuina*	Cleve-Euler																				
Licmophora *gracilis*	(Ehr.) Grun.	3	3.7	1.5	4.67	1.56	4	3.7	2.2	7.60	1.35										
Mastogloia *elliptica*	Cleve	14	3.0	6.8	3.32	0.64	15	3.0	7.2	7.65	0.90	11	3.0	5.7	0.44	0.40	11	3.0	5.7	−0.59	0.98
+ var. *dansei*	(Thwaites) Cleve																				
Mastogloia *lanceolata* var. *hungarica*	Pant.	2	2.2	1.9	4.56	1.30	2	2.2	1.9	7.40	0.78	2	2.2	1.9	0.47	1.14	2	2.2	1.9	−2.35	0.56
Mastogloia *pumila*	(Cleve and O. Müller) Cleve	6	1.8	2.7	4.27	0.62	5	1.8	2.2	7.45	0.27	6	1.8	2.7	0.33	0.30	6	1.8	2.7	−1.92	0.77
Mastogloia *smithii*	Thwaites	9	14.1	2.1	3.61	0.22	9	14.1	2.1	7.40	0.27	9	14.1	2.1	−0.12	0.48	9	14.1	2.1	−1.23	0.51
+ var. *amphicephala*	Grun.																				
+ var. *lacustris*	Grun.																				
+ *M. muradii*	Voigt																				
Melosira *varians*	Ag.	10	5.5	4.3	2.22	0.67	9	5.5	3.1	7.44	0.77	9	5.5	3.6	0.01	0.84	10	5.5	4.3	0.67	0.92
Navicula *aberrans*	Simonsen	2	1.3	1.5	3.76	1.55	2	1.3	1.5	7.80	1.72	2	1.3	1.5	1.68	0.04	2	1.3	1.5	0.02	0.00
Navicula *accomoda*	Hust.	6	2.9	3.0	2.08	0.76	4	2.9	1.6	6.84	1.02	3	2.9	1.5	0.70	0.71	3	2.9	1.5	0.38	1.07
Navicula *afroalpina*	Gasse	2	4.2	1.5	1.78	1.61	2	4.2	1.5	6.00	1.78										
Navicula *aguilhasica*	Cholnoky	25	6.9	10.4	4.40	0.50	24	6.9	9.7	7.91	0.61	25	6.9	10.3	0.38	0.29	25	6.9	10.3	−2.00	0.62
Navicula *ammophila*	Grun.	5	23.9	1.3	4.25	0.45	5	23.9	1.3	7.18	0.98	5	23.9	1.3	1.73	0.76	5	23.9	1.3	−1.28	1.11
Navicula *brekkaensis*	Petersen	2	2.6	1.2	1.78	2.23	2	2.6	1.2	6.00	2.47										
Navicula *bryophila*	Petersen	4	11.0	1.7	1.77	0.06	3	11.0	1.5	6.00	1.71	3	11.0	1.3	0.40	0.27	3	11.0	1.3	0.18	0.22
Navicula *bulnheimii*	Grun.	5	6.6	3.1	4.70	0.35	3	6.6	1.9	7.66	0.34	5	6.6	3.1	0.57	0.08	5	6.6	3.1	−2.04	0.45
Navicula *capitata* var. *hungarica*	(Grun.) Ross	13	10.1	5.2	3.49	0.63	12	10.1	5.1	7.40	0.49	13	10.1	5.2	0.03	0.28	13	10.1	5.2	−1.09	0.60
Navicula *cari*	Ehr.	13	10.7	2.2	3.76	0.94	12	10.7	2.1	8.97	1.31	11	10.7	2.0	1.75	0.97	11	10.7	2.0	0.13	1.01
Navicula *cari* var. *cincta*	Ehr.	61	20.0	16.4	3.20	1.16	55	20.0	14.7	8.17	0.82	52	20.0	12.1	0.42	0.56	53	20.0	12.4	−0.52	1.40
Navicula *cirfuga*	Lange-Bertalot	9	33.4	1.7	3.72	0.49	8	33.4	1.6	7.40	0.32	9	33.4	1.7	0.15	0.28	9	33.4	1.7	−1.41	0.86
Navicula *citrus*	Krasske	4	5.4	2.0	2.23	0.24	3	5.4	1.7	7.44	0.68										
Navicula *cocconeiformis*	Greg.	8	5.9	4.4	4.27	0.87	8	5.9	5.2	7.82	0.52	3	2.2	2.1	0.06	0.14	3	2.2	2.1	−0.72	0.13
Navicula *complanatoides*	Hust.	3	3.6	1.4	4.19	0.97	3	3.6	1.4	7.81	0.38	3	3.6	1.4	0.37	0.34	3	3.6	1.4	−1.73	1.36
Navicula *confervacea*	(Kütz.) Grun.	18	5.0	10.4	2.88	0.81	16	5.0	9.6	8.02	0.88	8	3.2	4.1	0.16	1.03	9	3.2	4.5	0.66	0.56
Navicula *cryptocephala*	Kütz.	47	14.9	14.8	2.61	0.74	41	14.9	13.0	7.62	0.85	41	7.8	19.5	0.27	0.61	42	7.8	20.5	0.11	0.83
Navicula *cryptocephala* var. *veneta*	(Kütz.) Grun.	69	37.8	19.6	3.25	0.66	66	37.8	17.5	7.46	0.71	57	37.8	16.3	0.19	0.42	57	37.8	16.2	−0.74	1.00
Navicula *cryptocephala* var. *exilis*	(Kütz.) Grun.	21	8.9	11.6	2.99	0.73	17	8.9	10.4	8.15	0.92	15	8.9	8.4	0.57	0.57	16	8.9	8.6	−0.03	0.66
Navicula *cryptotenella*	Lange-Bertalot	18	15.3	7.1	3.58	0.65	18	15.3	7.1	7.77	0.61	13	15.0	4.7	0.20	0.35	12	15.0	4.6	−1.54	0.91
Navicula *cuspidata*	Kütz.	16	2.8	8.0	3.26	0.75	14	2.8	6.8	8.37	0.70	12	2.8	6.2	0.81	0.79	12	2.8	6.2	0.28	0.60
+ var. *ambigua*	(Ehr.) Cleve																				
Navicula *damasii*	Hust.	4	20.1	2.2	3.21	0.38	4	20.1	2.2	9.35	0.40	4	20.1	2.2	0.83	0.88	4	20.1	2.2	0.47	0.35
Navicula *debilissima*	Hust.	3	1.4	2.4	3.73	1.17	3	1.4	2.4	8.87	0.96										
Navicula *decussis*	Ostrup	18	13.4	7.5	2.52	0.46	14	13.4	6.3	7.82	0.98	16	13.4	5.9	0.19	0.82	18	13.4	7.5	0.79	0.40
Navicula *difficilimoides*	Hust.	2	2.9	1.2	4.53	0.95	3	2.9	1.5	7.64	0.21										
Navicula *digitoradiata*	(Greg.) Ralfs	12	13.0	3.1	2.99	0.53	10	13.0	2.9	8.18	0.54	11	7.7	3.0	1.32	0.60	11	7.7	3.0	−0.49	0.48
+ var. *minima*	Cleve-Euler																				
Navicula *duerrenbergiana*	Hust.	12	4.4	5.4	3.82	0.54	10	4.4	4.1	7.93	0.46	9	1.8	5.7	0.33	0.29	9	1.8	5.7	−1.54	0.35
Navicula *elkab*	O. Müller	46	57.9	14.2	4.14	0.60	43	57.9	13.2	9.36	0.62	33	90.0	11.2	2.00	0.44	37	90.0	11.9	0.09	0.50
Navicula *feuerbornii* fo. *minor*	Cholnoky	8	7.8	2.3	2.70	0.44	8	7.8	2.3	8.48	0.47	4	1.3	3.3	0.08	0.12	4	1.3	3.3	−0.07	0.72
Navicula *gallica*	(W. Sm.) Lagerstedt	7	5.0	4.6	2.89	1.34	8	5.0	5.1	6.99	0.80	2	2.2	1.5	−0.32	0.77	3	5.0	2.0	0.37	1.11
Navicula *gastrum*	(Ehr.) Kütz.	6	2.0	3.0	2.49	0.35	6	2.0	3.0	8.35	1.06										
+ var. *signata*	Hust.																				
Navicula *gawaniensis*	Gasse	8	4.0	4.9	4.24	0.33	7	3.5	4.2	8.88	0.98	7	4.0	4.2	2.02	0.62	8	4.0	4.9	0.01	0.31
Navicula *gregaria*	Donkin	12	3.1	8.1	3.11	0.63	12	3.1	8.1	8.30	0.68	9	3.1	6.4	0.17	0.31	9	3.1	6.4	−0.55	0.71
Navicula *grimmioides*	Cholnoky	3	4.2	2.6	3.21	0.60	3	4.2	2.6	8.88	0.78	3	4.2	2.6	0.54	1.01	3	4.2	2.6	0.58	1.28
Navicula *halophila*	(Grun.) Cleve	58	4.7	13.4	3.47	0.72	55	4.7	32.5	8.25	0.92	51	24.3	8.8	0.92	0.92	53	24.3	9.0	−0.24	0.77
+ var. *robusta*	Hust.																				
+ var. *subcapitata*	Ostrup																				
Navicula *hambergii*	Hust.	2	1.3	1.9	1.78	0.60	2	1.3	1.9	6.00	0.78										
Navicula *heufleri*	Grun.	9	23.0	4.0	3.91	0.47	9	23.0	4.0	8.75	0.99	7	7.5	4.9	1.34	0.58	8	23.0	3.8	−0.46	0.60

Table 4 (*continued*)

Taxon name	Authority	Conductivity					pH					Cation ratio					Anion ratio				
		N	*Max*	N_2	Optimum	Tolerance	N	*Max*	N_2	Optimum	Tolerance	N	*Max*	N_2	Optimum	Tolerance	N	*Max*	N_2	Optimum	Tolerance
Navicula *insociabilis*	Krasske	2	1.4	1.5	2.07	0.26															
Navicula *iranensis*	Hust.	5	27.9	1.7	4.24	0.56	4	27.9	1.6	9.01	1.03	5	27.9	1.7	0.43	0.13	5	27.9	1.7	−0.69	0.33
Navicula *juernefelti*	Hust.	3	2.7	2.9	4.67	0.60	3	2.7	2.9	7.60	1.24										
Navicula *kotschyi*	Grun.	12	3.6	5.9	3.07	0.79	12	3.6	5.9	7.56	0.99	9	3.6	4.4	0.98	0.82	9	3.6	4.4	0.19	1.08
Navicula *lagerheimii*	Cleve	2	2.6	1.3	2.61	0.06	2	2.6	1.3	7.91	0.07										
Navicula *lanceolata*	(Ag.) Kütz.	7	5.3	2.7	3.20	1.01	6	2.0	3.2	8.01	0.64	6	5.3	1.9	−0.29	0.17	6	5.3	1.9	−0.75	0.65
Navicula *menisculus*	Schumann	12	6.0	3.9	2.26	0.40	9	6.0	3.1	7.00	1.16	7	1.1	4.2	0.12	0.38	8	6.0	2.1	0.30	0.45
Navicula *minima*	Grun.	26	3.6	12.6	2.51	0.91	22	3.6	9.8	7.53	1.26	19	2.3	11.3	0.17	0.51	20	2.3	12.0	0.46	0.59
Navicula *minuscula*	Grun.	9	15.1	2.4	2.38	0.65	8	15.1	2.3	7.51	0.92	8	15.1	2.3	−0.26	0.83	9	15.1	2.4	0.88	0.86
+ var. *muralis*	Lange-Bertalot																				
Navicula *molestiformis*	Hust.	9	9.1	3.3	3.38	0.99	6	9.1	2.2	9.29	0.58	8	9.1	2.5	1.62	0.97	8	9.1	2.5	0.41	0.19
Navicula *molissima*	Hust.	2	3.2	1.4	2.35	0.49	2	3.2	1.4	7.83	0.10										
Navicula *monoculata*	Hust.	4	3.4	2.1	3.20	0.22	4	3.4	2.1	7.62	0.31	4	3.4	2.1	0.19	0.22	4	3.4	2.1	−0.86	0.17
+ var. *omissa*	Lange-Bertalot																				
Navicula *muticuloides*	Hust.	3	7.6	1.4	2.92	1.00	3	7.6	1.4	7.94	1.04										
Navicula *mutica*	Kütz.	37	19.0	6.4	2.96	0.88	34	19.0	6.2	7.94	1.13	28	19.0	4.7	0.57	0.68	34	19.0	6.1	−0.06	0.86
+ var. *intermedia*	(Hust) Cholnoky																				
+ var. *nivalis*	(Ehr.) Hust																				
+ var. *tropica*	Hust.																				
+ var. *ventricosa*	Kütz																				
Navicula *nolens*	Simonsen	10	7.5	6.1	2.13	0.70	7	7.5	4.8	7.83	1.12	8	7.4	4.7	0.62	0.32	8	7.4	4.7	0.51	0.19
Navicula *oblonga*	Kütz.	2	1.1	2.0	3.26	0.20	2	1.1	2.0	7.70	0.78	2	1.1	2.0	0.04	0.35	2	1.1	2.0	−0.92	0.17
Navicula *pelliculosa*	(Bréb) Hilse	10	1.4	6.6	2.47	0.50	8	1.4	5.3	8.14	0.68	9	1.4	6.1	0.25	0.70	9	1.4	6.1	0.45	0.64
Navicula *permitis*	Hust.	5	1.3	3.8	2.65	0.18						4	1.3	3.2	−0.25	0.14	4	1.3	3.2	−0.24	0.50
Navicula *perventralis*	Hust.	3	1.1	2.2	1.86	0.50	3	1.1	2.2	7.69	0.72										
Navicula *phyllepta*	Kütz	13	3.8	7.3	4.55	0.63	10	3.8	5.4	7.75	0.35	10	3.8	5.3	0.49	0.29	10	3.8	5.3	−1.93	0.56
Navicula *pseudoreichardtii*	Patrick	11	23.3	5.1	3.35	0.51	11	23.3	5.2	9.03	0.32	11	23.3	5.1	1.01	0.60	12	23.3	5.4	0.51	0.32
Navicula *pupula*	Kütz.	34	9.3	0.4	3.41	0.79	32	9.3	11.3	8.44	1.12	19	4.9	8.7	0.31	0.66	23	4.9	10.5	0.12	0.69
+ var. *capitata*	Hust.																				
+ fo. *elliptica*	Hust.																				
Navicula *pygmaea*	Kütz.	32	26.7	5.6	3.37	0.57	29	26.7	5.3	8.05	0.70	27	26.7	5.0	0.94	0.78	27	26.7	5.1	−0.39	0.88
Navicula *radiosa*	Kütz	39	31.3	7.8	3.20	1.01	34	12.1	12.7	7.87	0.65	25	31.3	4.7	0.14	0.39	28	31.3	5.2	0.29	1.04
Navicula *ramosissima* var. *mucosa*	(Aleem) Hendey	3	1.6	2.4	4.01	0.80	3	1.6	2.4	7.73	0.51										
Navicula *rhyncocephala*	Kütz.	37	8.9	13.1	3.34	0.84	33	8.9	12.1	8.16	0.95	29	4.2	13.4	−0.02	0.30	31	8.9	8.8	−0.62	0.69
Navicula *salinarum*	Grun.	31	11.3	15.3	2.96	1.24	29	11.3	14.3	7.62	1.13	22	11.3	10.1	0.41	0.41	22	11.3	10.1	−0.14	0.83
Navicula *salinicola*	Hust.	14	19.0	6.9	4.47	0.46	14	19.0	6.9	8.25	0.73	14	19.0	6.9	0.69	0.36	14	19.0	6.9	−1.33	0.89
Navicula *scabellum*	Hust.	5	28.2	3.4	1.79	0.12	5	28.2	3.4	6.08	0.38	5	28.2	3.4	0.85	0.35	5	28.2	3.4	0.61	0.14
Navicula *schroeterii*	Meister	21	6.0	7.4	2.14	0.70	16	6.0	4.0	7.77	0.76	19	3.2	8.3	0.30	0.63	20	3.2	8.7	0.07	0.92
Navicula *scutelloides*	W. Sm.	3	1.2	2.0	2.61	1.46	3	1.2	2.0	8.47	1.71	2	1.2	1.3	−0.48	1.13	3	1.2	2.0	1.01	0.45
Navicula *secura*	Patrick	2	2.7	1.5	3.28	0.02	2	2.7	1.5	8.84	0.81	2	2.7	1.5	1.36	1.39	2	2.7	1.5	0.18	0.38
Navicula *seminuloides*	Hust.	21	12.9	6.6	2.99	0.98	14	12.9	4.0	8.37	1.33	16	3.5	9.9	0.39	0.65	17	9.5	6.2	0.68	0.51
Navicula *seminulum*	Grun.	24	3.1	15.3	2.34	0.69	23	3.1	14.7	7.56	1.28	19	3.1	12.2	0.54	0.68	21	3.1	13.1	0.45	0.83
Navicula *simplex*	Krasske	8	1.4	6.1	2.11	0.53	8	1.4	6.1	7.47	0.96	7	1.1	5.3	0.02	0.31	7	1.1	5.3	0.13	0.53
Navicula *soehrensis*	Krasske	2	5.2	1.2	1.72	0.87						2	5.2	1.2	0.84	0.45	2	5.2	1.2	0.59	0.04
+ var. *linearis*	Krasske																				
Navicula *soodensis*	Krasske	6	11.0	2.9	4.75	0.42	5	11.0	2.4	8.53	0.71	6	11.0	2.9	0.94	0.65	6	11.0	2.9	−1.87	1.21
Navicula *spicula*	(Hickie) Cleve	11	4.4	4.6	3.75	0.48	11	4.4	4.6	8.24	0.64	8	4.4	3.5	0.29	0.31	8	4.4	3.5	−0.71	1.14
Navicula *stroemii*	Hust.	2	1.2	1.5	3.33	0.60	2	1.2	1.5	8.41	0.15										
Navicula *subhalophila*	Hust.	4	15.1	1.4	2.07	1.48	4	15.1	1.4	7.61	1.83	3	15.1	1.2	1.25	0.81	4	15.1	1.4	0.61	0.27
Navicula *subminuscula*	Manguin	24	16.4	10.3	2.51	0.70	20	16.4	8.3	8.32	0.80	23	19.0	9.6	0.60	0.46	23	19.0	9.6	0.44	0.41
+ *N. perparva*	Hust.																				
Navicula *suboculta*	Hust.	4	4.4	2.0	2.41	0.48	4	4.4	2.0	7.64	0.90	4	4.4	2.0	−0.07	1.25	4	4.4	2.0	1.06	0.39
Navicula *subrhyncocephala*	Hust.	11	3.5	8.3	3.29	0.61	11	3.5	7.6	8.32	0.68	10	2.9	7.4	1.34	0.36	10	2.9	7.4	−0.54	0.46
Navicula *subrotunda*	Hust	3	2.5	2.1	1.72	0.27						3	2.5	2.1	0.63	0.54	3	2.5	2.1	0.48	0.26
Navicula *subtilissima*	Cleve	4	5.2	2.1	1.94	0.46	4	5.2	2.1	6.32	1.01										
Navicula *tantula*	Hust.	11	19.5	4.3	1.76	0.17	8	19.5	3.5	6.72	1.13	9	9.2	4.1	0.81	0.15	9	9.2	4.1	0.53	0.10
Navicula *tenelloides*	Hust.	12	23.2	2.0	3.98	0.43	11	23.2	2.0	9.05	0.82	8	23.2	1.2	0.86	0.66	7	23.2	1.2	0.49	1.01
Navicula *tenera*	Hust.	9	1.9	6.7	3.18	0.64	9	1.9	6.7	7.67	0.29	8	1.9	5.7	0.29	0.54	8	1.9	5.1	−0.46	1.05
Navicula *tenuicephala*	Hust.	2	3.0	1.2	3.33	2.08	2	3.0	1.2	8.44	0.15										
Navicula *tripunctata*	(O. Müller) Bory	5	39.0	2.3	4.66	0.23	5	39.0	2.3	9.38	0.29	4	39.0	2.3	1.99	0.26	4	39.0	2.3	−0.64	0.01
Navicula *trivialis*	Lange-Bertalot	6	15.0	1.6	2.89	0.82	6	15.0	1.6	8.61	0.31	2	3.4	1.1	0.91	0.39	2	3.4	1.1	0.59	0.03
Navicula *twymaniana*	Archibald	8	3.5	6.1	2.47	0.76	5	3.5	3.5	8.39	1.06	7	3.5	5.6	0.52	0.37	7	3.5	5.6	0.54	0.12
Navicula *ventralis*	Krasske	9	2.0	6.5	2.45	0.58	6	1.8	4.8	7.42	0.91	5	1.8	4.0	1.07	0.24	6	1.8	4.8	0.58	0.79
Navicula *viridula*	(Kütz.) Ehr.	26	5.0	11.6	3.34	0.92	23	5.0	9.7	7.52	0.60	24	5.0	10.9	0.29	0.48	24	5.0	10.9	−0.82	1.05
+ var. *rostellata*	(Kütz.) Cleve																				
+ var. *slesvicensis*	(Grun.) Van Heurck																				
Navicula *zanoni*	Hust.	7	6.8	4.3	2.56	0.73	8	6.8	5.1	7.50	1.40	5	6.8	2.9	−0.20	0.25	8	6.8	5.1	0.79	0.49
Neidium *affine*	(Ehr.) Cleve	6	5.0	3.6	2.49	0.45	4	1.2	3.8	7.04	0.63	2	1.2	1.9	1.33	0.06	3	3.0	2.3	0.95	0.32
+ var. *longiceps*	(Ehr.) Cleve																				
+ var. *amphirhynchus*	(Ehr.) Cleve																				
Nitzschia *acicularis*	(Kütz.) W. Sm	19	27.0	4.6	2.47	0.56	19	27.0	4.6	7.60	0.76	6	2.0	4.4	0.12	0.66	6	2.0	4.4	0.76	0.56
Nitzschia *acidoclinata*	Lange-Bertalot	4	25.9	1.5	1.80	0.15	4	25.9	1.5	6.03	0.21						2	2.1	2.0	0.21	0.14
Nitzschia *acuminata*	(W. Sm.) Grun	2	2.8	1.1	2.81	0.52	2	2.8	1.1	8.08	1.13	2	2.8	1.1	0.44	1.03	2	2.8	1.1	0.39	0.13
Nitzschia *acuta*	Cleve	6	1.9	4.2	2.69	0.13	5	1.9	3.4	8.24	0.48	6	1.9	4.2	−0.50	0.26	6	1.9	4.2	0.64	0.97
Nitzschia *adapta*	Hust	3	15.8	1.8	3.34	0.39	3	15.8	1.8	9.26	0.77	3	15.8	1.8	1.62	0.50	3	15.8	1.8	0.43	0.43
Nitzschia *alexandrina*	(Cholnoky) Lange-Bertalot	3	12.0	1.9	3.90	0.14	3	12.0	1.9	8.62	0.82	3	12.0	1.9	1.19	0.53	3	12.0	1.9	0.40	0.39
Nitzschia *amphibia*	Grun	90	36.3	26.9	2.66	0.75	78	36.3	23.2	7.85	1.07	75	36.3	21.7	0.40	0.61	79	36.3	23.8	0.41	0.66
Nitzschia *barata*	Hust.	27	10.0	10.4	2.04	0.42	21	10.0	7.3	6.76	1.13	25	10.0	9.3	0.56	0.47	27	10.0	10.4	0.53	0.44
Nitzschia *calida*	Grun. in Cl. and Grun	2	2.1	1.9	3.42	0.14	2	2.1	1.9	7.00	0.78	2	2.1	1.9	−0.26	0.01	2	2.1	1.9	−1.14	0.13
Nitzschia *clarissima*	H. and M. Peragallo	4	2.1	2.8	4.64	0.16	4	2.1	2.8	7.65	0.06	2	2.1	1.4	0.53	0.11	2	2.1	1.4	−2.15	0.20
+ var. *obtusa*	H. and M. Peragallo																				
Nitzschia *closterium*	(Ehr.) W. Sm.	13	6.4	3.4	4.19	0.98	12	6.4	3.0	7.86	0.57										
Nitzschia *communis*	Rab.	26	87.0	4.5	2.01	0.65	24	87.0	5.0	8.46	0.52	24	87.0	4.5	0.76	0.42	25	87.0	5.0	0.43	0.41
Nitschia *confinis*	Hust.	5	15.5	2.0	2.72	0.96	3	2.9	2.7	8.16	1.52	3	2.9	2.4	1.16	1.76	5	15.5	2.0	0.95	0.37
Nitzschia *constricta*	(Kütz.) Ralfs	20	33.2	4.0	4.26	0.49	20	33.2	4.0	7.61	0.45	15	33.2	3.6	0.38	0.20	16	33.2	3.7	−1.92	0.66
Nitzschia *denticula*	Grun.	23	18.0	5.5	3.23	0.37	21	18.0	4.9	8.14	0.59	15	3.0	8.1	0.05	0.50	14	3.0	7.1	−0.40	0.87
Nitzschia *desertorum*	Hust.	14	55.4	3.3	3.21	0.66	11	55.4	2.5	7.22	0.29	12	55.4	2.5	−0.08	0.29	13	55.4	2.8	−0.88	1.04
Nitzschia *dissipata*	(Kütz.) Grun	23	9.8	8.8	3.54	1.09	22	9.8	7.1	7.79	0.51	15	5.5	6.9	−0.17	0.47	16	5.5	7.7	−0.26	1.21
Nitzschia *dubia*	W. Sm.	2	1.2	1.5	3.99	0.48	2	1.2	1.5	7.72	0.07	2	1.2	1.5	0.07	0.63	2	1.2	1.5	−1.66	0.18
Nitzschia *elegantula*	Grun.	39	30.2	10.8	3.70	0.37	37	30.2	8.7	7.27	0.60	38	30.2	10.8	0.52	0.66	37	30.2	10.6	−0.87	0.87
Nitzschia aff. *elliptica*	Hust. [Ben Khelifa unpubl.]	10	66.2	3.3	4.82	0.20	10	66.2	3.3	7.88	0.37	10	66.2	3.3	0.61	0.09	10	66.2	3.3	−2.21	0.27
Nitzschia *epiphytica*	O. Muller	13	5.4	7.0	2.44	1.03	12	2.0	9.6	8.19	1.80	9	5.4	5.2	1.17	0.60	12	5.4	6.2	0.48	0.29
Nitzschia *epiphyticoides*	Hust	2	4.6	1.6	3.01	0.04	2	4.6	1.6	8.80	0.28	2	4.6	1.6	1.00	0.77	2	4.6	1.6	0.81	0.09
Nitzschia *epithemoides*	Grun.	12	6.0	6.2	4.51	0.19	10	6.0	5.0	8.50	0.92	12	6.0	6.2	0.50	0.19	12	6.0	6.2	−1.91	0.92
Nitzschia *etoshensis*	Cholnoky	6	10.9	4.7	3.92	0.67	5	10.9	3.8	9.30	0.70	6	10.9	4.2	2.05	0.56	7	10.9	5.1	0.27	0.23
Nitzschia *filiformis*	(W. Sm.) Van Heurck	4	1.0	3.5	3.87	1.19	4	1.0	3.5	7.94	0.66	3	1.0	2.5	0.42	0.38	3	1.0	2.5	−2.05	0.45
Nitzschia *fonticola*	sensu Gasse 1986	105	89.8	27.7	2.98	0.80	92	89.8	22.8	8.35	0.92	87	66.7	26.7	0.67	0.93	93	66.7	28.5	0.26	0.81
Nitzschia *frustulum*	(Kütz.) Grun	110	84.9	23.0	3.62	0.69	101	84.9	20.9	9.97	1.07	88	84.9	16.5	1.46	0.88	96	84.9	20.4	0.18	0.73
Nitzschia *gandersheimiensis*	Krasske	6	3.0	2.8	2.39	0.68															
Nitzschia *goetzeana*	O. Muller	17	2.8	11.2	2.87	0.70	15	2.8	9.4	8.20	0.68	15	2.8	9.6	0.95	0.89	16	2.8	10.5	0.59	0.35
Nitzschia *gracilis*	Hantzsch	27	69.5	2.2	2.70	0.41	23	69.5	2.1	7.52	0.62	22	69.5	1.9	0.03	0.46	22	69.5	1.9	0.73	0.65
Nitzschia aff. *graciloides*	Hust. [Ben Khelifa 1989]	10	70.0	3.1	4.65	0.15	10	70.0	3.1	8.91	0.56	7	70.0	2.9	0.73	0.11	7	70.0	2.9	−2.78	0.33
Nitzschia *hungarica*	Grun	48	10.3	17.7	4.01	0.64	44	10.3	16.9	8.69	0.88	35	10.3	13.5	0.88	0.80	38	10.3	14.5	−0.81	0.93

Table 4 (*continued*)

Taxon name	Authority	Conductivity					pH					Cation ratio					Anion ratio				
		N	*Max*	N_1	Optimum	Tolerance	*N*	*Max*	N_1	Optimum	Tolerance	*N*	*Max*	N_1	Optimum	Tolerance	*N*	*Max*	N_1	Optimum	Tolerance
Nitzschia *inconspicua*	Grun.	21	74.8	4.5	3.61	0.57	19	37.5	5.2	7.66	1.06	19	74.8	5.4	0.52	0.91	18	74.8	5.3	−0.73	0.70
Nitzschia *kuetzingiana*	sensu Hust.	63	48.4	16.3	2.75	0.66	56	48.4	14.2	7.52	0.93	48	48.4	8.8	0.74	0.72	50	48.4	9.7	0.04	0.77
Nitzschia *lacuum*	Lange-Bertalot	9	50.0	2.1	2.86	0.82	8	16.5	2.4	7.34	0.79	8	50.0	2.0	−0.19	0.13	8	50.0	2.0	−0.79	0.99
Nitzschia *lancettula*	O. Müller	21	55.9	3.0	3.28	0.80	17	55.9	2.8	8.51	0.76	20	55.9	3.5	1.15	1.00	21	55.9	3.5	0.20	0.50
Nitzschia *latens*	Hust.	16	75.2	2.4	3.72	0.63	15	75.2	2.3	9.17	0.87	14	75.2	2.1	1.65	0.60	15	75.2	2.1	0.39	0.41
Nitzschia *linearis*	(Ag.) W. Sm	38	15.0	14.8	2.73	1.15	32	15.0	13.3	6.89	0.81	30	11.1	13.2	0.43	0.49	30	11.1	12.4	0.18	0.74
Nitzschia *littorea*	Grun. in Van Heurck [Gasse unpubl.]	2	10.4	1.2	4.38	0.84	2	10.4	1.2	10.03	0.71	2	10.4	1.2	2.67	0.65	2	10.4	1.2	0.28	0.02
Nitzschia *microcephala*	Grun.	37	5.1	17.8	3.43	0.54	36	5.1	17.2	7.80	0.64	29	5.1	14.5	0.04	0.33	30	5.1	15.5	−0.99	0.49
Nitzschia *nana*	Grun.	3	23.3	1.2	2.77	0.07	3	23.3	1.2	7.06	0.56	2	23.3	1.1	−0.14	0.23	2	23.3	1.1	−0.51	0.80
Nitzschia *obtusa*	W. Sm	22	7.0	7.6	3.58	0.55	23	7.0	8.1	7.68	1.16	20	7.0	5.9	0.14	0.45	19	7.0	5.3	−0.78	0.86
Nitzschia *palea*	(Kütz.) W. Sm.	120	47.8	32.8	2.95	0.80	113	39.3	31.9	7.81	0.92	86	35.8	21.3	0.73	0.71	88	35.8	21.8	0.11	0.80
Nitzschia *palea* var. *debilis*	(Kütz) Grun.	28	69.3	6.5	3.46	0.56	28	69.3	5.5	7.22	0.55	21	69.3	4.4	−0.06	0.14	21	69.3	4.4	−1.16	0.28
Nitzschia *paleacea*	Grun.	36	20.9	11.0	2.48	0.40	32	13.3	8.4	7.67	0.81	29	13.3	7.9	0.23	0.52	31	20.9	7.6	0.78	0.89
Nitzschia *paleoides*	Hust.	3	24.3	1.3	2.98	0.42	2	24.3	1.0	8.71	0.92	3	24.3	1.3	1.37	0.79	3	24.3	1.3	0.77	0.20
Nitzschia *panduriformis*	Greg.	4	2.9	3.1	4.67	1.10	5	2.9	3.4	7.60	1.19										
Nitzschia *perminuta*	(Grun.) M. Peragallo	16	17.4	6.3	3.82	0.62	15	17.4	5.9	8.70	0.75	11	17.4	3.1	1.02	0.72	12	17.4	4.1	−0.71	0.76
Nitzschia *pseudofonticola*	Hust.	7	*****	1.2	2.92	0.72	5	4.2	2.7	7.95	1.48	4	*****	1.1	0.96	0.48	4	*****	1.1	0.61	0.14
Nitzschia *punctata*	(W. Sm.) Grun.	28	51.0	5.0	3.86	0.66	28	51.9	4.9	7.87	0.76	25	51.9	4.8	1.12	0.58	27	51.9	4.8	−1.08	0.89
Nitzschia *aff. pura*	Hust. [Ben Khelifa 1989]	2	66.4	1.0	4.63	0.48	2	66.4	1.0	10.86	1.34						2	66.4	1.0	0.14	0.33
Nitzschia *pusilla*	Grun.	73	68.8	17.3	3.96	0.57	68	51.6	18.2	8.46	1.09	60	51.6	15.0	0.59	0.71	63	68.8	15.8	−0.96	1.13
Nitzschia *recta*	Hantzsch	14	15.0	4.1	1.85	0.50	12	15.0	3.9	6.59	0.90	12	15.0	3.6	0.74	0.53	13	15.0	4.0	0.57	0.37
Nitzschia *sigma*	(Kütz.) W. Sm.	19	41.4	4.2	4.21	0.49	18	41.4	4.2	9.22	0.88	17	41.4	4.2	1.34	1.00	17	41.4	4.2	−0.26	1.20
Nitzschia *sociabilis*	Hust.	2	8.1	1.0	2.81	1.34															
Nitzschia *spiculum*	Hust.	15	30.5	3.0	2.75	0.18	13	30.5	2.6	7.86	0.71	13	30.5	2.6	0.01	0.31	14	30.5	2.6	0.71	0.41
Nitzschia *steynii*	Cholnoky	31	14.7	9.0	3.55	0.57	29	14.7	8.7	7.68	0.89	27	14.7	8.5	0.20	0.68	28	14.7	8.7	−0.80	0.88
Nitzschia *stompsii*	Cholnoky	21	23.8	7.7	4.01	0.29	20	23.8	7.1	7.41	0.38	19	23.8	7.4	0.30	0.48	18	23.8	7.3	−1.45	0.56
Nitzschia *subacicularis*	Hust.	21	41.5	4.9	3.86	1.18	19	41.5	4.8	9.46	1.43	17	41.5	3.6	2.13	1.36	18	41.5	4.3	0.33	0.25
Nitzschia *tropica*	Hust.	19	6.4	7.2	2.71	0.76	17	6.4	6.7	7.81	0.83	12	6.4	4.6	0.32	0.95	15	6.4	5.7	0.35	0.69
Nitzschia *tryblionella*	Hantzsch	19	7.7	5.8	3.22	0.77	18	7.7	5.7	8.17	0.99	11	7.7	3.0	1.24	0.76	13	7.7	3.9	−0.26	0.80
+ var. *levidensis*	(W. Sm.) Grun.																				
Nitzschia *umbonata*	(Ehr.) Lange-Bertalot	12	1.6	8.4	2.82	0.97	11	1.6	7.5	7.66	1.29	8	1.6	5.0	0.12	0.37	9	1.6	5.9	0.23	0.42
Nitzschia *vitrea*	Norman	111	4.0	6.8	4.04	0.36	9	4.0	6.5	9.25	0.30	5	4.0	2.6	1.85	0.86	6	4.0	3.5	0.16	0.39
+ var. *scaphiformis*	Wislouch and Poretsky																				
Nitzschia *vivax*	W. Sm.	3	4.4	1.5	4.33	0.49	3	4.4	1.5	9.63	1.58	3	4.4	1.5	2.53	0.71	3	4.4	1.5	0.22	0.18
Opephora *martyi*	Héribaud	6	4.2	2.5	3.54	0.41	6	4.2	2.5	7.19	0.39	5	4.2	2.3	−0.14	0.27	5	4.2	2.3	−1.15	0.19
Pinnularia *acoricola*	Hust.	2	3.6	1.7	1.78	1.39	2	3.6	1.7	6.00	1.54										
Pinnularia *acrosphaeria*	Rab.	10	2.0	5.5	2.26	0.83	10	2.0	5.5	7.18	1.02	7	2.0	3.9	−0.12	0.33	7	2.0	3.9	0.65	0.09
Pinnularia *appendiculata*	(Ag.) Cleve	7	3.5	4.1	2.77	0.97	6	3.5	3.6	6.87	0.89	5	3.2	2.8	0.05	0.31	5	3.2	2.8	−0.83	1.16
Pinnularia *borealis*	Ehr.	111	5.6	3.9	2.43	1.01	9	5.6	3.5	6.95	1.40	7	2.0	4.7	0.32	0.64	7	2.0	4.7	−0.16	0.69
+ var. *rectangularis*	Carlson																				
Pinnularia *braunii*	(Grun.) Cleve	2	3.9	1.5	2.10	0.04															
Pinnularia *cardinalis*	(Ehr.) W. Sm.	3	6.0	1.5	2.67	0.76	2	1.0	1.7	6.00	1.54										
Pinnularia *gibba*	Ehr.	19	13.0	4.0	2.53	0.50						13	3.6	5.0	0.61	0.69	14	13.0	2.6	0.94	0.41
+ var. *linearis*	Hust.																				
+ var. *sancta*	(Grun. ex Cleve) Meister																				
Pinnularia *gracilloides*	Hust.	5	5.6	1.8	1.79	0.11	2	1.0	1.7	6.00	1.57	4	5.6	1.4	1.17	0.63	4	5.6	1.4	0.75	0.34
Pinnularia *intermedia*	(Lag.) Cleve	2	2.8	1.6	1.78	0.60	2	2.8	1.6	6.00	0.78										
Pinnularia *interrupta*	W. Sm.	5	2.7	3.1	2.82	1.11	5	2.7	3.1	7.45	1.42										
+ fo. *biceps*	(Greg.) Cleve																				
Pinnularia *maior*	(Kütz.) Rab.	11	67.2	1.4	1.82	0.30	11	4.1	4.9	7.41	1.10	8	67.2	1.3	1.12	0.92	9	67.2	1.4	0.78	0.50
Pinnularia *microstauron* fo. *biundulata*	(O. Müller) Hust.	4	4.0	2.2	2.51	0.68	3	1.0	2.9	6.45	0.52						3	4.0	1.7	1.09	0.21
Pinnularia *obscura*	Krasske	5	3.8	3.8	1.89	0.18	4	3.8	3.0	6.15	0.32	2	2.0	1.6	−0.07	0.41	2	2.0	1.6	0.49	0.35
Pinnularia *stomatophora*	Grun.	5	7.9	3.0	1.87	0.50	5	7.9	3.0	6.19	0.50	3	3.3	1.8	1.10	0.68	3	3.3	1.8	0.31	1.20
Pinnularia *subcapitata*	Greg.	12	21.1	3.5	3.32	0.82	12	21.1	3.5	7.78	1.09	9	4.8	4.8	0.57	0.97	8	4.2	4.1	−0.22	0.52
Pinnularia *tropica*	Hust.	12	8.5	3.7	1.92	0.33	9	2.0	5.7	6.72	0.46	9	8.5	2.7	0.74	0.86	10	8.5	3.0	0.68	0.45
Pinnularia *viridis*	(Nitzsch) Ehr.	4	3.6	3.0	2.32	0.86	3	3.6	2.0	6.16	0.48						2	2.0	1.8	0.43	1.58
Pleurosigma *elongatum*	W. Sm.	7	5.7	3.7	4.27	0.49	9	5.7	4.1	7.63	0.16	4	5.7	1.3	0.26	0.61	4	5.7	1.3	−1.38	0.29
Pleurosigma *salinarum*	Grun.	3	3.2	1.4	4.57	0.83	4	3.2	1.6	7.62	0.14										
Rhoicosphenia *curvata*	(Kütz.) Grun.	8	17.2	1.3	3.23	0.82	7	17.2	1.3	8.115	0.99										
Rhopalodia *ascoidea*	O. Müller	11	2.6	7.4	2.78	0.70	8	2.6	5.0	8.58	1.31	10	2.6	6.7	0.25	1.19	12	2.6	8.4	0.55	0.47
+ *R. hirundiniformis*	O. Müller																				
+ *R. vermicularis*	O. Müller																				
Rhopalodia *gibba*	(Ehr.) O. Müller	23	11.4	7.1	2.80	0.68	23	11.4	7.1	8.14	0.96	20	11.4	6.4	0.45	0.78	20	11.4	6.4	0.30	0.35
+ var. *ventricosa*	(Kütz.) H. and M. Peragallo																				
Rhopalodia *gibberula*	(Ehr.) O. Müller	59	57.7	10.6	3.91	0.46	57	57.7	10.4	9.24	0.96	47	57.7	7.5	1.75	0.79	52	57.7	9.1	0.32	0.70
+ var. *debyi*	Pant.																				
+ var. *protracta*	Grun.																				
+ var. *vanheurckii*	O. Müller																				
Rhopalodia *musculus*	(Kütz.) O. Müller	21	17.5	3.9	4.65	0.63	21	17.5	3.9	8.50	0.85	18	17.5	3.7	0.79	0.58	19	17.5	3.7	−2.02	1.10
Stauroneis *abbottii*	Cholnoky and Klaus	2	3.6	1.8	1.78	0.60	2	3.6	1.8	6.00	0.78										
Stauroneis *acuta*	W. Sm.	2	1.0	1.7	2.17	1.01	2	1.0	1.7	6.78	2.04										
Stauroneis *aerophila*	Petersen	5	2.3	2.3	1.67	0.11	5	2.3	2.3	6.32	0.32	3	2.3	1.5	0.87	0.24	3	2.3	1.5	0.55	0.21
+ *S. nana*	Hust.																				
Stauroneis *anceps*	Ehr.	10	1.5	7.4	2.16	0.35	10	1.5	7.4	6.95	0.81	3	1.0	2.1	0.06	0.56	3	1.0	2.1	0.47	0.29
+ var. *gracilis*	(Ehr.) Brun																				
+ var. *linearis*	(Ehr.) Brun																				
Stauroneis *phoenicenteron*	(Nitzsch) Ehr.	11	5.0	4.9	2.55	0.53	7	1.5	5.5	7.03	1.02	7	1.5	5.2	0.24	0.55	8	5.0	3.5	0.69	0.55
Stauroneis *tackei*	(Hust.) Krammer and Lange-Bertalot	16	9.5	5.5	4.38	0.65	17	9.5	5.6	7.65	0.53	16	9.5	5.5	0.34	0.41	16	9.5	5.5	−1.90	0.50
Stauroneis *wislouchii*	Poret. and Anisimowa	9	16.2	1.5	3.85	0.24	8	16.2	1.4	7.36	0.37	9	16.2	1.5	0.11	0.21	9	16.2	1.5	−1.11	0.29
Stephanodiscus *astraea*	Grun.	64	31.0	8.9	2.67	1.03	62	31.0	8.8	8.37	1.20	48	31.0	7.3	0.47	0.83	54	31.0	9.2	0.51	0.50
+ var. *minutula*	(Kütz.) Grun.																				
Stephanodiscus *damasii*	Hust.	5	25.1	2.4	2.81	0.07	4	25.1	1.9	8.69	0.73	5	25.1	2.4	0.22	0.10	5	25.1	2.4	0.63	0.02
Stephanodiscus *hantzschii*	Grun.	4	17.0	1.9	2.80	0.26	3	17.0	1.2	8.90	0.72	3	17.0	1.8	0.27	0.03	3	17.0	1.8	0.62	0.07
Stephanodiscus *hantzschii* fo. *tenuis*	(Hust.) Håkansson and Stoermer	3	15.9	2.4	2.72	0.26	3	15.9	2.4	8.23	0.18	3	15.9	2.4	0.05	0.22	3	15.9	2.4	0.71	0.18
Stephanodiscus *hantzschii* var. *pusilla*	Grun	15	7.0	6.4	2.95	1.23	13	4.0	6.9	7.77	0.65	13	7.0	4.8	0.85	1.47	14	7.0	5.8	0.63	0.50
Stephanodiscus *minutus*	(Grun.) ex Cleve and O Müller	5	3.2	2.3	2.12	0.30	5	3.2	2.3	8.25	0.38	4	3.2	1.7	−0.47	0.77	4	3.2	1.7	1.01	0.69
Surirella *angusta*	Kütz.	3	2.9	1.6	2.10	0.36															
Surirella *bifrons*	Ehr.	6	3.3	2.6	2.75	0.85	6	3.3	2.6	8.77	1.00	6	3.3	2.6	0.34	1.34	6	3.3	2.6	0.71	0.66
Surirella *engleri*	O. Müller	8	34.1	1.2	2.91	0.42	7	34.1	1.2	8.97	1.20	7	34.1	1.2	0.20	0.15	8	34.1	1.2	0.70	0.17
Surirella *fasciculata*	O. Müller	6	27.8	1.5	3.20	0.24	6	27.8	1.5	8.88	0.19	6	27.8	1.5	0.53	0.34	6	27.8	1.5	0.55	0.28
Surirella *linearis*	W. Sm	10	3.1	4.8	2.25	0.39	9	2.6	4.4	6.84	0.78	5	3.1	2.1	0.40	0.24	5	3.1	2.1	0.49	0.24
Surirella *minuta*	Bréb. in Kütz.	4	1.5	3.5	2.22	0.62	2	1.5	2.0	8.31	0.80	3	1.5	2.5	0.50	0.53	3	1.5	2.5	−0.08	0.87
Surirella *mulleri*	Forti	3	3.7	1.3	2.25	0.70	3	3.7	1.3	8.20	0.62	3	3.7	1.3	−0.46	1.54	3	3.7	1.3	1.14	0.57
Surirella *nyassae*	O. Müller	6	9.9	1.7	2.29	0.17	6	9.9	1.7	7.90	0.33	6	9.9	1.7	−0.16	0.40	6	9.9	1.7	0.84	0.55
Surirella *ovalis*	Bréb.	8	1.5	5.6	3.18	0.78	8	1.5	5.6	7.69	1.11	7	1.5	4.8	0.48	0.46	8	1.5	5.6	−0.35	1.04
Synedra *acus*	Kütz.	61	78.5	10.6	2.38	0.38	56	78.5	10.9	7.61	0.64	48	78.5	10.1	0.22	0.45	51	78.5	10.3	0.59	0.34
Synedra *acus* var. *angustissima*	Grun.	2	10.1	1.1	2.40	0.03	2	10.1	1.1	7.82	0.42	2	10.1	1.1	0.77	0.76	2	10.1	1.1	0.90	0.05
Synedra *acus* var. *radians*	(Kütz.) Hust.	12	91.3	4.1	2.58	0.27	12	91.3	4.1	8.56	0.57	13	91.3	4.1	0.35	0.44	13	91.3	4.1	0.55	0.57
Synedra *berolinensis*	Lemmermann	7	19.1	4.2	2.21	0.34	6	9.5	4.5	8.08	0.59	7	19.1	4.2	−0.07	0.29	7	19.1	4.2	0.84	0.06

Table 4 (*continued*)

Taxon name	Authority	Conductivity					pH					Cation ratio					Anion ratio				
		N	*Max*	N_2	Optimum	Tolerance	*N*	*Max*	N_2	Optimum	Tolerance	*N*	*Max*	N_2	Optimum	Tolerance	*N*	*Max*	N_2	Optimum	Tolerance
Synedra *crystallina*	(Ag.) Kütz.	5	6.6	1.7	4.67	0.01	6	6.6	1.8	7.61	0.04										
Synedra *cunningtonii*	West	3	1.1	2.3	1.99	1.20	3	1.1	2.3	8.00	1.33	3	1.1	2.3	0.15	1.05	3	1.1	2.3	0.84	1.34
Synedra *dorsiventralis*	O. Müller	16	3.4	9.5	2.09	0.51	12	3.4	7.7	6.84	1.25	14	3.4	8.3	0.47	0.51	15	3.4	9.2	0.58	0.35
Synedra *hartii*	Cholnocky	18	17.4	7.9	3.71	0.27	17	17.4	8.0	7.42	0.39	19	17.4	8.4	0.11	0.43	19	17.4	8.4	−1.24	0.48
Synedra *pulchella*	(Ralfs ex Kütz.) Kütz.	5	8.5	1.9	3.48	0.87	5	8.5	1.5	7.62	0.31	5	8.5	1.5	0.15	0.17	5	8.5	1.5	−1.37	0.52
Synedra *rumpens*	Kütz.	44	50.0	5.8	2.34	0.29	38	50.0	5.3	7.80	0.65	34	50.0	3.1	0.43	0.57	38	50.0	3.8	0.55	0.68
+ var. *familiaris*	(Kütz.) Grun.																				
+ var. *fragilarioides*	Grun.																				
Synedra *rumpens* var. *neogena*	(Grun.) Hust.	6	56.5	1.5	2.56	0.28	6	56.5	1.5	7.70	0.51	4	4.7	2.7	0.56	0.57	4	4.7	2.7	0.75	0.26
Synedra *tabulata*	Ehr.	11	34.4	2.3	3.78	0.22	12	34.4	2.3	7.45	0.38	9	34.4	2.2	0.16	0.17	8	34.4	2.2	−1.41	0.27
Synedra *ulna* var. *danica*	(Kütz.) Van Heurck	3	2.7	2.4	2.46	0.20	3	2.7	2.4	8.01	0.65	2	2.7	1.9	0.43	0.72	2	2.7	1.9	0.20	0.99
Synedra *ulna*	(Nitzsch) Ehr.	103	40.7	24.0	2.59	0.60	93	40.7	21.5	7.71	0.89	87	40.7	18.8	0.14	0.49	90	40.7	19.0	−0.09	0.75
Synedra *sp1.*	Ben Khelifa (1989)	8	49.2	3.9	3.61	0.16	8	49.2	3.9	7.35	0.29	8	49.2	3.9	−0.05	0.25	7	49.2	3.9	−1.27	0.19
Thalassiosira *faurii*	(Gasse) Hasle	21	28.2	4.3	3.95	0.61	18	28.2	3.6	9.19	0.44	12	4.4	5.0	1.49	1.24	14	4.4	5.7	0.21	0.23
Thalassiosira *rudolfi*	(Bach.) Hasle	32	63.6	7.3	4.06	0.61	32	63.6	7.4	9.60	0.60	23	63.6	6.1	2.36	0.65	26	63.6	6.3	0.35	0.21
Thalassiosira *weissflogii*	(Grun.) Fryxell and Hasle	2	1.8	1.3	4.54	0.11	2	1.8	1.3	7.77	0.14										

permeable lake sediments. The effect of non-climatic factors can only be detected using other independent methods, such as the stable isotope content of associated minerals (Gasse et al., 1990).

Finally, a major constraint on the application of all biologically-based transfer functions is the lack of suitable modern analogues for fossil assemblages. For example, *Cyclotella choctawhatcheeana*, a species dominant in several Holocene lakes of the Sahara has not been recorded in our investigations of the modern African flora. However, this species is common in the salt lakes of the northern Great Plains of North America (Fritz et al., 1993). Merging of regional datasets may thus provide suitable analogues, even though they may be geographically distant.

We have shown in this paper that the merging of regional datasets can be used to generate new transfer functions without decreasing their predictive ability. One of the aims of the Climate and Salinity Project (CASPIA; Juggins et al., in press) is to merge the African and northern Great Plains datasets to further strengthen these diatom/hydrochemistry relationships by providing better analogues of fossil African assemblages.

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PALAEO

A 135,000-year record of vegetational and climatic change from the Bandung area, West-Java, Indonesia

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Abstract

Sedimentological and palynological analyses of sediment cores from the intramontane Bandung basin (West-Java, Indonesia) provide a first palaeoclimatic record for the Indonesian region covering continuously the last 135,000 years. Our data on palaeosol development indicate anomalously dry conditions for the final part of the penultimate glacial period, around 135,000 yr B.P., and very warm and humid interglacial conditions from 126,000 to 81,000 yr B.P. During the transition to the last glacial period, around 81,000 yr B.P., freshwater swamp forest of the Bandung plain was replaced by an open swamp vegetation dominated by grasses and sedges, indicating a change to considerably drier conditions, possibly related to reduced moisture uptake by the NW monsoon as a consequence of lower sea levels at the onset of glacial conditions. A strong reduction in *Asplenium* ferns from 81,000 to 74,000 yr B.P. suggests that drier conditions may also have occurred in the mountains of the Bandung area, while increased numbers indicate that from 74,000 to 47,000 yr B.P. it was slightly wetter again. Inferred depression of montane vegetation zones and reduced fern percentages suggests distinctly cooler and possibly drier climatic conditions prevailed in the Bandung area from 47,000 to approximately 20,000 yr B.P. For the Last Glacial Maximum 4–7°C lower temperatures are recorded.

1. Introduction

Earlier Quaternary palynological research in the Malay Archipelago included studies of highland, coastal and marine sites, but with the exception of a pollen record from the New Guinea believed to cover the last 60,000 years (Hope and Tulip, 1994) not one of these records reaches beyond 40,000 yr B.P. (Anderson and Muller, 1975: Borneo; Hope, 1976: New Guinea; Haseldonckx, 1977: Malaysia; Walker and Flenley, 1979: New Guinea; Maloney, 1980: Sumatra; Morley, 1981: Kalimantan, 1982: Sumatra; Hillen, 1984: Malaysia; Newsome and Flenley, 1988: Sumatra; Gremmen, 1990: Sulawesi; Van der Kaars, 1991: marine records; Barmawidjaja et al., 1993: Halmahera; Stuijts, 1993: Java). These studies suggest that in the last glacial period montane vegetation zones were depressed, indicating lower temperatures. But clear evidence for significantly drier conditions, as in other tropical regions i.e. northern Australia, South America or Africa (Flenley, 1979; Kershaw, 1986, 1994; Van der Kaars, 1991; Kuhry et al., 1993; Vincens et al., 1993) has so far not been found. In these regions sclerophyll and open dry vegetation types expanded during the last glacial period, indicating increased aridity. Only from some of the marine records indications for drier conditions during the last glacial period have been reported (Van der Kaars, 1991; Barmawidjaja et al., 1993). In these marine records fern spores percentages reduced strongly during the last glacial period, suggesting overall drier conditons in the Indonesian region.

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Campylodiscus clypeus (Ehrenb.) Ehrenb. in inland saline lakes

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Abstract

This paper is concerned with *Campylodiscus clypeus* in recognition of Urve Miller's interest in this taxon and her contribution to the study of shoreline displacement, a stage of Baltic sea level change characterised by *C. clypeus*. This species has also frequently been recorded from inland saline lakes, where the dominant anions are often carbonate and sulphate, rather than chloride. Diatom remains in the sediments of saline lakes can provide estimates of past salinity that can be used to infer past water level and climate. In an attempt to obtain more accurate reconstructions of past salinities we are merging saline lake diatom and water chemistry datasets from the Northern Great Plains (N. America) and Africa; ensuring taxonomic consistency is a vital prerequisite. We examined material from two localities cited by Ehrenberg and compared populations from the Baltic and from inland saline lakes, from Recent and Pleistocene and Holocene Sub-fossil material. We present new data on the frustule morphology of this taxon and show that the populations cannot be clearly separated, either morphologically or ecologically by salinity optima or ion type, and therefore, should be regarded as the same taxon.

both Recent and Pleistocene and Holocene Sub-fossil material. We present new information on frustule morphology and show that the populations cannot be clearly separated, morphologically or ecologically by salinity optima or brine type, and should be regarded as the same taxon.

Taxonomic background

Ehrenberg (1838a) first described the taxon, as *Cocconeis? clypeus*, from fossil deposits at Franzensbad (Františkovy Lázne), Czech Republic (50° 07´ N, 12° 22´ E). That same year he recorded it in abundance from fossil deposits nearby, at Eger, and transferred it to his new genus *Campylodiscus* (Ehrenberg, 1838b). There have, however, been few taxonomic treatments of members of this genus since Deby's monograph (1891). Miller (1969) published several SEM images of *C. clypeus* from Baltic Holocene deposits and Paddock and Sims (1977) surveyed the raphe structure of several advanced groups of diatoms, including *Campylodiscus*.

Material and Methods

Recent material taken from surface sediments in North American (Shinbone Lake, School Lake, Horseshoe Lake, and Lake Isabel) and African (Lake Kindai, Tanzania) saline lakes were examined together with Holocene sub-fossil material from deposits in West Africa (Adrar Bous, N. Niger). These were compared with fossil material from Franzensbad and Kützing material from Eger, held in the diatom herbarium at the Natural History Museum, London. Both appear to have assemblages identical to those Ehrenberg illustrated in Mikrogeologie (1854). The Eger material is rich in specimens of *C. clypeus* and was therefore chosen for SEM studies. Recent material from lagoons in Sweden (Forsmark) and Finland (Lammaslampi) and Pleistocene interglacial fossil material from Norinkylä, Finland (Grönlund, 1991) were also examined. Details of the North American sites are given in Fritz *et al.* (1993), and in Gasse (1986) and Dubar (1988) for the African sites.

canal (Fig. 5, arrowed). The areolae are particularly visible in partially dissolved valves (Fig. 6) and are found in the central area (Fig. 7) and between the costae of the marginal rays (Figs 5 & 8). However, there is a band, approximately 2 μm wide, around the margin of the valve face that is devoid of areolae (Fig. 8). Rows of poroid areolae can also be seen on the valve mantle (Fig. 9). The raphe endings, situated on the keel at either end of the axial axis, are slightly expanded when viewed externally (Fig. 9). The valve face and mantle are corrugated: they are slightly raised along the outer rows of puncta but form slight depressions along the lines of the costate fibulae (Figs 3 & 8).

← Plate 1

Baltic lagoon material (Figs 10-12)

Valves are 103-198 μm in diameter (mean: 135 μm) with 12-17 costae/100 μm (Table 1). The general areola distribution (Figs 10-11) is similar to that in the Eger material, although, due to dissolution, details of the areolae and fibulae could not be resolved (Fig. 12).

← Plate 2

Saline lake material (Figs 13-30)

Valves are 77-223 μm in diameter (mean: 116 μm) with 12-21 costae/100 μm (Figs 13-17). Internally 1, occasionally 2, non-costate fibulae were observed per fenestra (Figs 18-19). As in the material from Eger, the raphe endings are slightly expanded when viewed externally (Fig. 20). The areola distribution of the saline lake material (Figs 21-26) is similar to that found in the type material, although internal views (Figs 23-26) reveal that there is considerable variation in the shape and distribution of the central rows of areolae within and between samples. Valves from Holocene deposits at Adrar Bous (Figs 25-26) diverge most from the type valves as the areolae are more irregularly scattered and the central area more rounded, particularly in the larger valves from the former site.

← Plates 3 &

The internal view of a valvocopula and first copula were obtained for a valve from School Lake. The open copula has 2 rows of lineate pores. At the ligule, the row proximal to the valve bends towards the valve and 2 puncta are found between the 2 rows at this point (Figs 27-28). Another valve from this sample showed that, in external view, 1 of the rows of pores is usually hidden (Fig. 29). Six open girdle elements were also found with a valve from Adrar Bous (Fig. 30), 4 copulae and what appear to be used in palaeosalinity studies elsewhere, particularly in regions where *C. clypeus* is presently absent, or rare, such as East Africa. Its occurrence in carbonate-, sulphate- and chloride-dominated waters suggests that it cannot be used as a clear indicator of a particular brine type.

Acknowledgements

This paper is dedicated to Urve Miller, for whose help and support over the last 25 years Rick Battarbee expresses his thanks. The work was supported by an NERC research grant (GR3/8854) to Rick Battarbee, Steve Juggins, Pat Sims, and Eileen Cox and by British Council, UK/Ministère des Affaires Etrangères, France Alliance project 93.093. Thanks are due to Peter York for the light photomicrographs. Material was kindly provided by Sheri Fritz (Horseshoe Lake, Lake Isobel), David Ryves (Shinbone Lake), Platt Bradbury (School Lake), Francoise Gasse (Adrar Bous, L. Kindai), Tuulikki Grönlund (Norinkylä), Atte Korhola (Lammaslampi), and Pauli Snoeijs (Forsmark).

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Table 1. Measurements of valve diameter and costa density.

Site	No. of valves	Diameter (µm)		Costae/100 µm	
		Mean	Range	Mean	Range
Eger	15	114	92-132	15	14-17
Horseshoe	25	145	114-186	16	14-18
Isabel	50	101	77-143	19	17-21
School	25	109	92-134	16	15-17
Shinbone	15	116	104-141	17	16-19
Kindai	1	99	-	14	-
Adrar Bous	15	149	100-223	15	12-17
Lammaslampi	10	142	127-158	13	12-14
Forsmarch	15	170	136-198	14	13-16
Norinkylä	6	114	103-123	16	15-17

Figure Legends

Figs 1-9. Specimens from fossil deposits at Eger and Franzensbad, Bohemia. Figs 1-2. Light micrographs, scale bar = 25 μm. Figs. 3-10. Scanning electron micrographs of Eger material, scale bars = 25 μm (Figs 3-6) & 1 μm (Figs 7-9). Fig. 1. Franzensbad. Fig. 2. Eger, Sickle-shaped hyaline area. Fig. 3. External view of valve. Fig. 4. Internal view of valve and 4-cornered oval hyaline area. Fig. 5. Internal view of costate and non-costate (arrowed) fibulae subtending the raphe canal. Fig. 6. External view of partially dissolved valve showing areolae distribution on the valve face. Fig. 7. External view of areolae in the central area of the valve face. Fig. 8. External view of the margin of valve face, devoid of areolae. Fig. 9. External view of raphe endings.

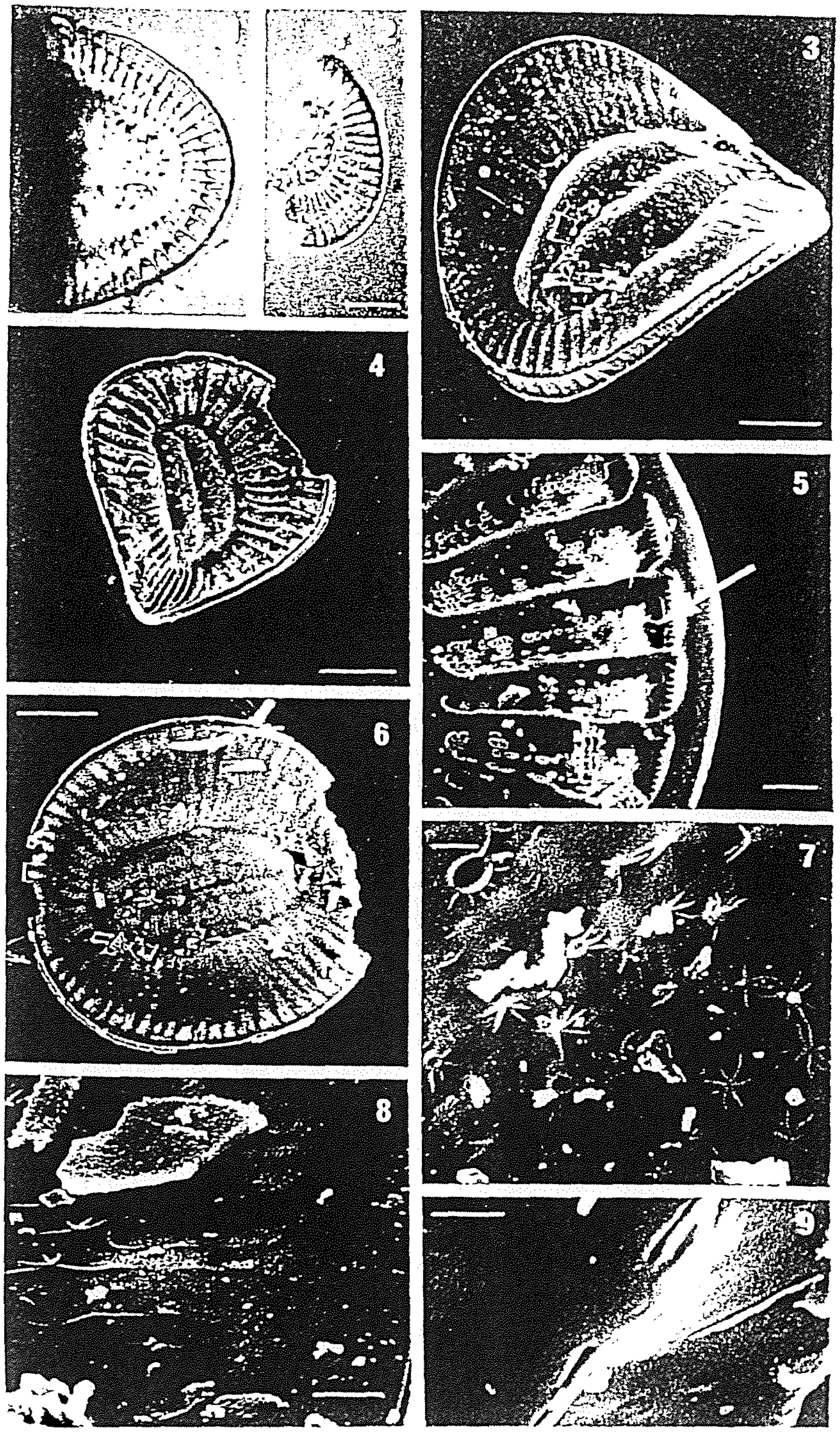
Figs 10-12. Specimens from the Baltic. Figs 10-11. Light micrographs. Fig. 12. Scanning electron micrograph. Scale bar = 25 μm. Fig. 10. Lammaslampi, Finland. Fig. 11. Forsmark, Sweden. Fig. 12. Norinkylä, Finland. Internal view of partially dissolved valve.

Figs 13-22. Specimens from saline lakes. Figs 13-17. Light micrographs, scale bar = 25 μm. Figs. 18-22. Scanning electron micrographs, scale bars = 2 μm (Figs 18, 20, & 22) & 10 μm (Figs 19 & 21). Fig. 13, Horseshoe Lake. Fig. 14, Shinbone Lake. Figs15 & 22, Lake Isabel. Figs16, 20-21, Adrar Bous. Fig. 17, Lake Kindai. Figs 18-19, School Lake. Figs 18-19. Internal views of costate and non-costate fibulae subtending the raphe canal. Fig. 20. External view of raphe endings. Fig. 21. External view of partially dissolved valve fragment showing areolae distribution on the valve face. Fig. 22. External view of the margin of valve face, devoid of areolae.

Figs 23-26, Internal view of valves from saline lakes. Scale bar = 25 μm. Figs 23-24 School Lake. Figs 25-26, Adrar Bous.

Figs 27-30, Girdle elements with valves from saline lakes. Scale bar = 2 μm. Figs 27-29 School Lake. Fig. 30, Adrar Bous. Figs 27-28, Internal view of valvocopula and first copula. Figs 29-30. External view of girdle elements.

Fig. 31. Relationship between relative abundance (%) of *C. clypeus* and salinity (g l^{-1}) for the combined NGP and African dataset, showing raw data and fitted Gaussian response curve. Only samples containing *C. clypeus* are shown in the main plot. The full range of samples within the dataset (n=303) are indicated by ticks on the upper x-axis.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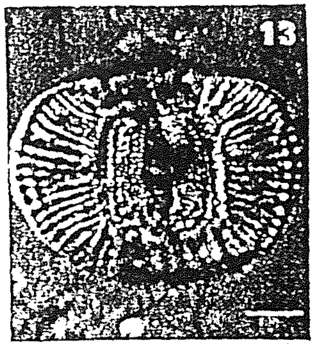

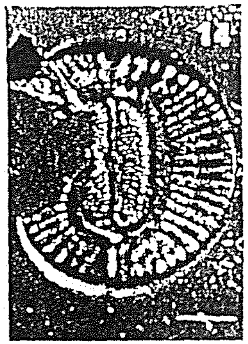

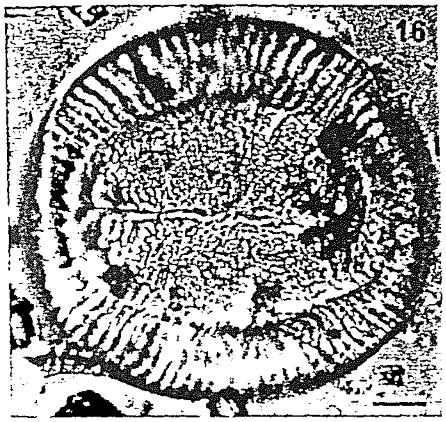

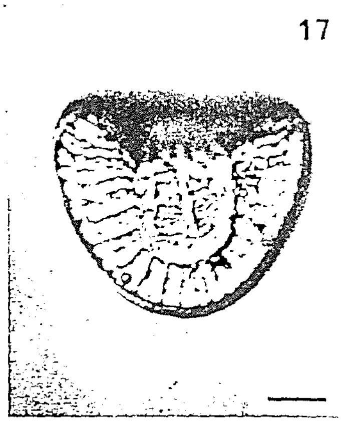

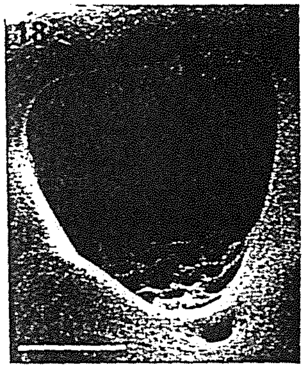

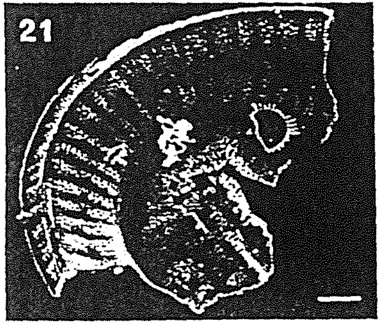

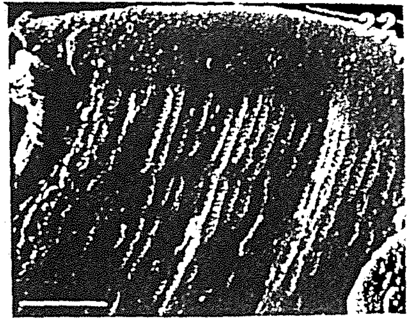

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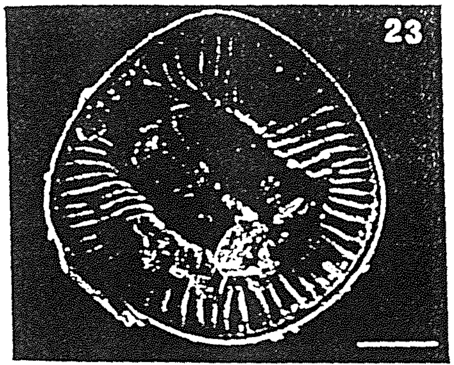
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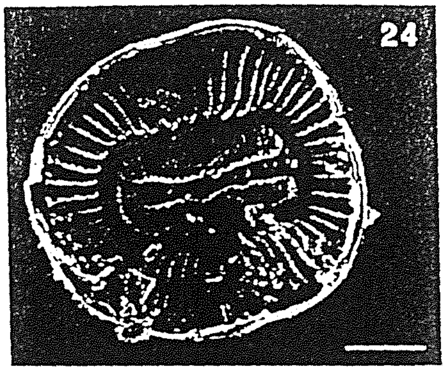
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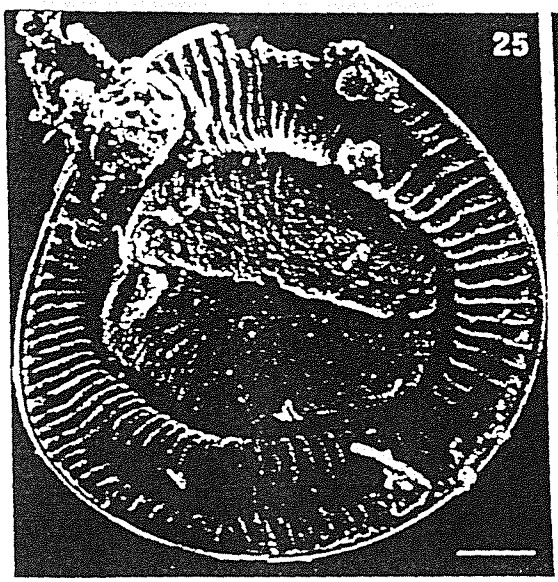
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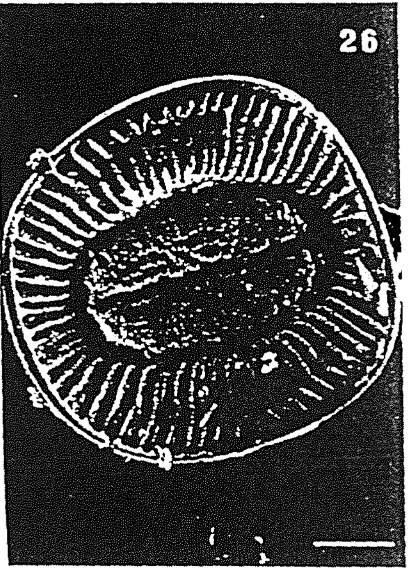
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COMPARISON OF DIATOM-BASED TRANSFER FUNCTION METHODS FOR INFERRING WATER-CHEMISTRY FROM AFRICAN PALEOLAKES

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Introduction

In arid and semi-arid regions the sediments of closed-basin saline lakes contain a unique archive of changing lake hydrochemistry (refs). Given the direct link between lake basin hydrology and lake water hydrochemistry, these hydrochemical fluctuations can be used to reconstruct changes in past hydrology, and ultimately, if we can control for non-climatic controls on local hydrology, changes in past climate (see examples in Gasse, 1994). Such palaeohydrological records are currently of great interest because they provide alternative and independent information that complements other paleoclimatic evidence (refs) and, often provide paleoclimatic data for particular periods or geographical zones for which other paleoclimatic indicators are lacking (refs).

Diatoms are one of the most useful palaeoenvironmental indicators preserved in the sediment of saline lakes(refs). In particular, the recent development of numerical transfer functions can now provide quantitative reconstructions of key hydrochemical parameters (refs). These transfer functions attempt to quantify the relationship between diatom taxa or diatom assemblages and particular environmental (hydrochemical) variables and are calibrated using a reference database of modern diatom assemblages and associated environmental information (refs). Several regional modern diatom datasets have now been developed, and a used to derive diatom transfer functions and palaeoenvironmental reconstructions for pH, salinity, conductivity and ionic facies (e.g.).

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Statement here on:
Require of TF - that it models taxa and produces accuarte and precise reconstructions.
Need large datasets - CASPIA project + acc Tfs combine datasets produce more accurate TFs
Also need to evaluate different numerical methods -
We need accurate Several numerical techniques have been used to derive diatom transfer functions but recently the method of weighted averaging has become the most popular(e.g.), primarily because both theoretical and empirical investigations have shown it to be well-suited to the species-rich, non-linear data that one finds in diatom-based palaeolimnology (refs). However elsewhere (pollen, marine micropalaeontology, the method of best analogues is widely used.....

In this paper we use a recently developed combined modern dataset to evaluate the performance of two methods BA & WA, both in terms of reducing RMSE for training set, and compare chemical reconstruction from two lakes with other palaeonvironmental data....

In this paper, we attempt to perform reconstruction with different statistical methods and compare their preferential application domains for inferring past lacustrine hydro-chemical conditions. In order to accurately discuss this methodological comparison, we have carried out the reconstruction using the two methods: the weighted averaging (WA) method and the best analogues (BA) method (fig. 1), on exactly the same diatom datasets, both for the modern reference and for the fossil data.

In order to discuss situations for which either method is the most suitable for the reconstruction of past lacustrine conditions, we have applied the two methods for inferring pH and conductivity values from diatom data, for two statigraphical profiles. Both sequences record the Upper Pleistocene, the Pleistocene-Holocene transition and the Holocene period. They both contain sediments for which the diatom assemblages are well preserved and other periods characterized by poorly-preserved floristic assemblages. If the diatom records exhibit commun features, they also present specific patterns, and thus provide complementary contribution for our case study.

Lake Abhé is a closed tectonic basin in the Afar (11°N, 42°E, 240 m asl) (fig. 5). It presently represents covers an area of 350 km^2, and is characterized by hyperalkaline waters, rich in sodium carbonate (in: Gasse, 1977).

We report here on the upper part of a 45 m-sediment core taken close to the margin of the lake (Gasse, 1975, 1977) and for which ^{14}C dates provide the chronological framework. The whole 45m-sequence may represent the last 70 kyr B.P. The core shows a paleosoil dated at 16-17 kyr B.P. at its base, with two interbedded diatom-bearing levels. There is a sedimentary gap during the Holocene period. The Middle Holocene is recorded by lacustrine sediment dated from 7.2 to 5.8 kyr B.P. The top of the Holocene has not been recovered in this core.

The fossil diatom record presented here (Fig. 6) (Gasse, 1975) includes quantitative counts for 51 samples, and for 99 taxa that were all represented in the modern dataset.

Bougdouma is currently an almost dry interdunal depression, in the Manga plateau, lying in the Nigerian Sahelian zone (13°19'N, 11°40'E, 337 m a.s.l.) (Fig. 5). Present-day waters are of the sodium-carbonate chemical type.

The sediment sequence documents the paleohydrological history of the last thirteen thousands years. A pluri-disciplinary climatic and hydrological interpretation of biological and isotope records (Gasse *et al.*, 1990; Téhet *et al*, 1990) evidenced that the Late Glacial corresponds to arid conditions, interrupted by sudden groundwater influxes before 12,000 yrs B.P., at c. 12,000 and from c. 10,800 to 10,600 yrs B.P. The stable isoptope ($\delta^{18}O$) variations then reaches its maximum value at 10,300 yrs B.P. However, diatom data indicate that diluted conditions persisted after that time, interpreted as seepage of heavy solutions throught the permeable lake bottom (Gasse, 1994). A brief episode of very saline-alkaline water is evidenced in the diatom record, reflecting the partial solution of a Na^+ carbonate crust previously deposited between c. 10,300 and 10,000 yr B.P. Before 10,300 B.P. the conductivity, therefore, cannot be considered as a climatic indicator. Its variations are mainly due to local factors, that obliterates the climatic changes signal. The period post-9,200 yr B.P. indicates diluted waters and the establishment of a freshwater lake. The Late Holocene records great fluctuations in the conductivity conditions and emphasizes rather saline waters, except around 4,000 yrs B.P. where a sudden brief humid episode occurs (Gasse & Fontes, 1992).

The fossil diatom record (Fig. 9) includes quantitative counts for 113 taxa from 51 samples; 103 taxa are present in the modern dataset.

Methods

The BA method (Overpeck, 1985) is based on a comparison between the modern and fossil diatom assemblages, each of them being considered as a single unit. This is a numerical interpretation of the similarity between the fossil diatom assemblage, and each assemblage in the modern dataset. The similarity, or more precisely, the dissimilarity between the the fossil and modern assemblages is estimated by a weighted log-transformed Euclidean distance (WLED) (Guiot, 1990a, b).

The first step in calculating the WLED consists of a time-series analysis of the fossil record to estimate the so-called "PaleoBioclimatic Operator" (PBO) (Guiot, 1990a). This is defined as a set of coefficients, one for each taxa, that quantifies the ability of each taxon to reflect the major environmental changes recorded in the fossil sequence; the higher the value of the PBO the more faithfully the taxon represents the main trends of the fossil record.

The second step integrates the PBO as weights in the calculation of the Euclidean distance between the fossil assemblage y_0 and each modern assemblage y_i, using log-transformed relative abundances:

$$D^2 = \sum_{k=1}^{m} w_k^2 \left(\ln(10 y_{ik} + 1) - \ln(10 y_{0k} + 1)\right)^2$$

The logarithmic transformation emphasizes the importance of rarer taxa, whose small variations may be more significative that the same variations of dominant taxa. The weighting procedure emphasizes the contribution, of the taxa that are the more important in the fossil sequence. It thereby minimizes the effect of the random part of the signal, that may be included in any biological proxy data through its natural variability.

Considering only the closest assemblage among the reference data and taking its environmental value as an estimate of the past environment would imply the unrealistic assumption that two diatom assemblages could be completely similar. Guiot (1990a) therefore introduced the necessary concept of "partial" analogues; each modern closer assemblage partially explains the floristic representation of the fossil diatom assemblage, and several modern analogues can then account for the total changes achieved in the fossil data. The final environmental estimate is therefore computed as the weighted mean of the chemical variable values measured for the 10 closest analogues sites (ie. minimum D^2), using $1/D^2$ as the weighting coefficient.

Data screening

Following the procedure described in Gasse *et al.* (1995), samples interpreted as statistical outliers were removed from the dataset as recommended in Martens and Naes (1989). These outliers are defined as the samples for which the estimate (diatom-inferred) differs from the value measured of more than one-quarter of the total range of the variable considered.

The results of the best analogues method reconstruction are plotted (Fig. 4) as a diatom-inferred estimate *versus* observed value diagram for the 4 hydrochemical parameters considered. Similar diagrams for the WA method are given in Gasse *et al.* (1995). The visual agreement between the diatom-inferred and measured chemistry is attested by the values of the squared correlation (Table 3): 0.81 for conductivity, 0.63 for pH, 0.60 for anion ratio and 0.59 for cation ratio. The squared correlation estimated-observed parameter value is lower in the BA reconstruction than it is, for the WA method for pH, conductivity, and anion ratio; it is slightly higher for the cation ratio.

The RMSE is slightly higher in the BA reconstruction than it is in the WA method, but the difference of value is negligeable for the cation ratio pattern.

The maximum bias also emphasizes slightly higher values in the BA reconstruction than in the WA, except for conductivity, for which the two maximum biases exhibit equal values. For the BA results, the maximum bias is systematically achieved for the extreme values of the total gradient lenght for the four parameters considered. This suggests that the estimated values in the intermediate values of the gradient are much lower biased than the maximum discussed here.

We therefore consider that the BA is also accurate enough for inferring the 4 hydrochemical parameters taken into account. For the following fossil reconstructions, we therefore applied and compared both the WA and the BA methods.

Fossil sites paleohydrochemical reconstruction

Fig. 7 represents the PaleoBioclimatic component of the sequence. The reconstruction of pH and conductivity carried out by the WA and the BA methods provides independent results that emphasizes general trend, similar whatever the method used. (fig. 8).

By using the BA method, few fossil diatom samples, especially located in the paleosoil level (fig. 8), could not be transfered into conductivity and pH quantitative estimates. For these fossil samples, the 10 modern analogue diatom assemblages were quite different from the fossil diatom one and even, eight among the 10 closer analogues were removed because they exhibited a too low similarity with the fossil assemblage. Indeed, a procedure of modern closer analogues removal is run as soon as the statistical distance between the fossil diatom assemblage and the modern analogue is higher that a value simulated, as representing the distance between two randomly drawn assemblages of the modern data. For these fossil samples, the only two modern closer analogues that were not removed originate from alkaline environments, what should be fairly realistic, if considering the estimates obtained for these samples by the WA method. However, we consider that two modern analogues are not enough to accurately explain the fossil feature and thereby to ensure the estimates. Moreover, the two valuable closer analogues exhibit a high distance value with the fossil assemblage. In such a case of a "no-analogues" situation, the BA method fails in performing any estimate. The WA method may be sucessfull in the reconstruction of the hydrochemical parameters, since it has the ability to extrapolate the calibrations between diatom and hydrochemistry, as defined on the modern dataset.

Except for these samples for which the conductivity and pH are given by the WA method only , the comparison of results achieved by the two methods provides a fairly valid cross-control of both estimate results. The lower part considered of the sequence (25-19 m depth interval) corresponds to a the freshwater assemblage . Such a discrimination enabled to quantify two conductivity values, that we assumed to represent the dry and the wet periods respectively, hence the seasonal or interannual contrast of the conductivity. The interpretation in climatic terms should also be facilitated by using the conductivity contrast, instead of a theoritical mean conductivity, that should not reflect any realistic feature. The partitioning of the two sub-assemblages were performed, by using the affinities of each taxa *versus* the conductivity conditions, as it is recorded in the whole modern data set, and that is summarized by the optimum value, calibrated in the WA method. This is a fairly rough approach, since results consists in two distinct values, even though the conductivity may have varied continuously during the year, or between several years of record. This tentative run (fig. 12) reconciles the inconsistencies well-marked between the two methods when estimating the mean conductivity, for both the lower and the higher conductivity values.

Comparison of methods

Need a section on this, which should summarise the performance of each, analyse the reconstructions, comment on the usefulness of each method and integrate the results of papers by ter Braak (1995), Le (1992) & Huton (1976).

Conclusion

The results obtained for the two transfer function methods are quite close for the modern dataset reconstruction of four environmental parameters.

For the application to the two fossil records, that are characterized by quite different present-day contexts, the results obtained by the WA and by the BA methods show, show rather good agreement. Some discrepancies appear, that question results achieved by one or by both methods.

For main discrepancies, explanation have been proposed, based on the characteristics and behaviour of each reconstruction procedure, facing a specific hydrological context and feature, or a particular pattern in the diatom data representation. Mis-interpretation revealed by comparison of the two independent methods would not have been detected by using one method only. No other clue that the intercomparison had pointed out erratic estimates. Moreover, solutions are tested to solve the inconsistencies between methods. They can be explained and solved, according to the consideration of the hydrological and climatic contexts of each site under investigation.

Our work demonstrates that, in addition to the fact that the climatic significance of the hydrochemical parameters have to be carefully checked according to the context for any site studied (Gasse, 1994), we have also to be aware that the study of the general context must help in the choise of the parameters that we are able to reconstruct. The Bougdouma record evidences that the conductivity contrast may be prefered in some sites for choosen periods.

Acknowledgments

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Captions of figures and tables

Fig. 1 - Schematic comparison of principles of the two transfer function methods:
a: weighted averaging method; b: best analogues method.

Fig. 2 - Location map of sampling sites for the modern diatom/water chemistry dataset (after Gasse & *al.*, 1995)

Fig. 3 - Selection of the modern data: criteria of removal and number of diatom taxa used in the reconstruction procedure.

Fig. 4 - Results of the reconstruction on modern data: diatom-inferred estimates against observed values. for (**a**) conductivity, (**b**) pH, (**c**) the cation ratio $(Na^{+} + K^{+})/(Ca^{2+}+Mg^{2+})$ and (**d**) the anion ratio $(CO_3{}^{2-}+HCO_3{}^{-})/(Cl^{-}+SO_4{}^{2-})$.

Fig. 5 - Location of the two fossil diatom record sampling sites: Lake Abhé (Afar, Ethiopia) and Bougdouma (Sahel).

Fig. 6 - Diatom record of the Lake Abhé sequence: dominant taxa percentages variations.

Fig. 7 - First PaleoBioclimatic Component of the fossil sequence from Lake Abhé.

Fig. 8 - Diatom-inferred conductivity and pH in the fossil sequence of Lake Abhé.

Fig. 9 - Diatom record of the Bougdouma sequence: dominant taxa percentages variations.

Fig. 10 - First PalaeoBioclimatic Component in the Bougdouma sequence.

Fig. 11 - Diatom-inferred conductivity and pH in the fossil sequence of Bougdouma.

Fig. 12 - Diatom-inferred conductivity range in the fossil sequence of Bougdouma.

Table 1 - Overall characteristics of the modern diatom data "subsets"

Table 2 - Summary statistics for the four hydrochemical variables, as recorded in the modern reference database.

Table 3 - Comparison of 3 statistical parameters to test the capability of each method in estimating the environmental parameters from diatom data.

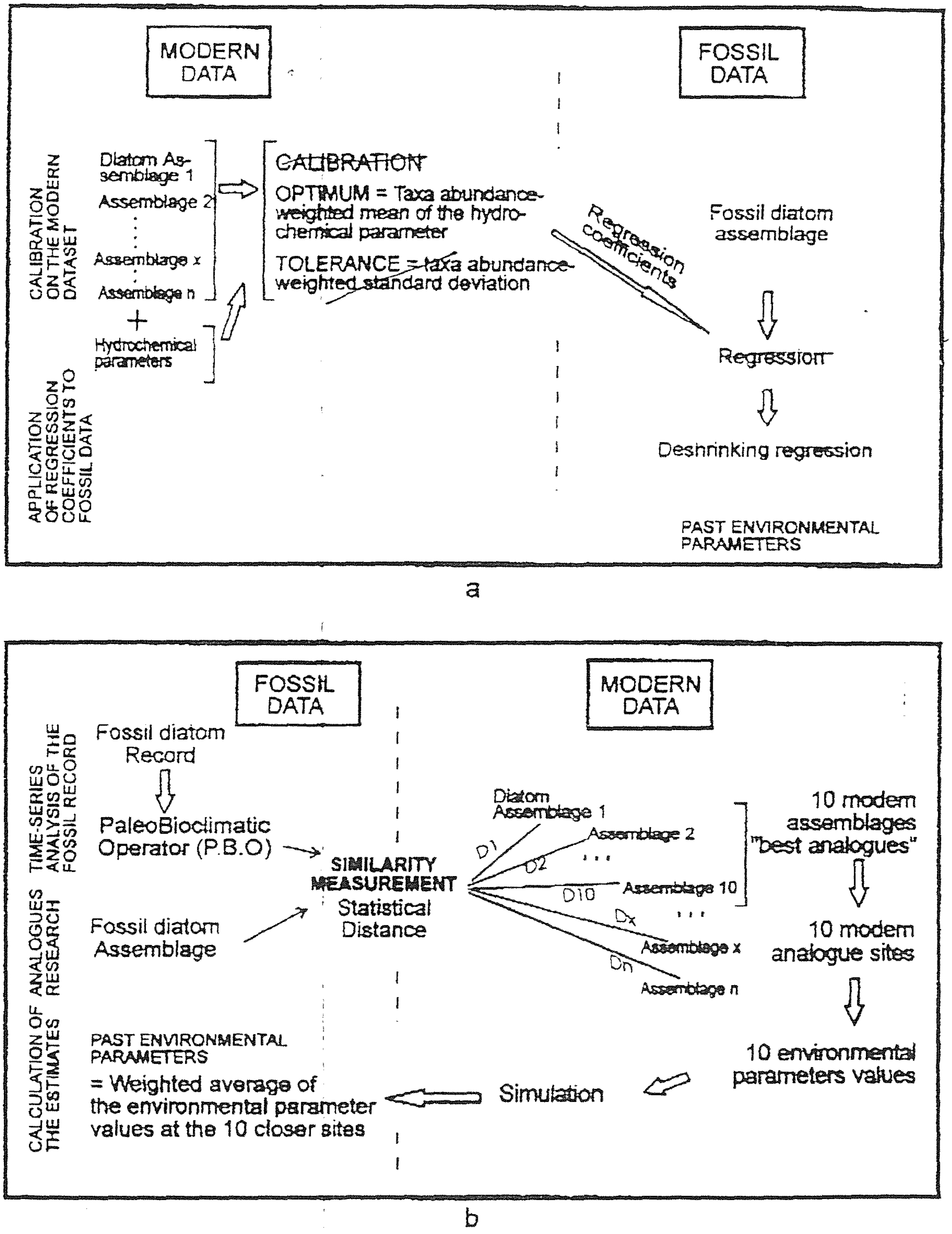


Fig. 1 - Schematic comparison of principles of the two transfer function methods. a: weighted averaging method; b: best analogues method

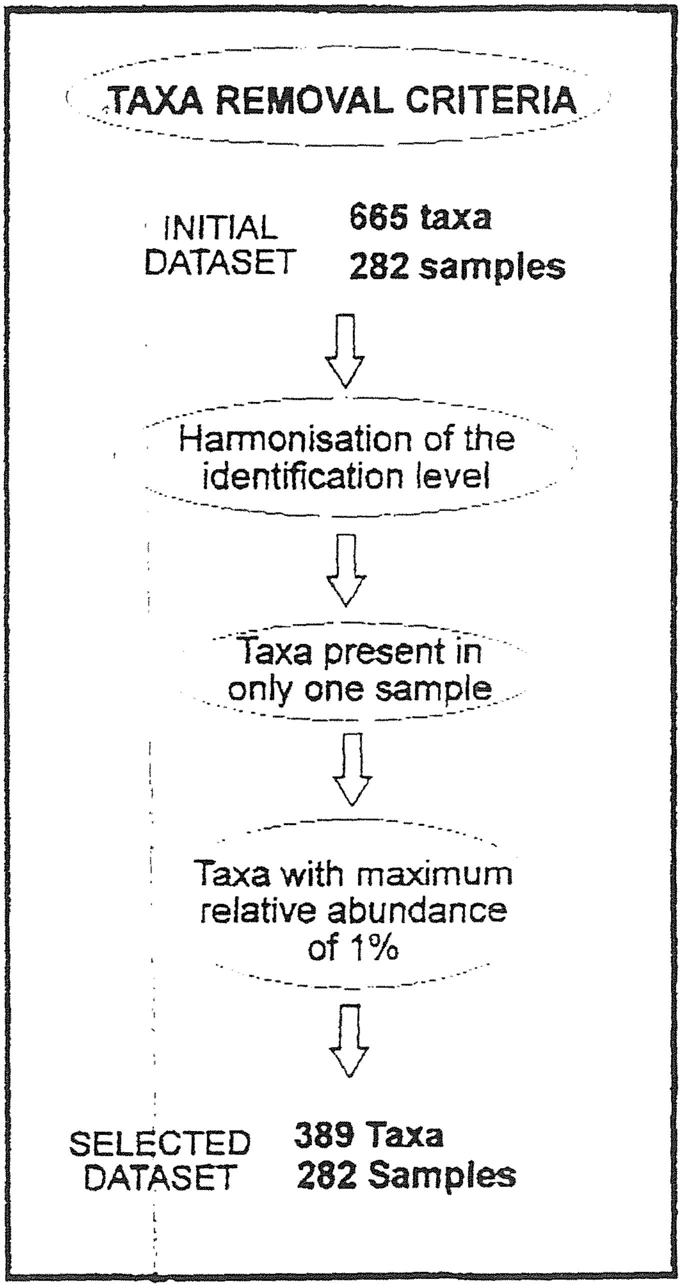


Fig.3 - Selection of modern data
(after Gasse et al., 1995)

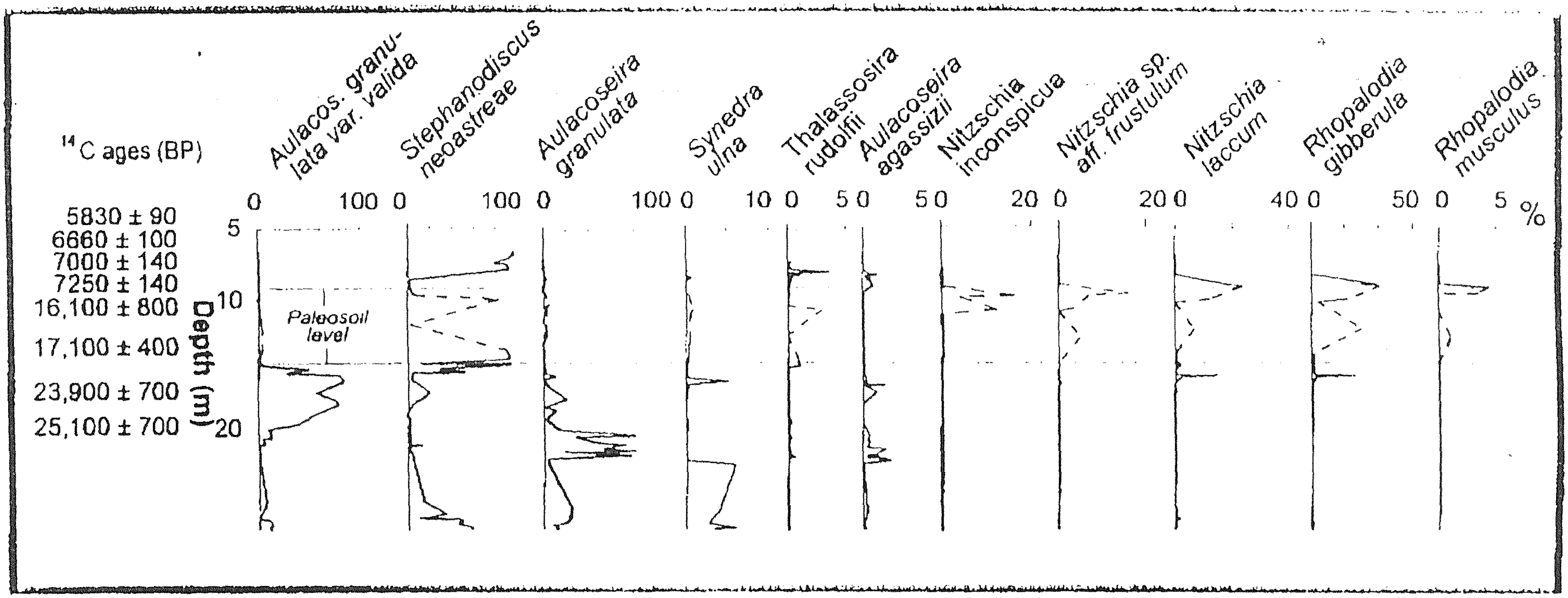
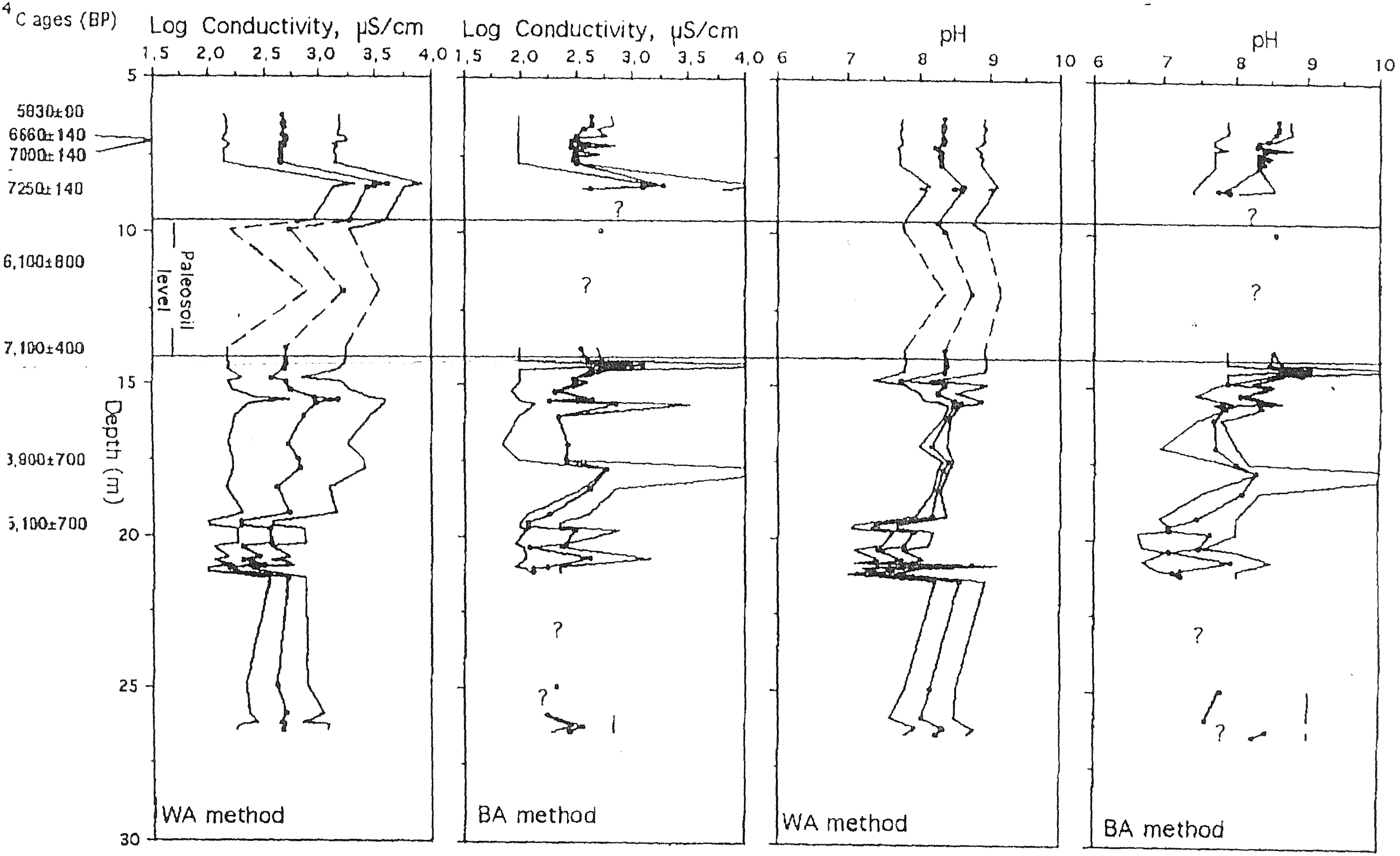

14C ages (BP)
Aulacos. granulata var. valida
Stephanodiscus neoastreae
Aulacoseira granulata
Synedra ulna
Thalassosira rudolfii
Aulacoseira agassizii
Nitzschia inconspicua
Nitzschia sp. aff. frustulum
Nitzschia laccum
Rhopalodia gibberula
Rhopalodia musculus
0 100 0 100 0 100 0 10 0 5 0 5 0 20 0 20 0 40 0 50 0 5 %
5830 ± 90
6660 ± 100
7000 ± 140
7250 ± 140
16,100 ± 800
17,100 ± 400
23,900 ± 700
25,100 ± 700
Depth (m)
5
10
20
Paleosoil level

Fig 6.



? : No estimate due to not enought modern analogues

Fig. 8

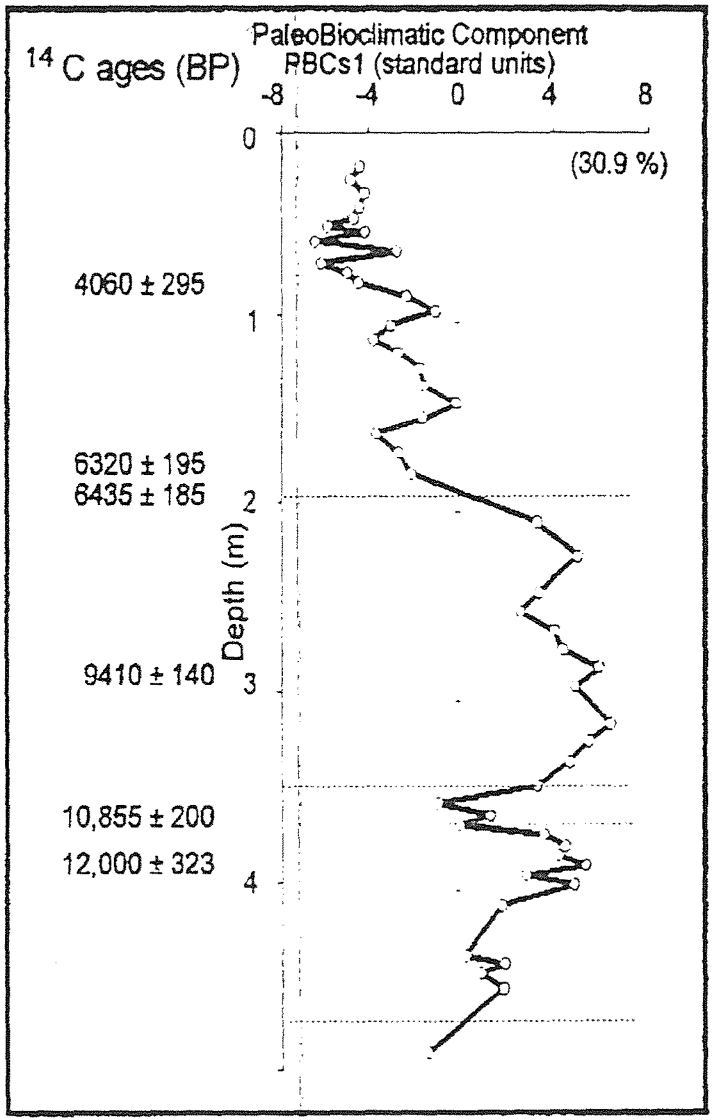


Fig.10 - First PaleoBioclimatic Component computed on the diatom fossil sequence of Bougdouma and used in the BA method reconstruction.

The identity and typification of some naviculoid diatoms reported from saline lakes.

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Introduction

Although the morphology of individuals belonging to a single diatom species varies within particular limits, which the species description should cover, for nomenclatural purposes a specific epithet is linked to a particular specimen or population, cited by the original author or chosen to represent his concept of the species (Greuter et al., 1994). However, in many cases the understanding of what constitutes a particular species has shifted as different workers have examined samples from a range of localities and allocated specimens to described taxa on the basis of written descriptions and published illustrations. Since some of the early descriptions, e.g. those of Kützing (1833, 1844, 1849), Ehrenberg (1838, 1843), Van Heurck (1880-1885) are extremely brief and the accompanying illustrations small, it is understandable that their specific epithets have sometimes been misapplied. Furthermore, it requires patience and care to link illustrations to specimens within mixed populations, unless the taxon in question is particularly distinctive. However, because early workers often distributed slides or samples containing specimens of their species, it is possible to obtain more detailed light microscopical information and photographic documentation of these specimens. Where material from the original locality is extant, it is also possible to supplement light microscopical studies with electron microscopy to present a comprehensive morphological account of the species for comparison with modern collections. The preparation of such accounts should preclude any future misidentification or nomenclatural confusion.

During the course of a project to harmonise diatom data sets from East African and North American saline lakes detailed morphological comparisons were made on the most abundant taxa from each area prior to the production of an iconograph (Carvalho et al., in press). Where possible, comparisons were also made with the type specimens of each species. This paper presents the results of observations of a number of naviculoid taxa whose types are held in The Natural History Museum, London and discusses their taxonomic position.

Materials and methods

Herbarium material and mounted slides held in The Natural History Museum, London, were examined with light and electron microscopy. Material was variously prepared for electron microscopy. Where cleaned samples had been dried onto mica slips, small sections of the mica were mounted on stubs (glued with araldite) before sputter coating with gold-palladium. When samples had been dried onto paper without prior preparation, a small sub-sample was removed with tweezers, gently cleaned in hydrogen peroxide and washed before mounting on a slide (in Naphrax) and on a stub. Any such slides and stubs have been deposited in the diatom collections at The Natural History Museum, London. Table 1 summarises the specimens examined, including the original name, indicating those which are now designated as types.

Material of *Navicula oblonga* collected from Anglesey, N. Wales was also prepared for comparative scanning electron microscopy following standard procedures (Cox 1995b).

Light micrographs were taken using a Zeiss Universal photomicroscope with Kodak T Max film, scanning electron micrographs on a high resolution Hitachi S-800 scanning electron microscope using Ilford HP4 or 100 Delta pro film.

Species descriptions and typifications

Craticula cuspidata (Kützing) D.G. Mann

Two morphologically distinguishable taxa have been recognised within *C. cuspidata sensu lato*: a larger, rhombic-lanceolate diatom with tapered apices, and a smaller, elliptic-lanceolate diatom with rostrate apices. Their taxonomic treatment has varied; some authors recognised them as separate species (W.Smith, 1853, Van Heurck, 1880-85, Mann & Stickle, 1991), some as varieties of a single species (Cleve 1894, Hustedt, 1961), while others grouped them together without any subspecific designation (Patrick & Reimer, 1966, Krammer & Lange-Bertalot, 1986). Before dealing with the taxonomic aspects, I will describe the two groups of specimens simply as non-rostrate and rostrate.

helictoglossae (Figs 17, 22). The girdle bands are narrow split rings, with a single row of pores along their length.

Kützing (1833) described and illustrated (Taf.16, Fig.26) a taxon, *Frustulia cuspidata*, "among *N. oblonga* and other diatoms from Halle, Weisenfels etc.", although he subsequently transferred it to *Navicula* Bory(Kützing, 1844), where it remained until Round et al. (1990) reinstated the genus *Craticula* Grunow. In his later publication, Kützing (1844) included "*Bacillaria fulva* Nitzsch, (ex parte) Beiträge p. 87. Taf. III. Fig. 19 (1817.)" within the synonymy of *N. cuspidata*. However, it is clear that although Nitzsch (1817) illustrated something resembling *C. cuspidata*, several different diatoms were included within *Bacillaria fulva* and therefore, although it is the earlier name, it cannot be used for the taxon we understand as *C. cuspidata*. Kützing (1844) indicated that he had seen material of *N. cuspidata* from de Brébisson although he does not give a locality for this or the species as a whole. It is simply recorded as occurring "In stehenden Gewässern durch ganz Europa."

Cleve (1894) subsumed *N. ambigua* into *N. cuspidata* as a variety, although Kützing (1844) had treated *N.ambigua* Ehrenberg as a discrete species and Smith (1853) and Van Heurck (1880-1885) had also kept them separate. Mann & Stickle (1991) similarly treated them as separate species based on *N. cuspidata* Kützing and *N. ambigua* Ehrenberg, as interpreted by Smith (1853) and Van Heurck (1880-1885). However it is unclear from his illustrations whether Kützing's concept of *N. cuspidata* excluded smaller, rostrate-ended specimens now called *C. ambigua*. Although the illustrations in his earlier work (Kützing 1833) show broadly lanceolate cells which taper to acute apices and have a marginal concavity near the apex, in 1844, Kützing illustrated four somewhat rhombic-lanceolate, tapered valves and two specimens with more markedly rostrate apices (Plate 3, Figs XXIVa and XXXII). Assuming that his drawings are magnified 420 times, all fall within the size range for *C. cuspidata*, whereas the drawing of *N. ambigua* (Plate 28, Fig. 66) is smaller, in the generally accepted size range for *C. ambigua*. Patrick & Reimer (1966) noted that BM slides labelled *N. cuspidata* Kütz. in the Kützing collection contained rostrate-ended, *C. ambigua*-like specimens (Fig.) rather than the larger, tapered cells which correspond to the modern concept of *C. cuspidata*. According to Eulenstein's catalogue of the Kützing collection held in the Natural History Museum (see Cox 1995a), *N. cuspidata* occurred in several packets of material, but none of the numbers is underlined to designate that Kützing used the material when describing the taxon. However, in the NHM copy of the Antwerp Catalogue (see Cox, 1995a), *N. cuspidata* the central raphe endings are more obviously hooked and less expanded than in the other species.

Grunow (Van Heurck 1885) described this as a variety of *Navicula cuspidata*, based on its smaller size, finer and more radiate striation and brackish rather than freshwater habitat. He gave the type locality as Blankenberghe and stated that it was present on Van Heurck Types du Synopsis No.12 *Amphora hybrida* Grun., although the locality is simply given as "Belgique". Cleve (1894) raised the taxon to specific level, as *Navicula halophila*, while with the reinstatement of *Craticula* as a genus (Round et al., 1990) it underwent another nomenclatural change to *C. halophila*. As multiple copies of the slides were distributed specimens on Van Heurck Types du Synopsis No.12 are isotypes.

Navicula digitoradiata (Gregory) Ralfs in Pritchard

Valves linear-lanceolate with obtuse apices, 33-46μm long, 8-9 μm wide (Fig. 7)(Duddingston Loch material). Striae alternately longer and shorter opposite the central raphe endings, radiate throughout much of the valve, 10-11 in 10μm, becoming convergent near the apices. The central area is laterally expanded, somewhat diamond-shaped. The central raphe endings are slightly expanded and lie in a broader portion of the raphe sternum; the polar fissures are hooked towards one side of the valve. The valve face is somewhat convex; the cells rectangular with rounded corners in girdle view; girdle bands plain.

Specimens of this taxon were found on BM 4633, Duddingston Loch, part of the Greville collection. Although Gregory slides are present in the Natural History Museum, they are poorly labelled and documented. However, because Greville frequently illustrated Gregory's taxa from material sent by Gregory, slides in the Greville collection are usually duplicates of the original gatherings.

Type material was not available for scanning electron microscopy.

This species was first described as *Pinnularia digitoradiata* by Gregory in 1856 from gatherings in Duddingston Loch, accompanied by an illustration drawn by Greville (Gregory, 1856, Plate 1, Fig. 32). Gregory's description recorded that the central five or six striae are alternately longer and shorter, but he commented that this feature is "a little too strongly marked in fig. 32". According to him the valves are narrowly linear elliptic or elliptic

Navicula species. The internal opening of the raphe slit is to one side, becoming central along the raphe rib only near the central endings and the relatively small, polar helictoglossae (Figs 28. 29). The central raphe endings terminate in a slight expansion of the raphe rib in the thickened central area. Distal to the slit opening the sternum is thickened, creating a groove on the distal side of the raphe rib and extending laterally to the axial end of the striae. This longitudinal thickening expands into a small mound at the poles beside the helictoglossae (Figs 28,29) and into a larger rounded thickening at the centre of the valve. The plain girdle bands are broad (Fig. 27), with an undulate margin abutting the valve.

First described as *Frustulia oblonga* (Kützing, 1833), Kützing (1844) subsequently transferred it to *Navicula* with an illustration (Taf. 4, Fig. XXI) and reference to his Alg. Dec. No.84 and a specimen from de Brébisson. On one of the herbarium sheets in the NHM diatom collection is a Kützing packet No. 404, labelled "Syn. *Frust. ocellata* Bréb. 1152 Eule". In the Eulenstein catalogue to Kützing's collection both these packet numbers are doubly underlined, indicating that Kützing used them to describe the taxon (cf. Cox, 1995a). A slide (BM 18728, made from packet 404) was designated the type of *N. oblonga* by Ruth Patrick although she did not cite this in the account of *N. oblonga* in Patrick & Reimer (1966).

Kützing (1833) stated that it often occurs in various areas of Germany , but was particularly numerous in a ditch near Tennstädt with *Melosira orichalcea* (i.e. *Melosira italica*), *Diatoma elongatum*, *Frustulia anceps* (i.e. *Stauroneis anceps*) and *Exilaria crystallina* (i.e. *Synedra ulna*).

Navicula radiosa Kützing

Valves lanceolate with acutely rounded apices 45-67μm long, 10-11μm wide (Kützing material; published range 40-120μm long, 10-19μm wide)(Fig. 9), very narrowly rectangular in girdle view. Striae clearly radiate at the centre of the valve and for at least half the distance towards the poles, 10 or 11 in 10μm, but then gradually becoming convergent at the apices. The central area is expanded laterally opposite the central two or three striae which are correspondingly shorter. The central raphe endings are slightly expanded and lie in a thickened area which is broader than the main raphe sternum. At the poles the raphe slits are hooked to one side of the valve.

This taxon was present on BM 18714, made from Kützing packet 406.

comprises many split rings (Figs 35, 37, 38) which externally appear as smooth narrow bands. However, each band is at least twice the apparent width, folded along its length, with a row of large pores along the internal portion (cf. *P. complanatoides* in Brogan & Rosowski, 1988).

Internally the valve presents a regular fretwork of pores (Figs 36, 39, 40), the raphe lying in a slightly thickened rib, with the slits opening to one side (Figs 39, 40). At the centre the raphe fissures are slightly expanded (Fig. 39), terminated at the poles by barely developed helictoglossae (Fig. 40). Opposite the central raphe rib thickening and distal to the raphe opening one stria is terminated by a rounded pore (Fig. 39), corresponding to the isolated pore under the external groove (Fig. 37).

This species was first described as *Navicula bulnheimii* Grunow in Van Heurck (1880) with an illustration (Van Heurck, 1885, Plate XIV, fig. 6a) bearing the legend "6. *N. bulnheimii* Grun. * forme, melé avec le *Nitzschia frustulum*, l'*Homoeocladia bulnheimiana* Rabh." The valve is narrowly lanceolate with acutely rounded apices, traversed by fine parallel striae, apparently of similar conspicuousness throughout the valve (Fig. 10) although the description states that the two central striae are stronger than the others. There is a slight indication that these are more widely spaced on the drawing. The girdle view is more or less rectangular (Fig. 11). Grunow also recognised a variety, *belgica,* from VH Type No. 113 (Figs 12,13). This was distinguished as having slightly more obtuse valvar apices and a deeper girdle view with finer longitudinal markings, but it is not illustrated in Van Heurck (1880). The locality for the type variety is given as "Marin? - Non encore signalé", *N. bulneimii* var. *belgica* as "Marin - Ostende", the locality of the Van Heurck slide, which should be considered isotype material of this variety.

Homoeocladia bulnheimiana Rabh. is listed for Rabenhorst's Algen Europas No. 1301, of which material was located in the Natural History Museum. Krammer & Lange-Bertalot (1986) illustrated a tranmission electron micrograph from duplicate material and suggested, on the basis of the appearance of its pores, that it belongs in *Navicula sensu stricto.* However, examination with SEM has shown that it is morphologically similar to *Proschkinia complanata* (cf. Cox, 1988, Figs 57-61) and *Proschkinia complanatoides* (cf. Brogan & Rosowski, 1988), ratifing Karayeva's combination of these taxa in a separate genus (Karayeva, 1978). Earlier, I (Cox, 1988) had considered this taxon in relation to *Parlibellus* E.J. Cox, because it had been placed in *Libellus* Cleve (Cleve, 1894), the conceptual basis of the new genus. However, after examining VH Types du Synopsis 113 (BM 26424) I concluded that *N. bulnheimii* did not collected at the type localities, although specimens of other *Navicula* spp. with strongly radiating striae are present. Furthermore, while the type localities are essentially freshwater sites, in more recent literature *N. digitoradiata* is usually considered a marine diatom.

Taxonomic problems also remain to be resolved within *Craticula*. The difficulty that some authors (Cleve, 1894, Hustedt, 1961, Patrick & Reimer, 1966, Krammer & Lange-Bertalot, 1986) have experienced in dealing with its range of morphology indicate that *C. cuspidata* should be examined more carefully. Comments on the variability of apices suggest that some large specimens may have rostrate apices, although they could not be placed in *C. ambigua*. Similarly the specimens that Mann & Stickle (1991) identified as *C. halophila* in their SEM studies differ in outline from the type specimens of this taxon and attention needs to be paid to this species too.

Scanning electron microscopical examination of Rabenhorst material of *N. bulnheimii* Grun. has confirmed its inclusion by Karayeva (1978) in a new genus, *Proschkinia*, with *P. complanata* and *P. complanatoides*. The validity of the order she erected is less certain.

Krammer, K. & Lange-Bertalot, H. 1986. *Bacillariophyceae. 1 Teil: Naviculaceae*. Süsswasserflora von Mitteleuropa (Begrundet von A. Pascher)(H. Ettl, J. Gerloff, H. Heynig & D. Möllenhauer, eds) 2 (1). 876 pp. G. Fischer Verlag, Stuttgart & New York.

Kützing, F.T. 1833. Synopsis Diatomacearum. *Linnaea*, **8**, 529-620.

Kützing, F.T. 1844. *Die Kieselschaligen Bacillarien oder Diatomeen*. 152pp. Köhne, Nordhausen.

Kützing, F.T. 1849,

Mann, D.G. & Stickle, A.J. 1991. The genus *Craticula*. *Diatom Research*, **6**, 79-107.

Nitzsch, C.L. 1817. *Beitrag zur Infusorienkunde*. Halle, J.C. Hendel, 128pp.

Patrick, R. & Reimer, C.W. 1966. The diatoms of the United States. Vol. 1. *Monographs of the Academy of Natural Sciences of Philadelphia*, **13**, 1-688.

Rabenhorst, L. 1864. *Flora Europaea. Algarum aquae dulcis et submarinae. Sectio I.* Lipsiae, Edward Kummer. 359pp.

Round, F.E., Crawford, R.M. & Mann, D.G. 1990. The diatoms. Biology and morphology of the genera. Cambridge University Press, 747pp.

Smith, W. 1853. A synopsis of the British Diatomaceae. Vol. 1. John van Voorst, London.

Van Heurck, H. 1880-1885. *Synopsis des diatomées de Belgique*. 235pp, 30 Plates. Anvers.

Figs 20, 25. External views of valve apices. The longitudinal ridges are lost at the apices and the external pore openings are clearly visible. The raphe fissures curve over the apices ending close to the valve margin;

Figs 21, 26. Internal views of valve apices. The helictoglossae are more or less straight;

Fig. 22. External and internal view of entire valves.

Figures 27-32. Scanning electron micrographs of *Navicula oblonga* from material collected by the author in Anglesey, N. Wales.

Fig. 27. External view of centre of valve showing the expanded central raphe endings and the lineate external pore openings.

Figs 28, 29. External views of the poles of the valve illustrated in Fig. 24. Note that the raphe fissures are deflected to the same side and then recurve slightly over the apices.

Fig. 30. External view of the end of a frustule in girdle view. Note that there are no pores in the girdle bands and the raphe fissure ends very close to the valve margin. There is a single row of lineate pores around the valve apex, arranged with their long axes perpendicular to the valve margin.

Figs 31, 32. Internal views of the ends of the valve showing the small helictoglossa, the thickening beside the raphe, distal to the slit opening which expands into a polar thickening. The elliptical internal pore openings are below the level of the virgae and the change in orientation of the striae near the poles is clearly visible.

Figures 33-37. Scanning electron micrographs of *N. radiosa* from Kützing packet 406.

Fig. 33. Internal view of an entire valve.

Fig. 34. External view of the central raphe endings. Note the hooked endings and the lineate external pore openings orientated perpendicular to the direction of the striae.

Fig. 35. . Internal view of valve apex showing the helictoglossa and the end of the additional rib.

Fig. 36. External view of valve apex, showing the hooked raphe fissure.

Fig. 37. Detail of the valve centre. Note the central raphe fissures open in a slight expansion of the raphe rib, flanked on one side by the broad development of the additional rib. The elliptical internal pore openings lie in depressions between the virgae

TABLE 1. **Details of slides examined in The Natural History Museum, London.**

Number	**Designated species**	**Locality / collector / date**	**Other information**
Van Heurck Types du Synopsis			
No.12	*Amphora hybrida* Grun.	Belgique	*C. halophila* *N. halophila*, isotype
No.113	*Navicula mutica* Kütz.	Belgique	*P. bulnheimii* var. *belgica* *N. bulnheimii* var. *belgica*, isotype
No.120	*Navicula cuspidata* Kütz.	Angleterre	
No.121	*Navicula ambigua* Ehr.	Angleterre	
Coll. Greville			
BM 4272	1 *Navicula ovalis* 2 *Nav.* 3 *Nav. elliptica*	Lochleven (Dl.1.A.) Gregory	
BM 4633	*Pinnularia*	Duddingston loch 55	*N. digitoradiata*, lectotype
BM 4636	*Navicula amphisbaena* *Pinnularia viridula* -- *radiosa* -- *oblonga*	Duddingston Loch	
Coll. Wm. Smith			
BM 23448	*Navicula cuspidata*	Lewes Sept 1850	
BM 23449	*Navicula cuspidata*	Lewes Sept 1850	*C. cuspidata* *N. cuspidata*, neotype
BM 23489	*Navicula ambigua*	Dec. 1853	*C. ambigua* *N. ambigua*, neotype
Coll. Kützing			
BM 18714	*Navicula radiosa* Kütz	Breckdorf 406	*N. radiosa* Kg det. R.P.
BM 18728	*Navicula oblonga* Kütz	404	*N. oblonga* Kg det. R.P.
BM 18767	*Navicula cuspidata* Kütz	De Brébisson Falaise 422	
BM 18882	*Navicula tenella* Kütz.	In ostreariis Calvadosii 1476	
Coll. Gregory			
BM 29158		A6	Gregory M.S. Page 89
BM 29159a		A7	Greg.M.S. Page 89
BM 29159B		A7	Gregory M.S. Page 89

Craticula ambigua (Ehrenberg) Mann in Round et al. 1990

Navicula ambigua
Navicula cuspidata var. ambigua (Ehrenberg) Cleve
Plate 2, Figs 1-4
Valves broadly-lanceolate with sub-rostrate apices.
Striae are ± parallel throughout the valve, slightly convergent at the poles, puncta just visible. The raphe is straight and lies in a thickened axial rib; central area not expanded or assymetrical, length greater than width (greater than 1.5 µm long).
40-60 µm long, 10-15 µm wide, 16-20 striae in 10 µm

Distributiion and Ecology: Present in both the NGP and E. Africa datasets but not distinguished from *C. cuspidata*. See *C. cuspidata* for combined distributional and ecological data.

Craticula cuspidata (Kützing) D.G. Mann1990

Navicula cuspidata Kützing 1844
Plate 1, Figs 5-8.
Valves lanceolate gradually tapering to rounded, sometimes rostrate, apices. Striae are parallel throughout the valve, sometimes slightly convergent at the poles. Puncta just visible, aligned longitudinally with the frets separating them often thickened so longitudinal striae are visible. The raphe is straight and lies in a thickened axial rib; central area not expanded or assymetrical, length greater than width (greater than 2 µm long). Internal craticular valves sometimes produced in response to osmotic stress (Schmid, 1979).
70-165 µm long, 15-30 µm wide, 15-20 striae in 10 µm

C. cuspidata is longer than *C. ambigua* and has a higher length to breadth ratio (5:1 compared with between 3:1 to 4:1). It can also be distinguished from *C. ambigua* by its more gradually tapering shape giving the appearance of less distinct rostrate apices.
C. halophila is shorter and narrower than both *C. cuspidata* and *C. ambigua* and has more strongly convergent striae at the poles.

Distributiion and Ecology: Present in both the NGP and African datasets. Not distinguished from *C. ambigua*, so distributional and ecological data summarises combined records.
C. cuspidata is recorded frequently in freshwaters as well as low salinity environments.

No. of sites	Max'm %	Optimum			
		Cond. (mS cm^{-1})	pH	$Na^+ + K^+ / Ca^{++} + Mg^{++}$	$CO_3^{--} + HCO_3^- / SO_4^{--} + Cl^-$
41	3	1.86	8.6	1.6	1.2

Craticula elkab (O. Müller 1899) nov. comb.

Navicula elkab Müller 1899
Plate 3, Figs 1-13.
Valves broadly-lanceolate to lanceolate with rostrate to sub-rostrate apices, sometimes narrowly rostrate or narrowly sub-capitate.
Striae are fine and ± parallel throughout the valve, punctae not clearly visible. The raphe lies in a narrow thickened axial rib, central area not assymetrical, small and rounded, slightly longer than wide (less than 1 µm long).
13-32 µm long, 3.5-6.5 µm wide, 23-26 striae in 10 µm

C. elkab can be distinguished from *C. halophila* as it is shorter and narrower and has a shorter central area, less than 1 µm long. A closely related taxon has been recorded (as *Navicula elkab*) from saline lakes in Central Mexico (Watts & Bradbury, 1982; Metcalfe, 1990). No clear distinction can be made with this and *C.elkab*; valves generally exhibit a more gradual sloping shape towards the poles compared to *C. elkab* and striae density is also generally lower than *C. elkab*.

Distribution & Ecology: *C. elkab* was recorded widely (44 sites) throughout East Africa and Niger, yet was absent from the Northern Great Plains dataset. Carbonate ions are a feature of both the African and Mexican sites. This preference may expain its absence from the sulphate-dominated saline lakes of the Northern Great Plains and from brackish estuarine and coastal waters.

No. of sites	Max'm %	Optimum			
		Cond. (mS cm^{-1})	pH	$Na^+ + K^+ / Ca^{++} + Mg^{++}$	$CO_3^{--} + HCO_3^- / SO_4^{--} + Cl^-$
46	58	13.8	9.4	101.0	1.2

Craticula halophila (Grunow *in* Van Heurck) Mann 1990

Navicula halophila (Grunow *in* Van Heurck) Cleve
Navicula halophila var. *subcapitata* Östrup
Navicula halophila forma *robusta* Hustedt
Plate 1, Figs 2-4.
Valves rhombic to linear-lanceolate with rounded to subrostrate apices.
Striae are ± parallel at the centre, slightly to strongly convergent at the poles. Longitudinal lines fine not always visible. Raphe straight, lying in a narrow thickened axial rib. Central area 1-2 µm long, sometimes slightly assymetrical.
30-60 µm long, 6-9 µm wide, 17-21 striae in 10 µm

C. halophila can be distinguished from *C. elkab*, *C. ambigua* and *C. cuspidata* by its more strongly convergent striae at the poles. The lengths of *C. halophila* stated by Hustedt and KLB (1986) are exceptional and are thought to be due to auxospore formation (Archibald & Schoemann, 1977).

Archibald & Schoemann (1977) give a detailed account of why *N. halophila* var. *subcapitata* Östrup and *N. halophila* forma *robusta* Hustedt should be regarded as synonyms

Distribution & Ecology: *C. halophila* is a cosmopolitan species, found in saline lakes in Africa, North America and Europe. It does not appear to be restricted by ion type. In addition to saline lakes, it is recorded in brackish estuarine and coastal waters.

No. of sites	Max'm %	Optimum			
		Cond. (mS cm^{-1})	pH	$Na^{+}+K^{+}$ / $Ca^{++}+Mg^{++}$	$CO_3^{--}+HCO_3^{-}$ / $SO_4^{--}+Cl^{-}$
82	12	4.05	8.6	3.9	0.4

Craticula vixvisibilis (Hustedt) nov. comb.

Navicula halophila forma *tenuirostris* Hustedt
Plate 1, Fig. 1.
Valves lanceolate with distinctly capitate apices.
Striae are ± parallel, slightly radiate at centre, indistinct (>35 in 10 µm) at the poles
Raphe straight, lying in a narrow thickened axial rib. Central area 1-2 µm long, length greater than width, sometimes slightly expanded.
20-45 µm long, 6-8 µm wide, 22-30 striae in 10 µm at the centre of the valve.

C. vixvisibilis is clearly distinguished from *C. elkab* and *C. halophila* by its distinct capitate apices and fine striae density at the poles.

Distribution & Ecology: It is a cosmopolitan species, found in saline lakes in Africa and North America.

No. of sites	Max'm %	Optimum			
		Cond. (mS cm^{-1})	pH	$Na^{+}+K^{+}$ / $Ca^{++}+Mg^{++}$	$CO_3^{--}+HCO_3^{-}$ / $SO_4^{--}+Cl^{-}$
4	9	1.4	8.4	0.3	0.4

Plate 1 (Figs 1-5 x2500, Figs 6-8 x1000)

Fig. 1:	*Craticula vixvisibilis* (Hustedt) nov. comb.
Figs 2-4:	*Craticula halophila* (Grunow *in* Van Heurck) D.G. Mann in Round *et al.* 1990
Figs 5-8:	*Craticula cuspidata* (Kütz) D.G. Mann in Round *et al.* 1990

Fig.1, 6-7:	Twin Lake, USA
Fig. 2-4:	Ain Toumbar, Tunisia (EH93)
Figs 5, 8:	L. Bogoria-Kibborit (H134)

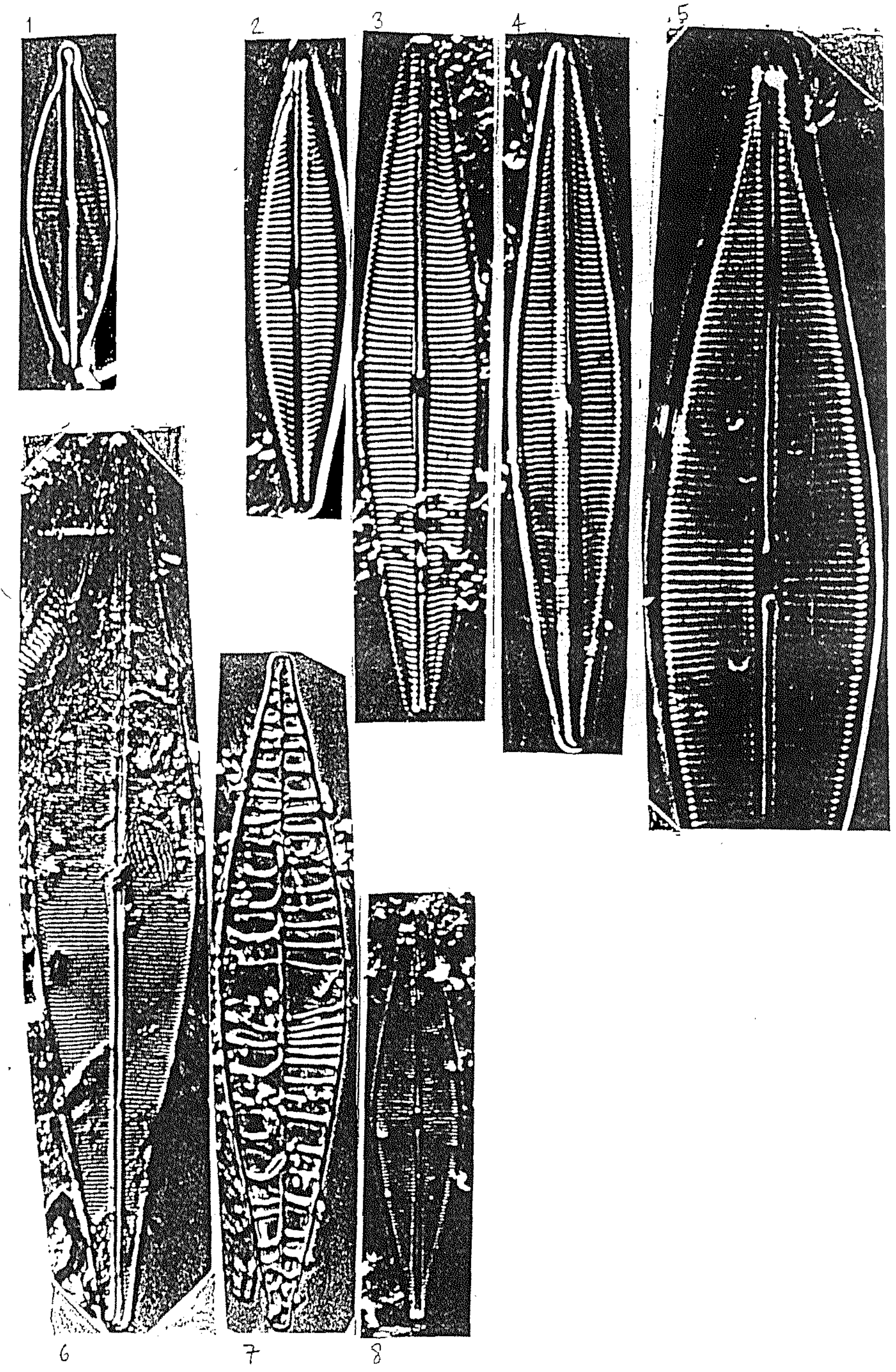

Plate 2 (x2500)

Figs 1-4: *Craticula ambigua* (Ehrenb.) D.G. Mann in Round *et al.* 1990

Fig.1: L. Bogoria, Kenya (H116)
Figs 2-4: Abbaitou, Djibouti (V24)

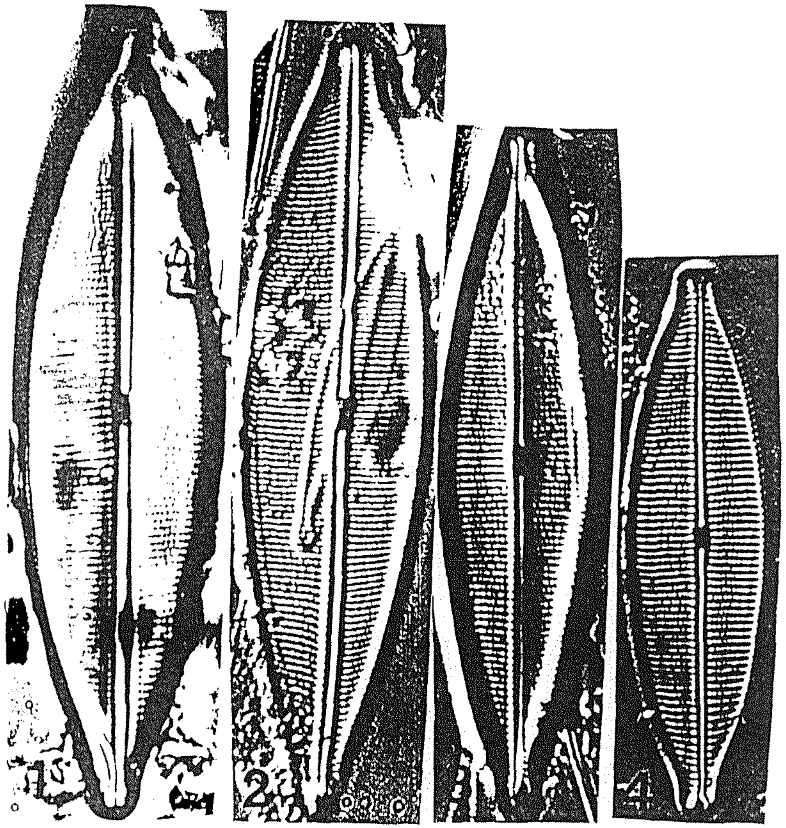

Plate 3 (x2500)

Figs 1-13: *Craticula elkab* (O. Müller) nov. comb.

Fig. 1: L. Biete Mengest, Ethiopia (BW16)
Figs 2, 4, 10-11: Bara Salt Swamp, Niger (Nig dII2e)
Figs 3, 5-9, 12: Abbaitou, Djibouti (V24)
Fig. 13: L. Shala, Ethiopia (JT13)