



## Swamps, springs and diatoms: wetlands of the semi-arid Bogoria-Baringo Rift, Kenya

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### Abstract

Lakes Bogoria and Baringo lie in a semi-arid part of the Kenya Rift Valley between 0° 15'–0° 30'N and 36° 02'–36° 05'E. Nevertheless, the area around these lakes contains numerous wetland systems that have been formed: along lake shorelines; along faults where hot, warm and cold springs have developed; and along river systems that cross the rift floor. Six major types of wetland are recognized: Proximal Hot Springs; Hot Spring Marshes; Blister Wetlands; *Typha* and *Cyperus papyrus* Swamps; Floodplain Marshes; Hypersaline Lake Littoral Wetlands; and Freshwater Lake Littoral Wetlands. These show significant variability in terms of geomorphic setting, water chemistry, temperature, plant communities and diatom floras. They are variously dominated by macrophytes, such as *Cyperus laevigatus*, *Typha domingensis* and *Cyperus papyrus*. In some cases macrophytes are absent. In hot spring settings and in hypersaline lake littoral zones bacterial mats are common.

Although absent in some samples, diatoms occur in at least parts of all of the wetlands, varying in diversity, abundance and species composition. Canonical correspondence analysis indicates that diatom floras show a close relationship with pH, temperature, and specific conductivity, with other environmental variables such as Si and nitrate being of secondary importance. Common diatoms include: *Anomoeoneis sphaerophora* var. *guntheri*, *Navicula tenella*, *N. cuspidata*, and *Nitzschia invisitata* in hot springs, where diversity is generally low and abundance is variable. Other wetland types contain distinctive diatom floras that variously include: *Fragilaria brevistriata*, *Gomphonema parvulum*, *Navicula tenelloides*, *Nitzschia communis*, *N. latens*, *N. sigma*, *Rhopalodia gibberula*, and *Stauroneis anceps*.

### Introduction

Diatoms have been a subject of study in East Africa for over 100 years (West & West, 1896), with these investigations based on both modern (Gasse, 1986a, b; Gasse et al., 1983, 1997; Haberyan, 1992) and fossil floras (Barker et al., 1990; Owen, 2002; Owen & Crossley, 1992; Owen & Renaut, 2000; Liutkus & Ashley, 2003). Modern studies have commonly been linked to particular geographical locations and environments. Gasse, for example, carried out research

into diatoms in hot springs and in Lakes Baringo and Bogoria (reported in Tiercelin & Vincens, 1987). In contrast, some investigations have used a statistical approach, based on data sets collected over many years and from different localities (Gasse & Tekaia, 1983; Gasse et al., 1995). Most of these works have focused on lakes and lake margins, with comparatively few studies being carried out in either fluvial (Pentecost et al., 1997) or wetland settings (Cholnoky, 1970; Gasse, 1987).

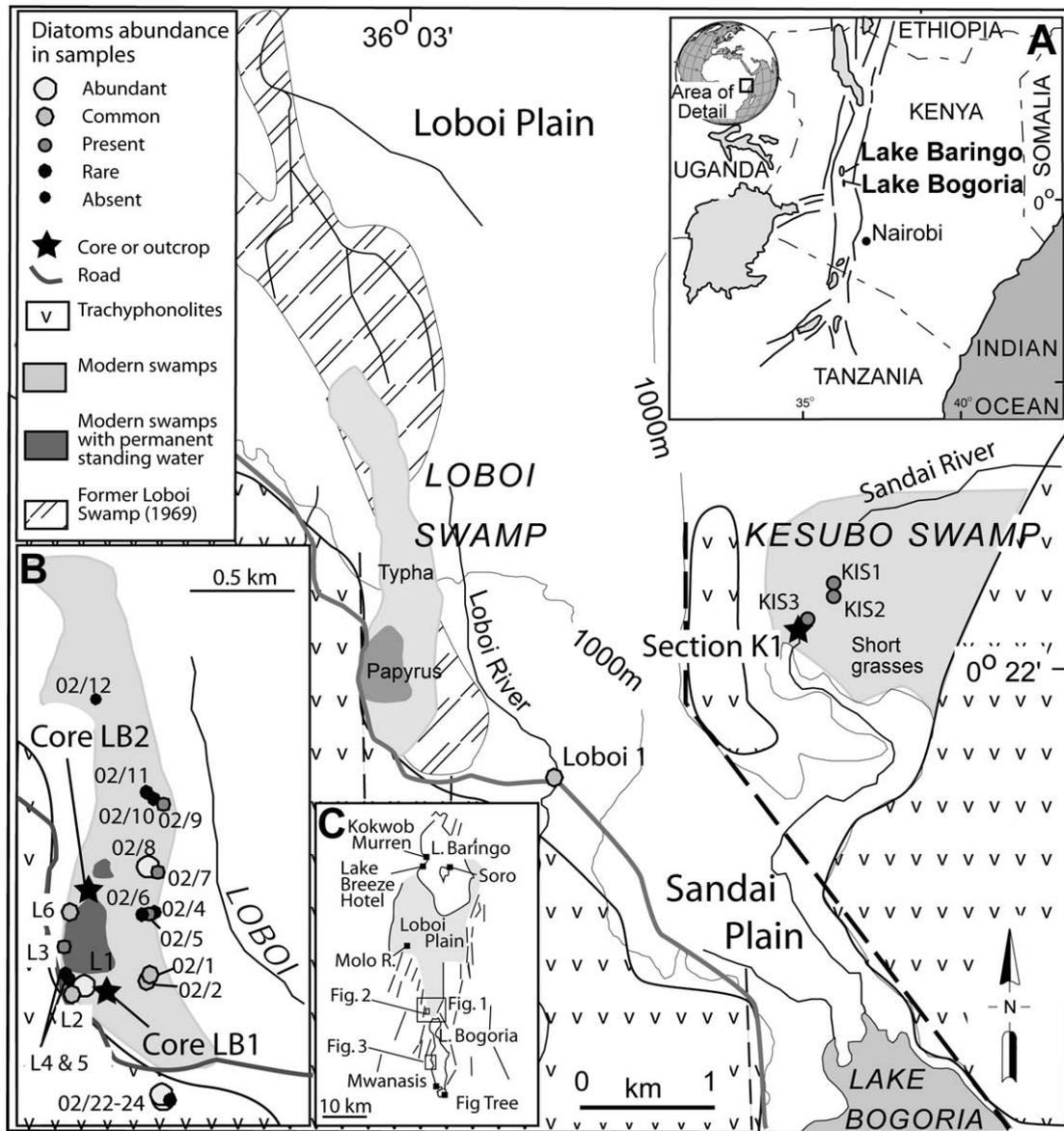


Figure 1. Location map and diatom abundance data for sample sites. The main map shows the locations of the Lobi Swamp and Kesubo Marshes. Inset (A) Overall location. (B) Detail showing sampling sites, with sample numbers, and diatom abundances in the Lobi Swamp. (C) Location of other sampling sites in the Bogoria-Baringo area.

The definition of wetlands can be difficult. Tarnocai (1980) defined wetlands as: 'having the water table at, near, or above the land surface, or which are saturated for a long enough period to promote wetland or aquatic processes as indicated by hydric soils, hydrophilic vegetation and various kinds of biological activity which are adapted to the wet environment'. Wetlands include a diverse range of habitats characterized by water saturation, with water being the

dominant control for soil development, plant types and animal communities (Cowardin et al., 1979). Often, the spatial extent of wetlands can be hard to define, especially where there are gradual changes from dry to wet conditions and seasonal variability. Such areas are present in many parts of East Africa, along lake margins, on deltas, adjacent to river systems, and in areas where the water table intersects low-lying surfaces (Thompson & Hamilton, 1983). In the Kenya



Plate 1. Wetlands of the Bogoria-Baringo Basin. (A) The Loburu Delta with proximal hot springs (Type 1A) and hot spring marshes (Type 1B). (B) Detail of a typical proximal hot spring with tufa and sandy gravel substrates. (C) Hot spring streamlet, with cyanobacterial filaments and marginal *Cyperus laevigatus* reeds. (D) Hot spring marshes (Type 1B wetland) and proximal hot springs (Type 1A). (E) Hot spring marshes with muddy substrate and *Cyperus laevigatus*. (F) Overview of the Lobo Swamp showing bounding horst to the left and *Cyperus papyrus* swamp (circular patch of vegetation) surrounded by *Typha domingensis* swamp. (G) Piston coring in the *Typha* swamp. (H) The Campground Wetlands showing a *Typha* swamp and blister mounds (arrows) dominated by graminoids. (I) Overview of the Kesubo Marshes, which are dominated by graminoids, and which subject to ephemeral flooding. (J) Erosion gully into the Kesubo Marshes revealing a section of pedogenically altered alluvial fan sediments. (K) Hypersaline lake littoral zone (Type 5 wetlands) on the flooded margins of Lake Bogoria. (L) Detail of bacterial mats in a hot spring streamlet entering the Type 5 wetland shown in 'L'. (M) Abundant *Typha* and *Cyperus* in the freshwater lake littoral wetlands of Lake Baringo (Type 6 wetland). (N) shoreline edge of a Type 6 wetland, Lake Baringo.

Rift Valley, springs also feed and generate wetlands. These may be supplied by shallow meteoric recharge (Ashley et al., 2002), or derive their water from deep aquifers, intercepted by faults, to produce hot springs (Renaut & Jones 2000). In this study, we refer to areas dominated by graminoids, short reeds, or sedges, and covered at times by water, as 'marshes'. The term 'swamp', in temperate locations, is often confined to permanently flooded areas with trees and shrubs. In

Africa, this term is commonly used for areas with tall reeds such as *Typha domingensis* Pers. and *Cyperus papyrus* L. (Thompson & Hamilton, 1983), which is the approach used here.

The study area lies to the west and north of saline-alkaline Lake Bogoria (~990 m height), which floods an asymmetric fault-bounded basin (~20 km long, 10 km wide) in the central Kenya Rift Valley (Fig. 1). A major border fault occurs to the east and

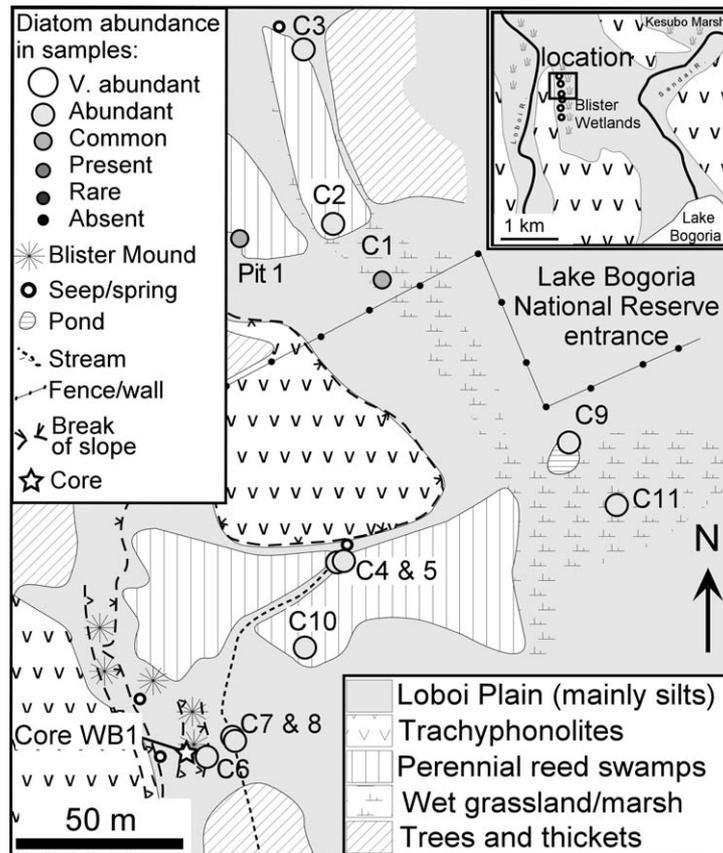


Figure 2. Location map and diatom abundances in the Campground Wetlands.

south with steep slopes preventing wetland development. Numerous gently sloping tilt-blocks cut through trachyphonolites to the west of Lake Bogoria, with north-south river valleys feeding delta lobes, upon which spring-fed wetlands have developed. The basin is open to the north, where Quaternary silts, sands and gravels form the gently sloping Sandai and Lobo Plains that gradually rise to a drainage divide that separates Lakes Bogoria and Baringo (Fig. 1). This area is characterized by semi-arid planar surfaces, and by extensive wetlands that are variously fed by ephemeral or perennial streams, and by spring systems.

The Sandai River feeds into the northern end of Lake Bogoria and dominates the hydrological inputs of this lake (Fig. 1), which has no outlet. Other streams, such as the Emsos to the south and the Parkirichai to the west, are ephemeral, flowing only after heavy rains. Over 200 fault-controlled hot and cold springs and seeps also contribute significantly to the water budget (Renaut & Tiercelin, 1994). Precipitation ranges from about 700 mm on the Lobo Plain

to 1200 mm on the adjacent highlands, with most of the rain falling in and around April and November. Potential evaporation is  $>2500$  mm, producing a budget deficit and semi-arid conditions over most of the lower parts of the Bogoria Basin. El Niño years are correlated with increased rainfall (LaVigne & Ashley, 2002), and flooding around the shores of Lake Bogoria. The dominant vegetation is *Acacia* savanna (Vincens, 1986), with wetlands being dominated by *Cyperus* or *Typha*.

Several types of wetland can be distinguished in the Bogoria-Baringo area (Plate 1). These include: Type 1A – Proximal Hot/Warm Springs, characterized by small streamlets, exposed ground (carbonate and/or siliciclastics), high water temperatures ( $>40^{\circ}\text{C}$ , reaching up to  $99^{\circ}\text{C}$  at vents), and microbial mats composed of bacteria and less common diatoms; Type 1B – Hot/Warm Spring Marshes that lie downstream of springs and adjacent to spring streamlets. These are dominated by dense stands of short reeds, mainly *Cyperus laevigatus* L., in very shallow

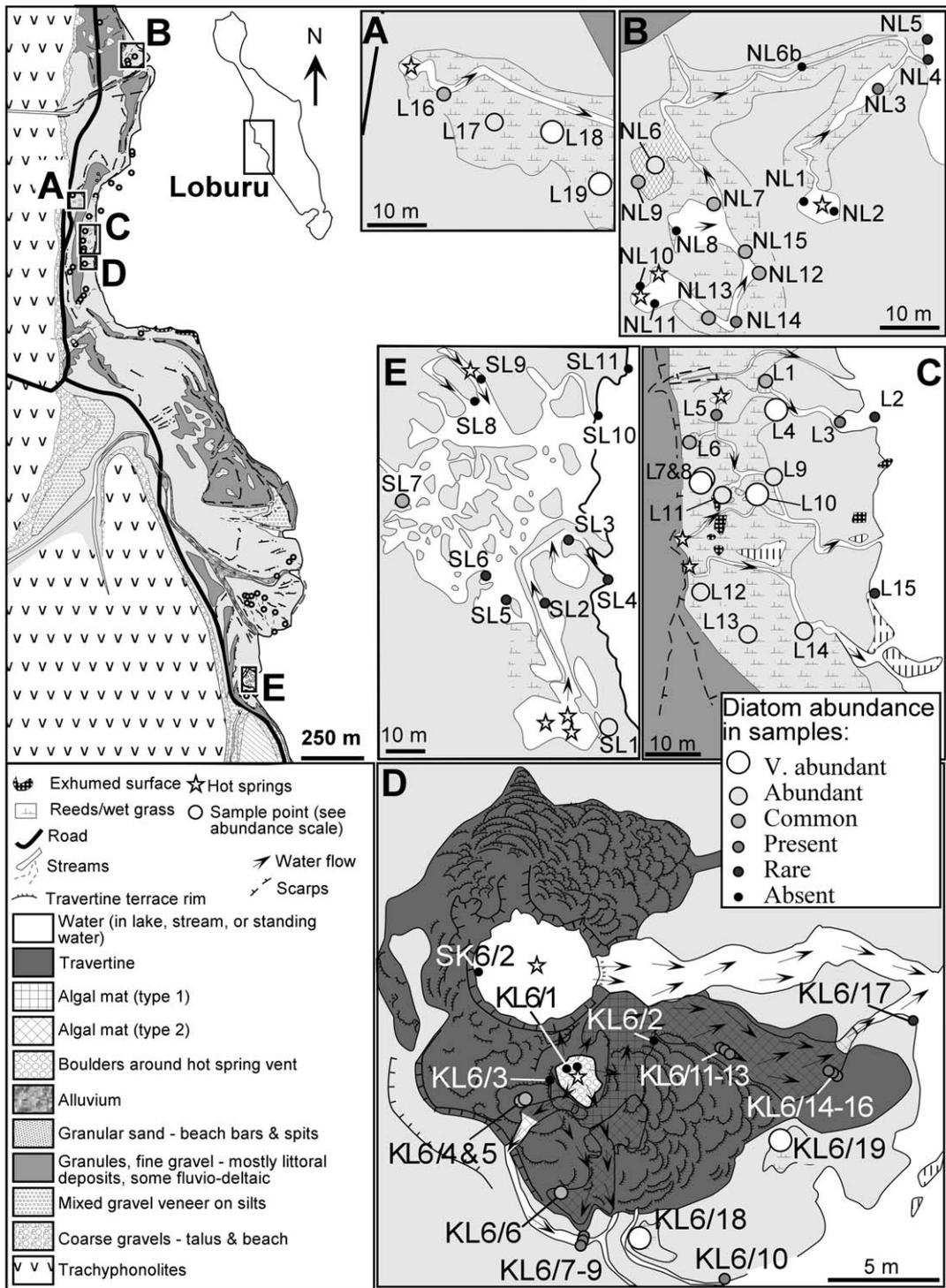


Figure 3. Location map and sediment types on the Loburu Delta. Details of sample locations and sampling numbers are shown together with abundance data in insets. (A–D) include areas of Type 1A (Proximal Hot Springs) and Type 1B (Hot Spring Marshes) wetlands. (E) shows a Type 5 (Hypersaline Lake Littoral) wetland.

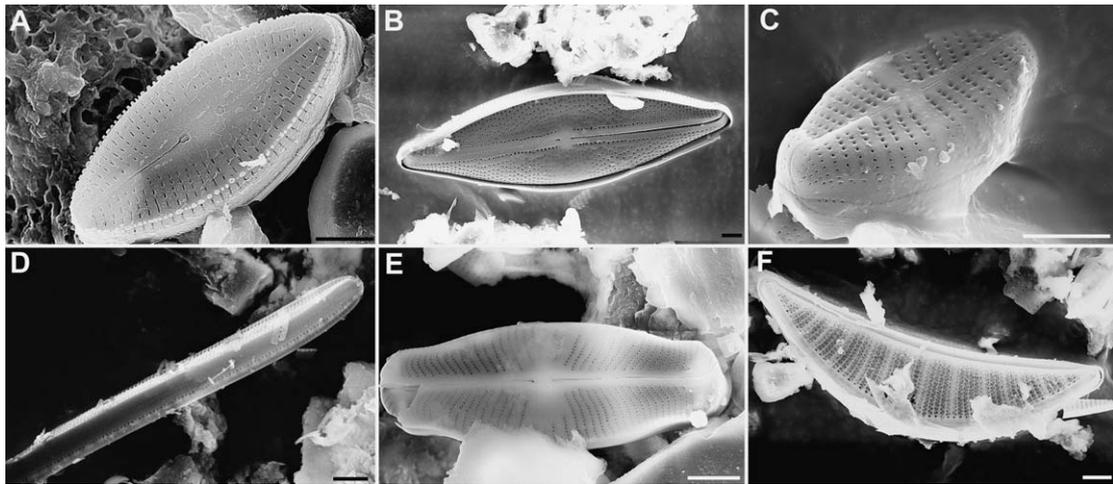


Plate 2. Common diatoms in the Bogoria-Baringo wetlands. A: *Navicula confervacea*; B: *Anomoeoneis sphaerophora*; C: *Achnanthes exigua*; D: *Nitzschia sigma*; E: *Navicula pupula*; F: *Rhopalodia gibberula*. Scale bar = 3  $\mu\text{m}$ .

(ca. 2 cm) standing water, with temperatures ranging between 30–40 °C; Type 2 – Artesian Blister Wetlands that include a variety of settings on and downslope of cool springs (30–33 °C). These areas are characterized by short (mostly <10 cm) graminoids, *Cyperus laevigatus*, and sedges on circular blister mounds (15 m diameter, 1–2 m high). Small areas of *Typha* and wet meadows tend to occur downslope of some of these mounds, and below other water seeps; Type 3 – *Typha* and *Cyperus* Swamps that are fed by various combinations of surface streams, groundwater seeps, or warm springs. These are dominated by tall (>2 m) *Typha domingensis*, where standing water is shallow and ephemeral, or by floating *Cyperus papyrus*, where permanent water (25–30 °C) occurs in broad depressions; Type 4 – Floodplain Marshes characterized by short grasses on floodplains that are seasonally flooded. Type 5 – Hypersaline Lake Littoral Wetlands. These occur along the margins of Lake Bogoria (pH ~ 10, alkalinity ca. 1000 meq l<sup>-1</sup>) and consist of flooded (<10 cm), gently sloping, siliciclastic delta margins, often modified by flamingo nesting. In some cases, hot springs also feed into these sites. Macrophytes are lacking. Cyanobacteria (mainly *Spirulina platensis* Norstedt) dominate, with scarce diatoms also occurring. Type 6 – Freshwater Lake Littoral Wetlands. These form narrow to extensive fringes around the relatively fresh water Lake Baringo (pH ~8.9, alkalinity ca. 13 meq l<sup>-1</sup>), and are dominated by a diverse range of wetland vegetation.

This study focuses on diatom variability and species patterns in wetlands (Types 1–5) to the north and

west of Lake Bogoria, and attempts to link wetland types with specific water chemistry to diatom assemblage composition and abundance. Data are based on samples from four main locations: 1. the relatively large and perennial Lobo Swamp (Type 3); 2. the relatively large and ephemeral Kesubo Floodplain Marshes (Type 4); 3. a series of small wetlands (Types 1A, 1B, 5) on the Loburu Delta, and 4. a series of wetlands (Types 2 and 3) near the Lake Bogoria National Reserve entrance, and referred to as the ‘Campground Wetlands’.

#### Site descriptions

The Lobo Swamp lies along the base of a north-south trending horst block (Plate 1F). Radiocarbon data suggest that it developed only 700 years ago from a former floodplain environment, perhaps as a result of faulting (Ashley et al., in review). In 1969, the swamp extended 6 km in a north-south direction (Fig. 1), but by 2001, as a result of water diversion, this had been reduced to 3.5 km, with a width of about 0.5 km. The swamp is fed by at least three warm springs and by groundwater inputs. The Lobo River also contributes to the hydrology, but is subject to periodic avulsion events that change its relative role in the development of the swamp. The river is cool, slightly alkaline and has a low total alkalinity (e.g. sample G02/15, Table 1). The springs have similar chemistry, but are warmer, have higher nitrate content, and are slightly acidic (G02/22, Table 1). Lobo Swamp waters are

also slightly alkaline, and generally reflect the mixing of fluvial, spring and groundwater inflows (L1, L3, L6, Table 1). *Typha domingensis* dominates in areas of semi-permanent or seasonal standing water (Plate 1G), with *Leersia hexandra* Sw., *Ipomoea aquatica* Forsk., and other taxa also being present. This *Typha*-zone forms an outer fringe (Plate 1F) that surrounds a central wetter area characterized by near pure stands of *Cyperus papyrus* that is rooted or floating in water up to 1.5 m deep. Acacia scrub occurs on an adjacent horst block to the west, with grasses such as *Sporobolus spicatus* (Vahl) Kunth. on adjacent plains.

The Kesubo Floodplain Marshes lie to the east of the Lobo Swamp (Fig. 1) and rest on the southern part of an extensive alluvial fan formed by the Sandai River (Plate 1I, J), which flows into the northern end of Lake Bogoria and is its main influent (Renaut & Tiercelin, 1994). The Sandai River lies close to the watershed between Lakes Bogoria and Baringo, and in the past has flowed northwards into Baringo. The Kesubo Floodplain Marshes are seasonally flooded and lie between the rift valley boundary faults, to the east, and a small horst block, to the west. The river waters are slightly alkaline, cool, and have a low total alkalinity (WS02-SR-1, Table 1). The marshes are similar in their general water chemistry, but are slightly acidic and have a distinctly lower NO<sub>3</sub> content. Short grasses are the dominant vegetation type and cattle graze the area.

The Campground Wetlands lie near the Lake Bogoria National Reserve entrance, to the south of the Lobo Swamp (Fig. 2), and are developed on the boundary between faulted volcanic uplands and colluvial-alluvial sediments. They have been characterized as an 'Artesian Blister Wetland' by Ashley et al. (2002), and contain a variety of habitats. These areas are named after cool artesian springs that emerge at the surface and support an arched semi-permeable cap of short graminoids such as *Pycreus mundtii* Nees, *Leersia hexandra* and *Cyperus laevigatus*. The edges of these 'blister mounds' are dominated by *Leersia hexandra* mixed with other grasses and sedges. Areas distal to the springs contain *Sporobolus spicatus*. Cyanobacterial and algal mats occur interspersed with the graminoid vegetation. Water from the blister mounds, and other seeps and springs, support wet meadows and *Typha* swamps (Plate 1H). The blister mounds and *Typha* swamps (C6 and C2, Table 1) show water chemistries with circum-neutral pH, low conductivities and total alkalinity. Slightly acidic, nitrate enriched, warm springs (C4, Table 1) are also present.

The Loburu Delta lies on the western shore of Lake Bogoria and is composed of silts and gravels formed in a variety of fluvial, deltaic, and beach settings (Fig. 3, Plate 1A). The delta is also characterized by active hot springs that feed into a series of marshes dominated by *Cyperus laevigatus* (Plate 1B–E). The springs are alkaline, of the Na-HCO<sub>3</sub> type, contain high silica and nitrate, and are extremely hot (>96 °C) close to the vents (e.g., NL10, KL6/1, Table 1). The areas immediately adjacent to the vents and in nearby streamlets are devoid of macrophytes, though microbial mats composed of *Phormidium*, *Pseudanabaena*, *Spirulina*, *Synechococcus* and *Calothrix* are common. Short reeds (<20 cm) dominate the *Cyperus* marshes, which have similar water chemistries. Temperatures vary, ranging upwards from about 32 °C to about 60 °C at hot spring streamlets that cross the marshes. Algal and cyanobacterial mats are also present in these areas. The Lake Bogoria shoreline at Loburu (and other shorelines) lacks extensive development of aquatic macrophytes (Plate 1K, L). The lake brine is of Na-CO<sub>3</sub>-HCO<sub>3</sub>-Cl composition and has a pH range of 9.3–10.6 (Renaut & Tiercelin, 1994). Salinities exceeding 100 g l<sup>-1</sup> occur in shallow marginal lagoons. A typical analysis (L02/2) for part of the Loburu shoreline is given in Table 1. Temperature at the time of sampling ranged between 28 and 33 °C, but exceed 60 °C at sublacustrine hot spring vents. However, cyanobacteria (mainly *Spirulina platensis*) are abundant and support up to 2 million flamingoes.

Other supplementary sampling sites were also examined for their diatom floras. These include the littoral zone of the, comparatively, freshwater (Table 1) Lake Baringo, at Kokwob Murren and near the Lake Breeze Hotel (Fig. 1C; Plate 1M, N), the hot springs of Soro on Ot Kokwe Center Island (Fig. 1C), samples from the Lobo and Molo Rivers, and hot and warm springs from the Mwanasis and Fig Tree sites near the southern shores of Lake Bogoria (Fig. 1C).

### Sampling methods and data analysis

A total of 145 samples, containing 160 diatom taxa, were collected from a variety of wetland habitats in the Bogoria and Baringo rift basins (Fig. 1C). These consist mostly of surficial sediment, supplemented by rock scrapings and vegetation samples. Collections were made in June 2001 and 2002. Smear slides were prepared for each sample using naphrax. Diatoms were identified to species level using light microscopy

Table 1. Representative chemical analyses for wetlands in the Lake Bogoria-Baringo Basin. Sample number locations are given in Figs 1, 2, and 3.

Sample type	Sample no.	Temp. (°C)	pH	Cond. (mS cm <sup>-1</sup> )	Ca (mg l <sup>-1</sup> )	Na (mg l <sup>-1</sup> )	K (mg l <sup>-1</sup> )	Si (mg l <sup>-1</sup> )	Fe (mg l <sup>-1</sup> )	F (mg l <sup>-1</sup> )	Cl (mg l <sup>-1</sup> )	NO <sub>3</sub> (mg l <sup>-1</sup> )	SO <sub>4</sub> (mg l <sup>-1</sup> )	Total alk (meq l <sup>-1</sup> )
Lake Baringo	KM1	27.6	8.9	1.67	8.46	376	36.55	10.35	0.63	11.50	118.50	14.50	63.50	13.00
Lake Bogoria	L0 LO2/2	30.9	10.0	19.50	1.05	27033	471.50	123.70	0.45	1246.00	6105.00	20.00	210.00	1011
Loboi River	G02/15	23.2	8.3	0.56	13.48	116	12.95	31.98	0.11	4.57	9.64	4.16	11.96	5.99
Typha swamp	L1	21.3	6.7	0.78	20.81	181	13.67	26.34	2.27	6.61	3.86	0.14	1.12	9.35
Papyrus swamp	L3	27.3	7.2	0.63	7.33	136	17.51	40.70	0.12	3.90	9.70	0.90	9.70	6.28
Loboi water ditch	L6	22.6	7.1	0.59	7.98	127	14.72	34.82	0.41	4.92	8.69	0.22	2.02	6.73
Sandai River	WS02-SR-1	21.8	8.0	0.24	9.06	32	8.82	16.76	0.05	0.60	12.5	1.00	5.80	1.85
Kesubo Marsh,	KIS 1	23.1	6.5	0.15	5.80	23	9.04	13.50	0.50	0.57	11.03	0.17	10.85	1.03
Typha Swamp	C2	24.2	7.1	0.67	5.96	140	13.10	42.06	0.24	6.21	10.33	0.12	8.10	6.79
Blister Bog	C6	23.7	6.8	0.74	7.22	140	13.64	34.04	0.05	5.83	10.59	0.11	6.10	7.33
Warm Spring	G02/22	36.7	6.4	0.52	6.61	108	11.50	38.54	0.12	4.19	8.92	7.53	11.07	5.41
Warm Spring	C4	33.4	6.6	0.57	5.99	127	12.46	39.98	0.15	5.25	9.33	6.19	11.38	5.97
Hot Spring	NL10	99.0	7.6	6.09	0.74	1200	40.69	41.20	b.d.l.	58.50	213.00	23.50	80.50	47.78
Hot Spring	KL6/1	96.0	8.3	6.53	1.11	1276	23.97	40.29	0.01	60.50	213.50	18.00	80.00	50.01

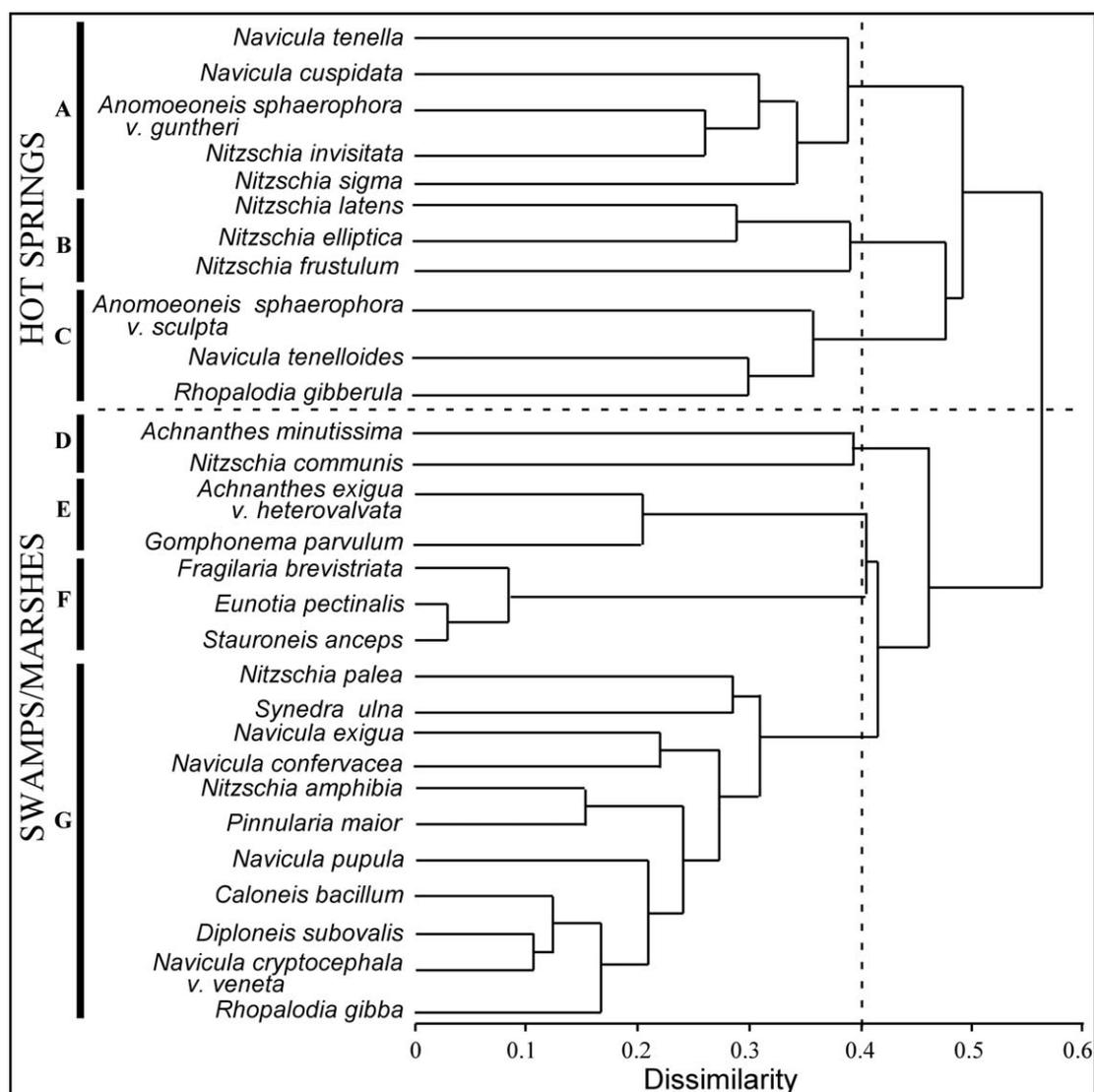


Figure 4. Cluster dendrogram of diatom species in wetlands of the Bogoria-Baringo Basin, constructed using Pearson dissimilarity and aggregation by unweighted pair-group averaging.

with phase contrast, and the taxonomic works of Gasse (1986a), Hustedt (1927–1930), Krammer & Lange-Bertalot (1986–1991), Patrick & Reimer (1975), and Schoeman & Archibald (1976). A minimum of 400 diatoms were counted per smear slide, except where diatoms were rare, in which case all diatoms on a slide were counted. Some diatom identifications were confirmed using a Leo 1530 Field Emission Scanning Electron Microscope.

Water samples were collected from fluvial, spring, and swamp settings. Temperature, pH, and conductivity were measured with portable instruments, cal-

ibrated in the field. Aliquots of surface waters were filtered at the time of sampling. Cation aliquots were acidified with concentrated  $\text{HNO}_3$ . Total alkalinity measurements were carried out within 48 hours of collection by potentiometric titration. The Si analysis was carried out at the Lab of Dr. Anna M. Martini, Amherst College, MA by ICP-AES (Inductively Coupled Plasma-Atomic Emission Spectrometry) using a Leeman Labs Instrument. Nitrate was determined by IC (ion chromatography), using a DIONEX instrument. Other analyses will be published elsewhere.

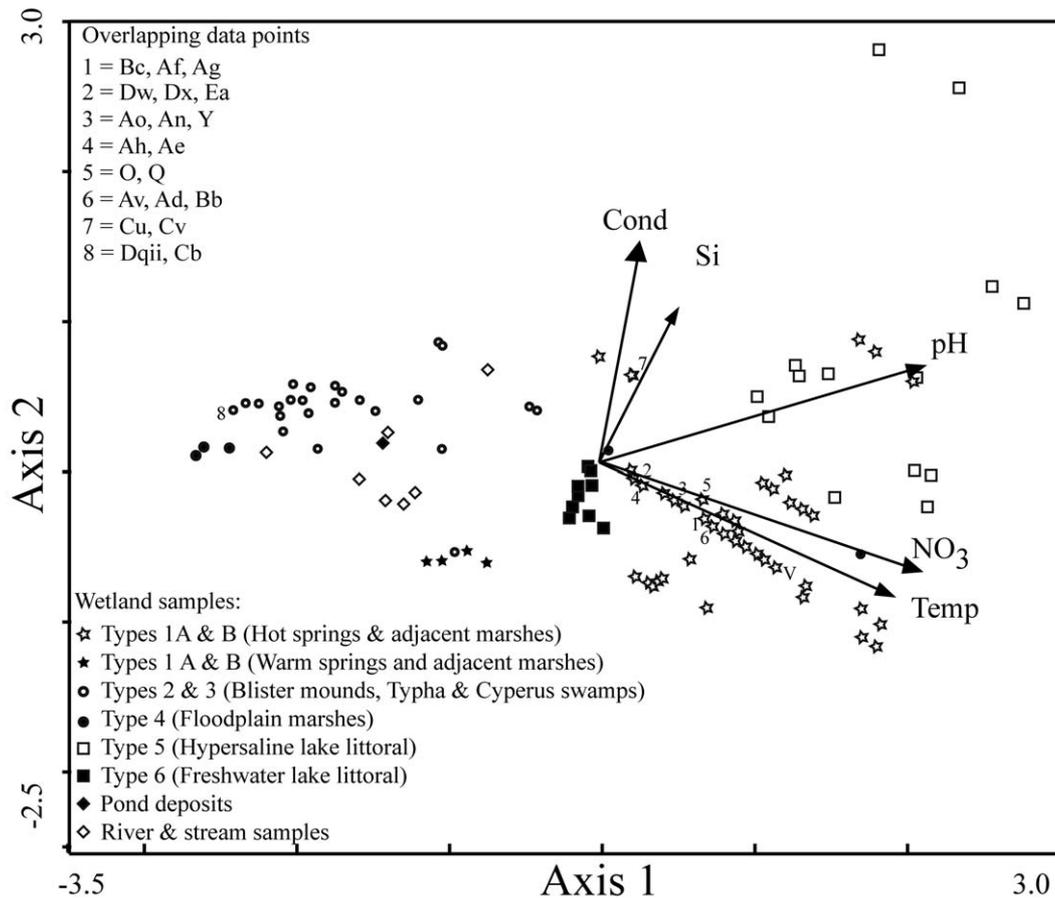


Figure 5. Canonical Correspondence Analysis of geochemical and temperature data from the Bogoria-Baringo wetlands with samples. The vectors for the geochemical data are shown (multiplied by 2) in relation to the first and second axes. Samples are classified according to wetland types discussed in the text. Overlapping data points are indicated by numbers, with original sample designations indicated.

Diatom assemblage patterns were examined using several approaches. Agglomerative Hierarchical Clustering (AHC) was carried out in order to group diatom taxa according to relative abundance data. Only diatoms that formed >5% of the flora in at least one sample, and which were present in at least five samples, were included. This yielded 29 diatoms for analysis. Several clustering models were tested, with good results being obtained for Pearson dissimilarity and aggregation by unweighted pair-group averaging.

Multivariate techniques were used to identify environmental parameters that were most strongly associated with species and sample distributions. Detrended Correspondence Analysis suggested that unimodal analyses were appropriate. Subsequently, the data were examined using Canonical Correspondence Analysis (CCA) (ter Braak, 1986). The axes in a CCA are linear combinations of environmental variables,

with the first axis representing the greatest proportion of variance in the distribution (Cooper et al., 1999). Ordinations were carried out using CANOCO 4.51. A broader diatom database was used than for the AHC analysis, with species that occurred in at least 3 samples at >1%, or in at least 1 sample at >4%, being included. This yielded 65 taxa for study. Inference models were also developed for pH, specific conductivity, nitrate, temperature, and Si, using weighted averaging. The strength of the different models was tested using the correlation between root mean square error (RMSE) and the RMSE associated with bootstrap analysis (Siver, 1999). These analyses were carried out using a data analysis program (C2, version 1.3), which was also used to generate stratigraphic transfer data for Cores LB1 and WB1 from the Lobo Swamp (Fig. 1) and the Campground Wetlands (Fig. 2), respectively.

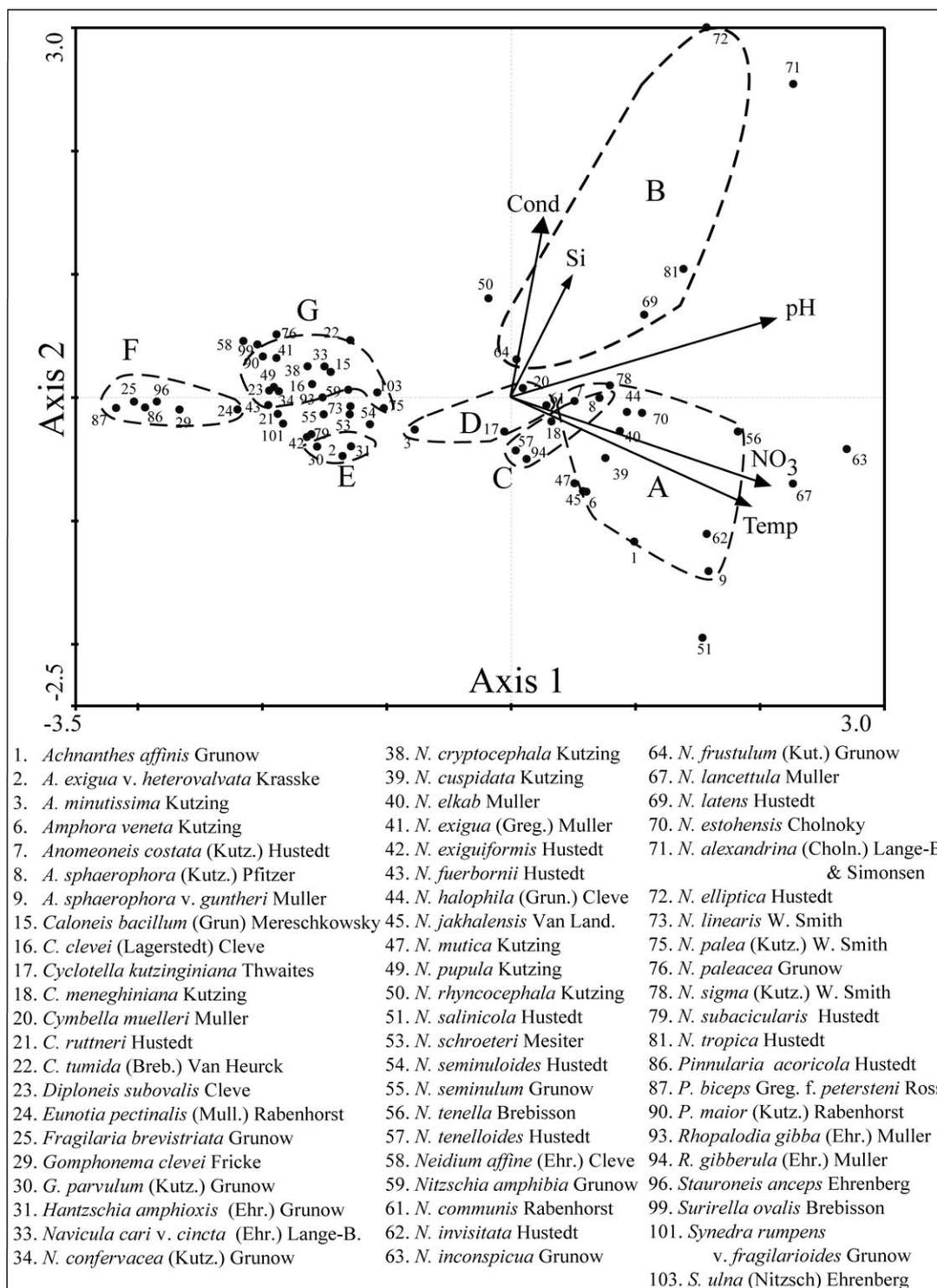


Figure 6. Canonical Correspondence Analysis of geochemical and temperature data from Bogoria-Baringo wetlands with diatom species. The vectors for the geochemical data are shown (multiplied by 2) in relation to the first and second axes. Numbers correspond with diatom names given below the CCA. Areas circled and labeled include taxa groups A–G, as distinguished by AHC in Fig. 4.

## Results

### *Diatom taxa*

A total of 160 diatom species and 26 genera were identified in the various wetland samples. The Shannon-Weaver diversity index for the diatom communities ranged from 0.06 to 2.75 with the lowest diversity occurring in Type 1A (hot spring) environments, in which diatom abundances ranged from absent to common. Diatom abundances (Figs 1B, 2 and 3), and diversity, were generally highest in Type 1B wetlands (hot spring marshes), followed by Type 2 and 3 wetlands, though with *Cyperus papyrus* Swamps showing very low abundance. Diatoms were common in Type 6 wetlands (Freshwater Lake Littoral), but rare in Type 5 (Hypersaline Lake Littoral).

Hill's N2 measure of diversity (Pielou, 1966), which is sensitive to the more common taxa in an assemblage, varied substantially between the wetland habitats. Diatoms were absent in Proximal Hot Springs with water temperatures >56 °C. However, in water where temperatures varied between 40–56 °C (Type 1A wetlands) N2 ranged between 1.17 and 3.98, averaging 2.13. Diatom abundances were low in these areas (Fig. 3). The adjacent hot spring marshes (Type 1B) show a greater diversity (average 5.67, range 2.2–13.2), and also some of the highest abundances recorded from any of the wetland systems. Types 2, 3 and 4 wetlands show similar average diversities, averaging N2 values of 5.8, 5.1 and 5.6, respectively. However, individual samples showed considerable variation (N2 = 1.1 to 10.1). Diatom abundances in these areas ranged from rare to common. Type 5 wetlands (Hypersaline Lake Littoral) showed a low diversity (2.18) and very low diatom abundance. Type 6 wetlands also showed relatively low diversity (2.5), but with diatoms being more common in samples.

Twenty diatoms exceeded 20% of the total flora in at least one sample, several of which are shown in Plate 2. These were: *Achnanthes affinis* Grunow, *A. exigua* var. *heterovalvata* Krasske, *A. minutissima* Kützing, *Anomoeoneis sphaerophora* var. *sculpta* (Ehr.) O. Müller, *A. sphaerophora* var. *guntheri* Müller, *Caloneis bacillum* (Grun.) Mereschkowsky, *Fragilaria brevistriata* Grunow, *Gomphonema parvulum* (Kütz.) Grunow, *Navicula cuspidata* Kützing, *N. exigua* (Gregory) O Müller, *N. pupula* Kützing, *N. tenella* Brébisson, *N. tenelloides* Hustedt, *Nitzschia communis* Rabenhorst, *N. elliptica* Hustedt, *N. in-visitata* Hustedt, *N. latens* Hustedt, *N. palea* (Kütz.)

W. Smith, *N. sigma* (Kütz.) W. Smith, and *Rhopalodia gibberula* (Ehr.) O. Müller. A further nine taxa exceeded 10%.

A cluster analysis for the 29 most common diatoms, based on dissimilarities between assemblages, is shown in Fig. 4. Two major clusters, diatom groups A–C and D–G, occur at the highest level of dissimilarity. These represent hot spring and swamp/marsh diatom communities. A useful clustering can also be recognized at the 0.4 dissimilarity level, and this has been used to distinguish each of the diatom groups shown in Fig. 4. Group 'A' diatoms are very closely associated with Type 1A wetlands (Proximal Hot Springs), which are areas of high water temperatures, typically 40–56 °C, above which diatoms are absent. These environments lack macrophytes, but frequently contain microbial mats. The diatom floras are usually sparse and typically of low diversity. *Nitzschia sigma* though placed in this cluster, shows a strong tendency to be found in Type 1B wetlands (Hot Spring Marshes), especially in areas close to hot spring streamlets. Diatoms belonging to cluster 'B' (Fig. 4) occur in both hot springs and in the littoral zone of Lake Bogoria. Cluster 'C' diatoms are present as common components in a wide range of habitats including Hot Spring Marshes, Type 3 (*Typha* Swamps) and Type 5 wetlands (Hypersaline Lake Littoral). *Navicula tenellodies* or *Rhopalodia gibberula* tend to occur more often in the Type 3 wetlands, whereas *Anomoeoneis sphaerophora* var. *sculpta* shows a stronger association with the Type 5 habitats.

Diatom groups D–E occur in swamps, marshes, and shallow ponds. Group 'D' is clustered at a relatively high node and could be split further. *Achnanthes minutissima* occurred with *Nitzschia communis* in Type 6 wetlands (Freshwater Lake Littoral), but also occurred in *Typha* Swamps where very few *N. communis* were present. Group 'E' diatoms were found mainly in shallow ponds surrounded by wet meadows and/or *Typha* Swamps. Group 'F' diatoms appear to be associated with Type 3 and Type 4 wetlands. *Fragilaria brevistriata*, *Eunotia pectinalis* (O. Müller) Rabenhorst, and *Stauroneis anceps* Ehrenberg were particularly closely associated with a variety of *Pinnularia* spp. on the Kesubo Floodplain Marsh. Group 'G' was mainly associated with Type 2 and 3 wetlands in a range of swamps, wet meadows, and blister mounds.

### Canonical correspondence analysis and inference models

Canonical correspondence analysis (CCA) was used to generate simultaneous ordinations of both samples (Fig. 5) and diatoms (Fig. 6) that were related to several environmental variables. The first two axes had eigenvalues of 4.45 and 2.45 and together accounted for 77.5% of the variance in the species-environment relationship. The species-environment correlations for CCA Axis 1 (0.89) and Axis 2 (0.78) are high and statistically significant ( $p = 0.01$ ). The results of the analysis suggest that Axis 1 is most closely related to temperature, nitrate, and pH and that the secondary axis is correlated with specific conductivity and to a lesser extent with Si.

Figure 5 clearly shows that different wetland environments plot in contrasting parts of the CCA, and that this probably reflects variations in temperature, nitrate, and pH gradients. Type 1A and 1B wetland samples (Proximal Hot and Warm Springs and Marshes) show a particularly strong relationship with the temperature and nitrate environmental variables, with Warm Springs in quadrant 4 and Hot Springs largely in quadrant 3. The Type 2 and 3 wetlands (Blister Mounds, *Typha* and *Cyperus* Swamps) occur along Axis 1 between scores of 0.5 and 2.5, within quadrant 1. Type 4 (Floodplain Marsh) is comprised of a restricted sample set that plots along Axis 1, with scores above 2.5. Type 5 wetlands (Hypersaline Lake Littoral areas) largely plot within the second quadrant. Type 6 wetlands (Freshwater Lake Littoral zones) form a tight grouping in the center of the CCA diagram. A number of small pond and river samples were also examined. These largely plot in quadrant 4, with Axis 1 values of 1.2 to 2.2.

As with samples, diatom species are well separated along axes 1 and 2, showing a close relationship with pH, nitrate and temperature (Fig. 6). The diatoms groups A–G are based on the 29 most common taxa recognized by cluster analysis. The CCA diagram shows data for 65 taxa. Diatoms belonging to Group A occur in quadrant 2, reflecting higher pH and temperatures than for other groups. Group B diatoms tend to follow the conductivity, Si, pH variables. The other diatom groups are closely aligned along Axis 1, with progressively more negative scores from Group D, through E & G, to Group F. This corresponds with a gradient towards lower pH and temperature.

Inference models for the environmental variables were also constructed. Simple weighted averaging

(WA), without tolerance downweighting, produced the best statistical data and the smallest differences between bootstrapped and non-bootstrapped (classical and inverse) methods. For example, pH models constructed with and without bootstrapping yielded  $r^2$  values ranging between 0.72 to 0.74, and 0.83 to 0.86, respectively. RMSE of prediction values ranged between 0.52 and 0.57 for bootstrapped models, and 0.34 to 0.37 for non-bootstrapped models. Fig. 7 shows the results for WA, without tolerance downweighting, for pH, specific conductivity, nitrate, and temperature. High  $r^2$  values were noted for pH (0.86) and specific conductivity (0.78), with lower values for nitrate (0.63) and temperature (0.60). Si produced the poorest correlation (0.49) and has not been included in Fig. 7.

## Discussion

### Wetland diatoms and indicator species

Many studies of East African diatoms have emphasized lakes. The wetland habitats near Lake Bogoria, with the exception of the papyrus sector of the Loboï Swamp, are comprised mainly of very shallow water (<5–10 cm) or damp ground. Consequently, planktonic taxa do not form a major part of the flora recognized in this study, with only a few examples occurring in Type 5 (e.g., *Cyclotella meneghiniana* Kützing, *Thalassiosira rudolfii* (Bachman) Hassle) and Type 6 (*Aulacoseira granulata* (Ehr.) Simonsen, *A. granulata* var. *angustissima* (O. Müll.) Simonsen, *A. ambigua* (Grun.) Simonsen) lake littoral habitats. Assemblages are dominated by benthic diatoms, and include epiphytic, epipsammic, epipellic, and epilithic forms. Macrovegetation, water chemistry, and substrate type are of major importance in determining the composition of the observed floras, with water depth playing a comparatively minor role in these shallow-water settings.

The diatom analyses demonstrate clear correlations between species abundances and pH, conductivity, nitrate, and temperature gradients. Several of the taxa have characteristics that may make them useful indicator species. This is possible where the environmental data include a broad range of conditions, and where three criteria are met (Cooper et al., 1999; Stevensen et al., 1991). Firstly, the species should show a strong relationship with an environmental variable. Secondly, the diatom has a narrow tolerance

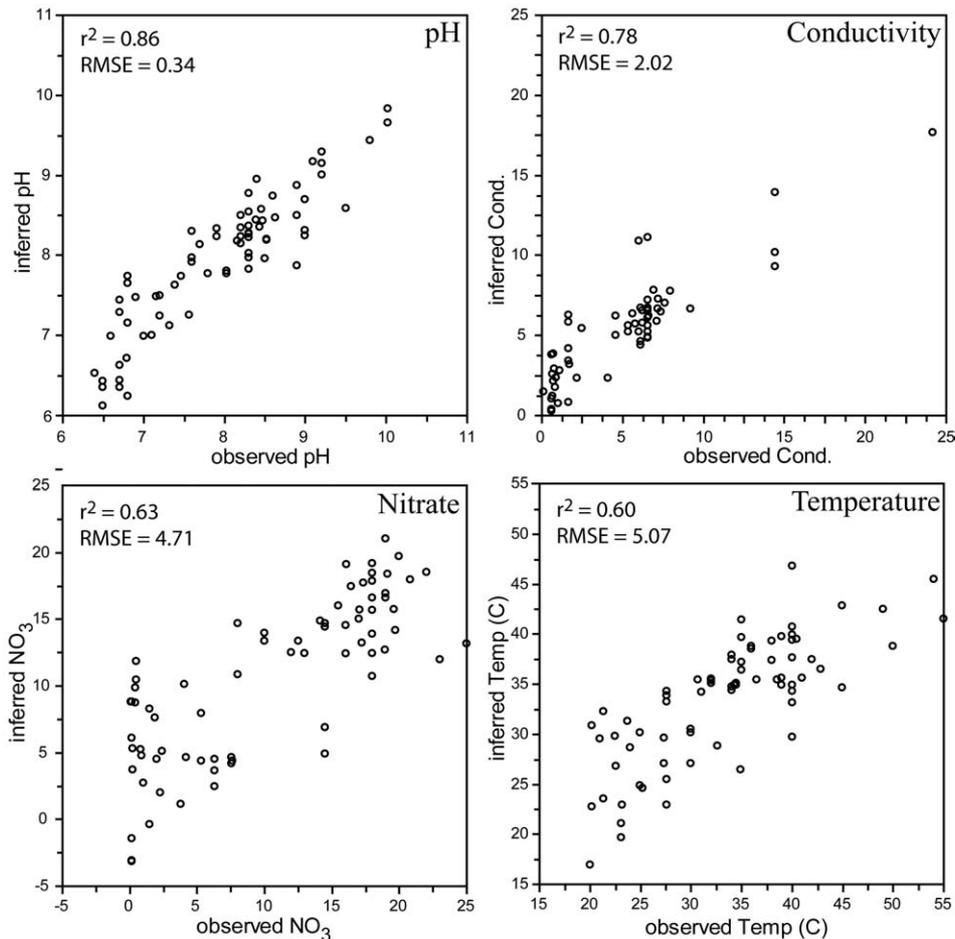


Figure 7. Weighted-averaging calibration models for the wetland sites. The relationships between measured and diatom-inferred values for pH, conductivity, nitrate, and temperature. The strength of the models are assessed by the correlation coefficient ( $r^2$ ) between the measured and inferred values and the root mean squared errors (RMSE) of prediction.

range around the optimum, and, finally, the diatom should be common in the sampling set. Table 2 is based on the inference models and shows the optima and tolerances for 29 common wetland diatoms, ranked by pH.

Diatoms with high WA optima for pH that might be useful indicator species of such conditions include: *Nitzschia elliptica*, *N. latens*, *N. invisitata*, *Anomooneis sphaerophora* var. *guntheri* and *Navicula tenella*. However, of these species, *A. sphaerophora* var. *guntheri*, *N. invisitata* and *N. tenella* show lower WA tolerances (Table 2), suggesting that these three diatoms may be more useful indicators for pH paleoenvironmental studies. The same five diatoms also show the highest conductivity optima, but with the tolerance levels being more variable. For example, *N. latens* shows a high value (Table 2), whereas *A.*

*sphaerophora* var. *guntheri* and *N. invisitata* exhibit low tolerances, suggesting that these are better indicators of conductivity. Similar observations can also be made for the nitrate and silica data (Table 2) with some species being potentially better indicators than others.

Figure 8 shows diatom stratigraphies for two piston cores from the wetlands. Core WB1 was collected from a blister mound at the Campground Wetlands site, near the Lake Bogoria National Reserve entrance (Fig. 2), and Core LB1 is from the Lobo Swamp (Fig. 1). Only diatoms forming >5% in at least one interval are shown. Diatoms occur throughout WB1, but appear suddenly above a floodplain deposit in LB1. Transfer functions were used to model pH, conductivity and temperature, which are all broadly stable through the diatomaceous parts of these cores, though with a slight increase suggested for conduct-

Table 2. Environmental optima and tolerances for common wetland diatoms based on a weighted averaging model. Diatom taxa are arranged according to their pH optima.

	pH opt.	pH. toler.	Cond. opt.	Cond. toler.	NO <sub>3</sub> opt.	NO <sub>3</sub> toler.	Temp. opt.	Temp. toler.
<i>Nitzschia elliptica</i> Hustedt	9.52	0.87	5.94	3.29	12.26	4.19	37.61	6.11
<i>Navicula tenella</i> Brébisson	8.92	0.57	11.25	4.64	18.23	2.81	43.14	8.60
<i>Nitzschia latens</i> Hustedt	8.67	0.82	6.35	5.62	14.21	6.05	32.96	5.88
<i>Anomoeoneis sphaerophora</i> v. <i>guntheri</i> O. Müller	8.50	0.40	6.59	0.09	18.00	4.63	43.19	7.84
<i>Nitzschia invisitata</i> Hustedt	8.46	0.48	6.45	0.92	17.44	3.03	43.17	8.42
<i>Navicula cuspidata</i> Kützing	8.20	0.55	6.05	1.88	16.60	5.20	37.94	5.94
<i>Nitzschia communis</i> Rabenhorst	8.17	0.55	4.11	2.46	9.37	8.07	37.42	7.96
<i>Navicula tenelloides</i> Hustedt	8.13	0.77	4.15	3.03	13.76	7.68	33.72	8.01
<i>Anomoeoneis sphaerophora</i> v. <i>sculpta</i> (Ehr.) O. Müller	8.11	0.59	5.22	3.20	11.45	8.82	34.90	5.93
<i>Nitzschia sigma</i> (Kütz.) W. Smith	8.11	0.35	6.00	0.80	12.46	4.59	35.00	6.26
<i>Nitzschia palea</i> (Kütz.) W. Smith	7.88	0.84	1.10	0.74	6.43	5.72	26.14	4.80
<i>Rhopalodia gibberula</i> (Ehr.) O. Müller	7.59	0.74	3.87	2.95	9.90	8.52	33.31	9.58
<i>Nitzschia frustulum</i> (Kützing) Grunow	7.58	1.05	2.65	4.61	5.79	7.82	30.08	8.30
<i>Achnanthes minutissima</i> Kützing	7.51	0.68	1.12	0.65	4.32	2.59	25.69	7.96
<i>Caloneis bacillum</i> (Grun.) Mereschkowsky	7.29	0.85	2.11	5.03	4.46	5.71	29.15	8.01
<i>Nitzschia amphibia</i> Grunow	7.21	0.50	0.92	1.04	1.86	3.35	24.75	3.84
<i>Navicula cryptocephala</i> v. <i>veneta</i> Kützing	7.17	0.61	2.05	2.58	7.95	8.90	33.81	10.16
<i>Rhopalodia gibba</i> (Ehr.) O. Müller	7.14	0.63	1.61	2.36	5.23	6.87	28.90	7.77
<i>Achnanthes affinis</i> Grunow	6.95	0.22	0.67	0.14	0.45	0.58	24.49	3.08
<i>Pinnularia maior</i> (Kützing) Rabenhorst	6.95	0.26	0.59	0.23	1.91	2.69	28.04	5.56
<i>Synedra ulna</i> (Nitzsch) Ehrenberg	6.95	0.62	0.91	2.05	2.10	5.54	25.87	5.48
<i>Diploneis subovalis</i> Cleve	6.89	0.30	0.62	0.32	2.99	3.35	29.55	8.58
<i>Navicula pupula</i> Kützing	6.84	0.24	0.57	0.14	4.18	2.92	29.11	4.70
<i>Navicula exigua</i> (Gregory) O Müller	6.80	0.28	0.70	0.16	1.68	2.78	26.71	8.28
<i>Eunotia pectinalis</i> (O. Müller) Rabenhorst	6.76	0.37	0.39	0.87	1.00	2.86	24.69	4.16
<i>Gomphonema parvulum</i> (Kütz.) Grunow	6.74	0.38	0.61	0.75	4.91	3.52	33.62	6.48
<i>Achnanthes exigua</i> v. <i>heterovalvata</i> Krasske	6.73	0.48	0.89	1.47	6.74	3.06	35.94	6.07
<i>Stauroneis anceps</i> Ehrenberg	6.70	0.25	0.15	0.01	0.29	0.69	23.61	2.92
<i>Fragilaria brevistriata</i> Grunow	6.58	0.20	0.16	0.10	0.19	0.25	23.10	0.43

ivity. It would appear that once wetland conditions were initiated they remained broadly stable in terms of these parameters. Variability in individual diatom contributions does exist, but probably reflects factors such as the speed of water flow through the swamps, macrophyte type and density that were not modeled.

#### Wetland sedimentation

The geomorphic setting of the wetland types noted in this study are shown in Fig. 9, together with data on diatom diversity and abundance, species characteristics, and tectonic setting. The wetlands display a variety of sedimentologic, geometric, and location characteristics that reflect their origins and the processes involved in their formation. Types 1A and 1B

are essentially contrasting parts of one wetland system, with both depending on a source of hot spring waters. Cioni et al. (1992) suggested that heated meteoric groundwater that has seeped down faults and mixed with a small percentage of Lake Bogoria waters might be the major source for the hot springs. This is returned from depth along fault lines giving rise to an overall linear distribution of Type 1A and 1B wetland habitats, which in detail are derived from point sources. Deposits that have accumulated, or which are actively forming, in Type 1A areas include travertine, and to a lesser extent siliceous sinter and diatom remains (Jones & Renant, 1995, 1997). Diatomaceous, organic-rich, clays and silts dominate in Type 1B locations. At Loburu (Fig. 2), the wetland sedimentary

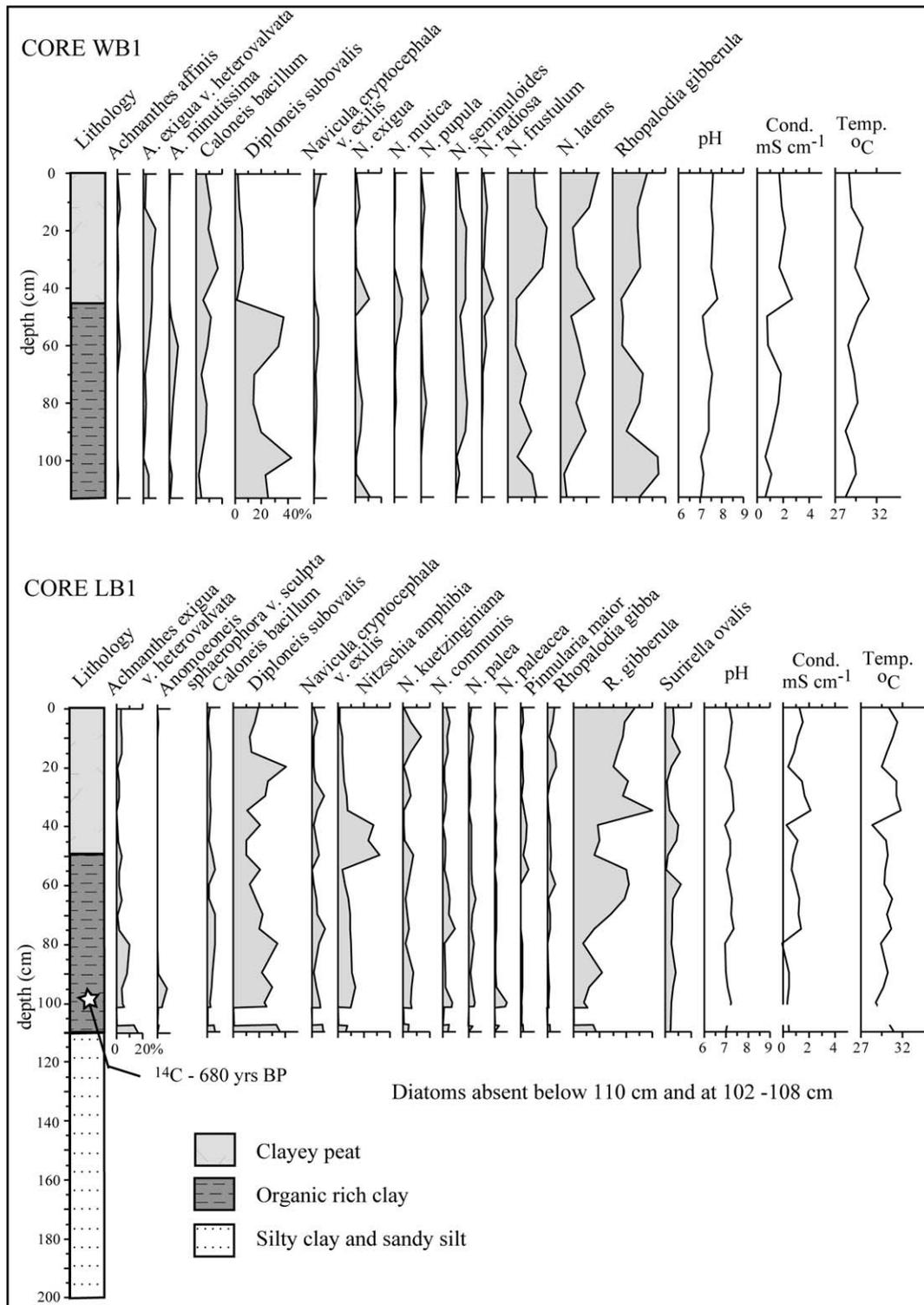


Figure 8. Diatom stratigraphies of Cores WB1 (Campground Wetlands, Fig. 2 for location) and LB1 (Loboi swamp, Fig. 1 for location). Only diatoms forming >5% in at least one sample are shown. Parameters to the right are based on inference models and suggest broad stability of the wetlands in terms of these parameters.

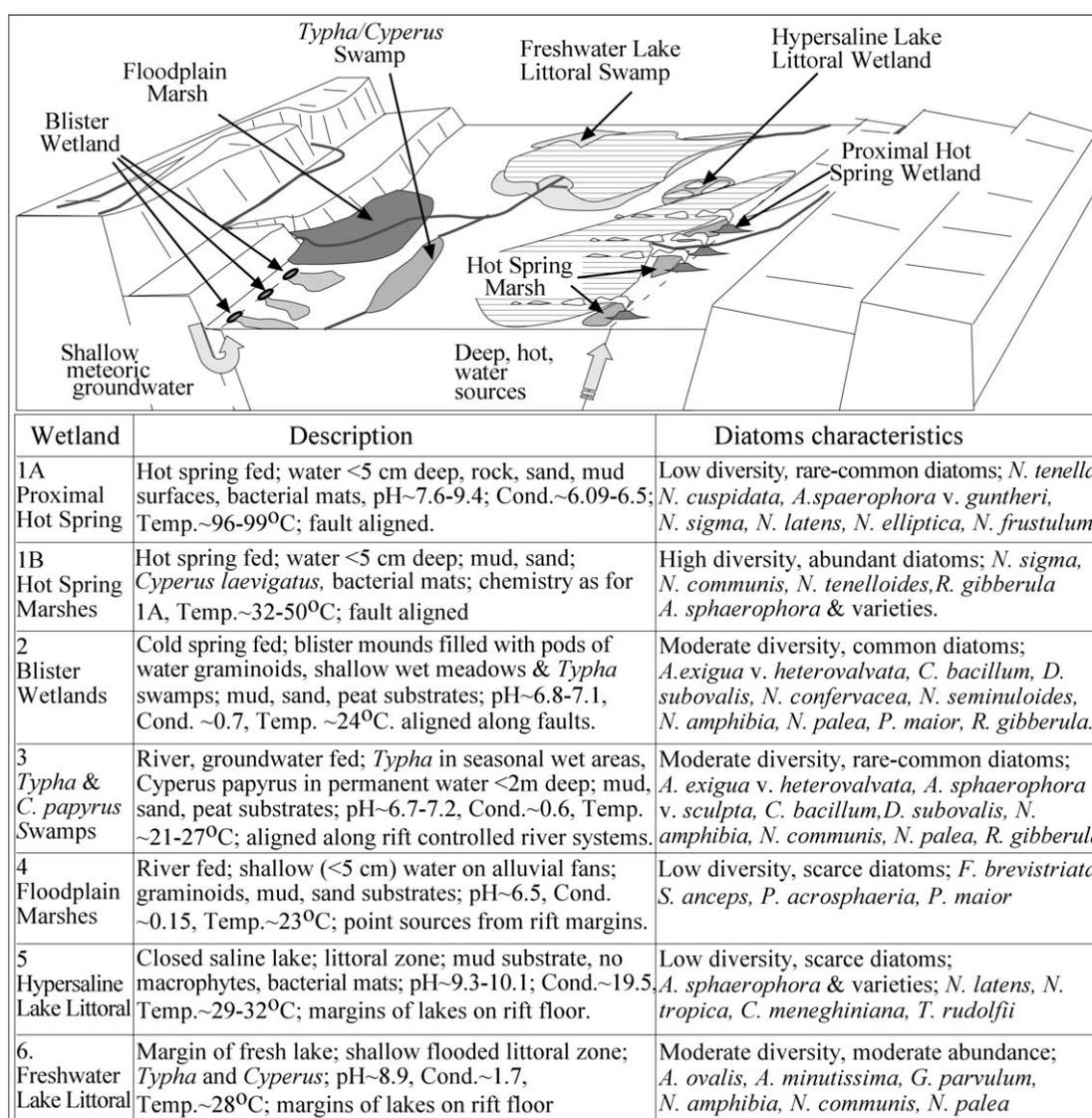


Figure 9. Geomorphic model showing the location and characteristics of the six major wetland types. Summary data for each wetland are given below the model. See text for discussion.

sequences are thin (mostly <50 cm), which may reflect a balance between sediment accumulation during low lake levels, and erosion by wave action during high lake level stages. These wetter periods have been linked to El Niño events by Johansson & Svensson (2002) and LaVigne & Ashley (2002).

Cool springs and seeps generally feed Type 2 Artesian Blister Wetlands. Sediments are comprised of organic-rich clays and silts, and peat formed in a complex mix of blister mounds (Ashley et al., 2002), swamps comprised of *Typha*, wet meadows, streamlets, and small ponds. Wetland sediments appear to

vary in thickness from 0 to about 1 m, reflecting the local setting. Core WB1, for example, is from a blister mound and is 115 cm long, with a gradual transition from inorganic silts to diatomaceous, organic-rich, clayey peat at about 45 cm. A sediment section examined at the site of Pit 1 (Fig. 3) was comprised of about 1 m of blocky silty clays, underlying a swamp dominated by *Typha*. Type 2 wetlands also appear to be fault controlled with linear alignments (Fig. 2, inset; Fig. 9). The cold springs and seeps are probably fed by shallow meteoric water, rather than the deep

re-circulated waters associated with Type 1A wetlands (Ashley et al., 2002).

Type 3 wetlands are comprised of *Typha* and *Cyperus* Swamps. These are predominantly fed by river systems, with spring seeps and groundwater inputs varying in their contributions. The Loboï Swamp belongs to this category and was examined at seven piston core locations. The basal deposits consist of floodplain silts and sands. In Core LB1 (Figs 1, 8), these give way to wetland sediments, comprised of organic-rich clay and peat, at a sharp boundary at 110 cm. The wetland units thin northwards, towards Core LB2 (Fig. 1), which consists mostly of floodplain silts and sands lacking in diatoms, overlain by only 20 cm of diatomaceous peaty wetland deposits. The sharp boundary suggests a rapid change, which may reflect a strong tectonic influence on the initiation of this swamp, perhaps by changing river flow patterns or by altering groundwater discharges. The distribution of these swamps reflects river patterns on the axial parts of the rift valley, with fault-controlled springs making local additional water contributions to areas such as the Loboï Swamp. In this latter case, part of the swamp is aligned parallel to a fault-controlled horst.

Type 4 wetlands were examined at the Kesubo Marshes. These rest on a gently sloping, poorly drained, alluvial fan of the Sandai River. Flooding of this surface is ephemeral and the sediments are comprised of clayey, lithic, silts and sands altered by pedogenesis, overlain by an organic rich surface horizon (up to 10 cm) that supports a graminoid vegetation. These pedogenically altered (Driese et al., in review) fluvial sediments show little direct indication of a wetland environment, other than a sparse diatom flora, and would be difficult to recognize as such in the fossil record. The geometry of the wetland resembles that of the alluvial fan, being broadly circular. Its location is closely associated with the rift border fault from which the Sandai River issues.

Type 5 and 6 wetlands are essentially similar in being the littoral fringes of lake systems and occur as linear belts at relatively low elevations on the axial rift floor. The sediments are dominated by silt or gravel, with varying organic contributions (Fig. 9). Saline-alkaline Lake Bogoria lacks macrophytes, but is dominated by cyanobacteria, and is characterized by scarce diatoms. In contrast, the Lake Baringo wetlands include a wide range of macrophytes, with diatoms being moderately abundant and of low diversity.

## Concluding remarks

The wetlands of the Bogoria-Baringo area are developed in a semi-arid rift setting. Several types can be recognized that reflect variability in terms of their water chemistry, macro- and micro-floral composition, and geomorphic setting. Although climate change must exert an influence on these wetlands, faulting and its effects on groundwater movements and river systems is of major importance. Water chemistry, for example, is influenced by the depth reached (fault-controlled) by meteoric water sources, which also controls the development of cool, warm and hot springs. Many wetland types show strong alignments parallel to fault lines.

Wetland sediment preservation potential appears to vary with geomorphic setting, being low, for example, in areas subject to periodic lake flooding and wave action. Wetland sequences that were sampled were thickest in association with rift-axial river systems ponded against horst blocks. Sediment compositions vary from site to site, reflecting fluvial, lacustrine and colluvial contributions and perhaps an aeolian element as well. In some cases (e.g., Kesubo), there is a pedogenic overprint reflecting periods of desiccation, with sediment brecciation. Organic-rich sedimentation appears to be a common feature of the wetlands, but this varies in its nature (bacterial mats, macrophytes and diatoms).

The diatom floras are varied in terms of composition, diversity, and abundance, and show clear differences between contrasting wetland types (Fig. 9). A number of habitat and geochemical variables influence the floras. Among the geochemical parameters examined, pH, conductivity, and nitrate appear to be particularly closely related to diatom development, as was water temperature. Some species show good potential as indicators of habitat, pH, conductivity, and temperature.

In recent years, the Bogoria and Baringo wetlands have been subject to increasing human impacts. The Loboï Swamp has been reduced in size by about 70% as a result of irrigation. The Kesubo Marshes have also been affected by irrigation. Tourism has impacted on several of the hot spring sites. These wetlands represent a model for the variability of contemporary semi-arid rifts that may be of use in paleoenvironmental studies. However, they may not remain such ideal analogues if human activities continue to degrade them further.

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## References

- Ashley, G. M., M. Goman, V. C. Hover, A. M. Muasya, R. B. Owen & R. W. Renault, 2002. Artesian blister wetlands, a perennial water resource in the semi-arid rift valley of East Africa. *Wetlands* 22: 686–695.
- Ashley, G. M., M. Maitima Mworira, A. M. Muasya, R. B. Owen, S. G. Driese, V. C. Hover, R. W. Renault, M. F. Goman, S. Mathai & S. H. Blatt, in review. Evolution of a freshwater wetland in a semi-arid environment, Lobo Marsh, Kenya, East Africa. *Sedimentology*.
- Barker, P., F. Gasse, N. Roberts & M. Taieb, 1990. Taphonomy and diagenesis in diatom assemblages: a Late Pleistocene palaeoecological study from Lake Magadi, Kenya. *Hydrobiologia* 214: 267–272.
- Cholnoky, B. J., 1970. Bacillariophyceen den Bangweolosumpfen. *Exploration Hydrobiologique du Bassin du Lac Bangweolo et du Lualaba. Cercle Hydrobiologique de Bruxelles* 5: 1–71.
- Cioni, R., G. Fanelli, M. Guidi, J. K. Kinyariro & J. Marini, 1992. Lake Bogoria hot springs (Kenya): geochemical features and geothermal implications. *Journal of Volcanology and Geothermal Research* 50: 231–246.
- Cooper, S. R., J. Huvane, P. Vaithyanathan & C. J. Richardson, 1999. Calibration of diatoms along a nutrient gradient in Florida Everglades Water Conservation Area-2A, USA. *Journal of Paleolimnology* 22: 413–437.
- Cowardin, L. M., V. Carter, F. C. Golet & E. T. Laroe, 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Department of the Interior Fish and Wildlife Service, Report No. FWS/OBS-79/31. Washington, D.C.
- Driese, S. G., G. M. Ashley, Z. H. Li, V. C. Hover & R. B. Owen, in review. Micromorphology, geochemistry, and stable carbon isotopes of late Holocene wetland and floodplain soils, Lobo Plain, Kenya: wetland pedogenesis in a semi-arid setting. *Palaeogeography, Palaeoclimatology, Palaeoecology*.
- Gasse, F., 1986a. East African Diatoms. Taxonomy, Ecological Distribution. *Bibliotheca Diatomologica* 11, J. Cramer, Stuttgart, 202 pp.
- Gasse, F., 1986b. East African diatoms and water pH. In Smol, J. P., R. W. Battarbee, R. B. Davis & J. Merilainen (eds), *Diatoms and Lake Acidity*. Dr W. Junk Publishers, Dordrecht: 149–168.
- Gasse, F., 1987. Diatoms for reconstructing palaeoenvironments and palaeohydrology in tropical semi-arid zones, examples of some lakes from Niger since 12,000 BP. *Hydrobiologia* 154: 127–163.
- Gasse, F., S. Juggins & L. B. Khelifa, 1995. Diatom-based transfer functions for inferring past hydrochemical characteristics of African lakes. *Palaeogeography, Palaeoclimatology, Palaeoecology* 117: 31–54.
- Gasse, F., J. F. Talling & P. Kilham, 1983. Diatom assemblages in East Africa: classification, distribution and ecology. *Revue d'Hydrobiologie Tropicale* 16: 3–34.
- Gasse, F. & F. Tekaia, 1983. Transfer functions for estimating paleocological conditions (ph) from East African diatoms. *Hydrobiologia* 103: 85–90.
- Gasse, F., P. Barker, P. A. Gell, S. C. Fritz & F. Chalie, 1997. Diatom-inferred salinity in palaeolakes: an indirect tracer of climate change. *Quaternary Science Reviews* 16: 547–563.
- Haberyan, K., 1992. Algal communities near Cape MacLear, southern Lake Malawi. *Hydrobiologia* 215: 175–188.
- Hustedt, F., 1927–1930. *Die Kieselalgen Deutschlands, Osterreichs und der Schweiz, Band 7, Die Kieselalgen*. Akademische Verlagsgesellschaft.
- Johansson, J & J. Svensson, 2002. Land degradation in the semi-arid catchment of Lake Baringo, Kenya. Project Report No. B343, Earth Sciences Centre, Göteborg University, 79 pp.
- Jones, B. & R. W. Renault, 1995. Noncrystalline calcite dendrites from hot-spring deposits at Lake Bogoria, Kenya. *Journal of Sedimentary Research* 65: 154–169.
- Jones, B. & R. W. Renault, 1997. Controls on aragonite and calcite precipitation in hot spring travertines at Chemerkeu, Lake Bogoria, Kenya. *Canadian Journal Earth Sciences* 34: 801–818.
- Jones, B. & R. W. Renault, 1998. Origin of platy calcite crystals in hot-spring deposits in the Kenya Rift valley. *Journal of Sedimentary Research* 68: 913–927.
- Krammer, K. & H. Lange-Bertalot, 1986–1991. *Bacillariophyceae* (4 vols). In Ettl, H., H. Heynig & D. Mollenhauer (eds), *Susswasserflora von Mitteleuropa* 2/1–4. Gustav Fischer Verlag, Jena.
- LaVigne, M. & G. M. Ashley, 2002. *Climatology and Rainfall Patterns: Lake Bogoria National Reserve (1976–2001)*, Department of Geological Sciences, Rutgers University, Piscataway, NJ, U.S.A.
- Liutkus, C.M. & G.M. Ashley, 2003. Facies model of a semi-arid freshwater wetland, Olduvai Gorge, Tanzania. *Journal of Sedimentary Research* (in press).
- Owen, R. B., 2002. Sedimentological characteristics and origins of diatomaceous deposits in the East African Rift System. In Renault, R. W. & G. M. Ashley (eds), *Sedimentation in Continental Rifts*. SEPM Special Publication No. 73: 233–246.
- Owen, R. B. & R. Crossley, 1992. Spatial and temporal diatom variability in Lake Malawi and ecological implications. *Journal of Paleolimnology* 7: 55–71.
- Owen, R. B. & R. W. Renault, 2000. Spatial and temporal facies variations in the Pleistocene Olorgesailie Formation, southern Kenya Rift Valley. In Gierlowski-Kordesch E. H. & K. K. Kelts (eds), *Lake Basins through Space and Time*. American Association Petroleum Geologists: 553–559.

- Patrick, R. & C. W. Reimer, 1975. The Diatoms of the United States. Monographs of the Academy of Natural Sciences of Philadelphia 13, 213 pp.
- Pentecost A., R. G. Bailey, H. Busulwa & A. Williams, 1997. Epilithic diatom communities of the Bujuku-Mubuku River system, Rwenzori Mountains, Uganda. *Archiv fur Hydrobiologie* 139: 479–493.
- Pielou, E. C., 1966. The measurement of diversity in different types of biological collections. *Journal Theoretical Biology* 13: 131–144.
- Renaut, R. W. & B. Jones, 2000. Microbial precipitates around continental hot springs and geysers. In Riding, R. & S. Awramik (eds), *Microbial Sediments*. Springer-Verlag, Berlin: 187–195.
- Renaut, R. W. & J. J. Tiercelin, 1994. Lake Bogoria, Kenya Rift Valley – A sedimentological overview. In Renaut, R. W. & W. M. Last (eds), *Sedimentology and Geochemistry of Modern and Ancient Saline Lakes*. SEPM Special Publication 50: 101–123.
- Schoeman, F. R. & R. E. M. Archibald, 1976. The Diatom Flora of Southern Africa, CSIR Special Report 50, Pretoria.
- Siver, P. A., 1999. Development of paleolimnological inference models for pH, total nitrogen and specific conductivity based on planktonic diatoms. *Journal of Paleolimnology* 21: 45–59.
- Stevenson, A. C., S. Juggins, H. J. B. Birks, D. S. Anderson, N. J. Anderson, R. W. Battarbee, F. Berge, R. B. Davis, R. J. Flower, E. Y. Haworth, V. J. Jones, J. C. Kingston, A. M. Kreiser, J. M. Line, M. A. R. Munro & I. Renberg, 1991. The Surface Waters Acidification Project Palaeolimnology Programme: Modern Diatom/Lake-Water Chemistry Data-set. ENSIS Publishing, London, 86 pp.
- Tarnocai, C., 1980. Canadian wetland registry. In Rubec C. D. A. & F. C. Pollett (eds), *Proceedings of a Workshop on Canadian Wetlands*. Environment Canada, Ecological Land Classification Series 12, Ottawa, Ontario: 9–21.
- Thompson, K. & A. C. Hamilton, 1983. Peatlands and swamps of the African continent. In Gore, A. J. P. (ed.), *Ecosystems of the World, 4B, Mires: Swamp, Bog, Fen and Moor, Regional Studies*. Elsevier, Amsterdam: 331–373.
- ter Braak, C. J. F., 1986. Canonical correspondence analysis: a new eigenvector method for multivariate direct gradient analysis. *Ecology* 67: 1167–1179.
- Tiercelin, J. J. & A. Vincens (eds), 1987. *Le Demi-Graben de Baringo-Bogoria, Rift Gregory, Kenya, 30,000 and d'histoire hydrologique et sedimentaire*. Bulletin Centres Recherches Exploration-Production, Elf Aquitaine 11: 249–540.
- Vincens, A., 1986. Diagramme pollinique d'un sondage Pleistocene superieur-holocene du Lac Bogoria, Kenya. *Revue de Palaeobotanie et Palynologie* 47: 169–192.
- West, G. S. & F. L. S. West, 1896. Algae from Central Africa. *Journal of Botany British & Foreign* 34: 377–384.