Diatom assemblages in East Africa : classification, distribution and ecology

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ABSTRACT

Based on widespread sampling of diversified waterbodies from East Africa, relationships between the quantitative composition ofdiatom communities and some major environmental variables—concentrations and ratios of major ions, conductivity, pH, and temperature—were shown. Water balance, climate, and some other habitat characteristics (silica concentration, turbidity, water depth, and substratum) were also taken into account.

Diatom analyses were carried out on 210 samples containing a total of 579 taxa. The diatom results were treated by Factor Analysis of Correspondence in order to define the diatom assemblages. Seventeen assemblages, distributed in five major groups (I-V), were distinguished.

The relationships between the diatom assemblages and the combination of environmental variables were then depicted. Of these, variables connected with the chemical water types (ionic ratios) and their increasing ionic concentration (e.g. conductivity, $HCO_3^- + CO_3^{2-}$ alkalinity, pH) appear to be influential both between and within Groups I, III and IV; Group V relates to high salinity and concentration of sodium chloride. Temperature, linked to the altitude, does not appear influential; neither does the silica concentration. The microhabitat appears important in water having low mineral content, and periphytic assemblages largely constitute Group II.

The results are discussed in relation to previous records and hypotheses concerning the distribution of diatom communities in East Africa. They are only based on field observations, and a full understanding of the causative mechanisms controlling the diatom community composition have not yet be attained.

KEY WORDS : Diatoms — East Africa — Ecology — Assemblage — Water chemistry.

RÉSUMÉ

LES ASSOCIATIONS DE DIATOMÉES D'AFRIQUE DE L'EST : CLASSIFICATION, DISTRIBUTION ET ÉCOLOGIE

Ce travail est basé sur l'échantillonnage de nombreux milieux aquatiques d'Afrique de l'Est, très diversifiés au point de vue écologique. Le but est de montrer les relations entre la composition quantitative des communautés de diatomées et quelques facteurs écologiques — concentrations et rapports des ions majeurs, conductivité, pH et température. Le climat, le bilan hydrologique, et quelques autres caractéristiques du milieu (concentration en silice, profondeur d'eau, turbidité, et substrat) sont également considérés.

L'analyse quantitative des diatomées a été effectuée sur 210 échantillons contenant au total 579 taxons. La définition des associations de diatomées a été établie avec l'appui d'Analyses Factorielles des Correspondances. Dix-sept associations, réparties en cinq groupes principaux, ont été distinguées.

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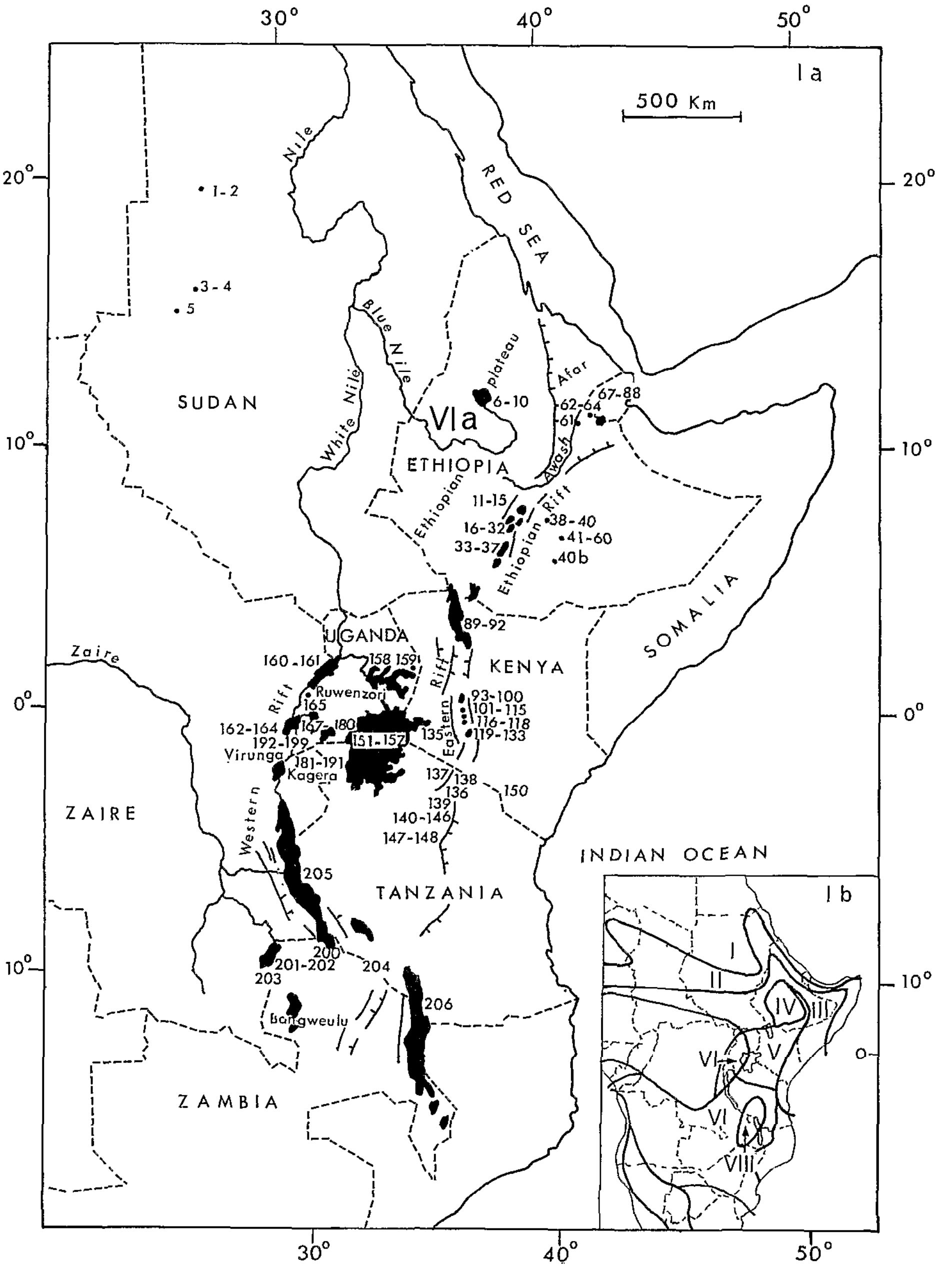


FIG. 1. — East Africa. Ia: Location map of the investigated stations. Arabic numbers indicate the sample numbers. Names and detailed locations of the waterbodies are given in table 1. Ib: climatic zonation (according to GRIFFITHS, 1972). Roman numbers: climatic zones (CZ) used in the text.

Les relations entre les associations de diatomées et quelques variables écologiques sont ensuite mises en évidence. Parmi ces variables, les types hydrochimiques (rapports ioniques), et les facteurs liés à la concentration ionique (conductivité, alkalinité, pH) semblent influencer la distribution des associations appartenant aux Groupes I, III et IV. Le Groupe V correspond à une salinité élevée et une forte concentration en chlorure de sodium. Le rôle de la température, liée à l'altitude, et celui de la concentration en silice, n'apparaissent pas clairement. Le microhabitat semble important dans les milieux de faible salinité. Le Groupe II est principalement constitué d'associations périphytiques.

Les résultats sont discutés en tenant compte des données et des hypothèses préalablement établies, et concernant la distribution des communautés de diatomées en Afrique de l'Est. Ils sont basés sur des observations de terrain; il est encore difficile de cerner les mécanismes et les facteurs déterminants qui contrôlent la composition et la distribution des associations de diatomées.

MOTS-CLÉS : Diatomées — Afrique de l'Est — Écologie — Associations — Chimie des eaux.

INTRODUCTION

The aim of this study is to provide a survey of the present-day diatom communities of East Africa and their habitats. It is based on the sampling of a wide diversity of waterbodies. F. GASSE, J. F. TALLING and P. KILHAM have participated in collecting diatom samples and environmental information. F. GASSE undertook the detailed taxonomic work, the definition and interpretation of the diatom assemblages, the statistical analyses, and the construction of this paper.

East Africa is a particular suitable region for diatom studies because of its wide range of ecological conditions. Furthermore, diatoms can be used for interpreting the history of the East African lakes which have undergone enormous changes in water level and water chemistry during the late Quaternary (RICHARDSON and RICHARDSON, 1972; HARVEY, 1976; HOLDSHIP, 1976; GASSE, 1974a, b, 1975, 1977, 1978, 1980a, b).

Central and East African lakes have been the subject of intensive floristic and taxonomic research on diatoms for almost 80 years, including the investigations of MÜLLER (1903-1910), WEST (1907), HUSTEDT (1922), ERLANDSSON (1928), ZANON (1938, 1941), MONTEIRO (1960, 1963) and MÖLDER (1961). HUSTEDT (1949) made the first explicit attempt to characterize chemically different waters in terms of their diatom flora. During the last two decades, CHOLNOKY (1960, 1964, 1970) published the first quantitative analyses of species composition, from Mt Kenya, Ruwenzori lakes and Bangweulu swamps. Hustedt's typology was expanded and refined by RICHARDSON (1968, 1969), HECKY and KILHAM (1973), and RICHARDSON *et al.* (1978).

The diatom flora of African desert regions is less well known. DE TONI (1892) and FRENGUELLI (1919) recorded diatom taxa from Somalia and Abyssinia. BROOK (1954), PROWSE and TALLING (1958), BASTOW (1960), and KARIM (1968, 1975) studied diatoms from Sudan. Some diatom samples from the Afar were analyzed by GASSE (1975).

Few of these works provided quantitative data on both the diatom assemblages and their corresponding environments. The present investigation is based on quantitative analyses of 210 contemporary diatom samples from 98 localities for which ecological conditions are known.

MATERIALS AND METHODS

Investigated biotopes

A wide variety of recent diatom-bearing environments (lakes, swamps, peat-bogs, thermal springs) was studied. The investigated stations are situated between 19° N and 14° S in latitude, and between 27° E and 43 °E in longitude (fig. 1). They range from Afroalpine bogs at altitudes exceeding 4,000 m to salt lakes lying far below sea-level. Samples from L. Abhé, L. Afrera, L. Asal (Afar), L. Birira, L. Balangida, L. Haubi, L. Ikema, L. Laja, L. Mihindi and L. Milayi (Central East Africa) contained no diatoms or very few fragments.

ORIGIN

Ethiopian alpine lakes and bogs are the results of glaciation (PERROTT, 1981). L. Tana is a volcanic-barrier lake, as numerous lakes situated in the Virunga area. Crater lakes (Bishoftu area, L. Kirongoro, L. Embagai, etc.) are common along the major tectonic faults. Great lakes, of tectonic origin, lie on the floor of the Western Rift flanked by precipitous escarpments (L. Malawi, L. Tanganyika, L. Edward = L. Idi Amin, L. Mobutu sese Seko = L. Albert). The eastern Rift and the Ethiopian Rift are occupied by chains of closed lakes usually shallow and small. The gently sloping land surface between the Western Rift and L. Victoria is drained by a branching system of rivers which are choked with swamp vegetation and which drain numerous shallow lakes (Kagera river lakes, L. Kioga, L. Bisina). The Kagera river is the major permanent inflow to L. Victoria. L. Mweru, like L. Bangweulu (BEADLE, 1974), with its great expanse of associated wetlands, also lies in a great area of tropical swamps in the southeast part of the Zaire Basin. Only springs and residual lakes, hydrologically dependant on the highlands occur in the lowest region (Afar depression).

CLIMATE

The climatic zonation shown on figure 1b (GRIFFITHS, 1972, p. 13, fig. 6) is based on a classification using temperature efficiency and precipitation/evaporation ratio. The investigated biotopes lie in 8 major climatic zones (CZ), more detailed and quantitative data on the used criteria being given by GRIFFITHS (1972).

— CZ I : tropical, arid, rainfall deficiency all seasons. Samples 1-6 are taken from this zone.

— CZ II : tropical, semi-arid, rainfall deficiency in winter. Samples 62-92 (Afar) are situated in zones CZ I and CZ II.

— CZ III : tropical, sub-humid, rainfall deficiency in winter. This zone corresponds to the Ethiopian areas of medium elevation (samples 61, 16-37).

— CZ IV : tropical, humid, rainfall deficiency in winter. This is represented by the Ethiopian highlands (samples 6-10 b, 38-60).

— CZ V : mesothermic, sub-humid, rainfall adequate all seasons. This zone lies on the eastern side of L. Victoria and in the Kenyan Rift (samples 93-157).

— CZ VI : mesothermic, humid, rainfall adequate all seasons. This zone extends from the Western Rift to L. Victoria (western part) (samples 158-199).

— CZ VII : tropical, sub-humid, rainfall deficiency in winter. Samples 200-205 are taken from this zone.

— CZ VIII : mesothermal, humid, rainfall deficiency in winter. The northern part of L. Malawi (sample 206) is situated in CZ VIII.

Climate and vegetation in the catchment areas are closely related. CZ I and II correspond to desert, semi-desert and scrub, or desert grass savanna. CZ III is covered by desert grass savanna and *Acacia* woodland. Vegetation on CZ IV, V, VI and VIII ranges from thorn tree and tall grass savanna to tropical montane forest and Afroalpine woodland. Tropical evergreen and deciduous forest prevails on CZ VII (GRIFFITHS, 1972, p. 8).

HYDROLOGY

At a given locality, the hydrological regime (water balance and turnover time) depends on the topography and on the climate of the catchment area, and on the lake itself. The water balance (WB) of a lake at equilibrium can be described by the following equation:

$$\begin{array}{cc} \text{Inflow} & \text{Outflow} \\ \Sigma_i: P + R_i + G_i = & \Sigma_o : E + R_o + G_o \end{array}$$

(P: direct precipitation on the lake; R_i: surface runoff from the catchment; G_i: groundwater inflow; E: evaporation from the lake; R_o: surface outflow; G_o: groundwater outflow=seepage).

In most cases, the water balance of the investigated waterbodies was not calculated because insufficient hydrological data were available. The water balance of 12 lakes in East and Central Africa (including L. Mobutu, L. Kioga, L. Edward, L. Tanganyika, L. Ziway, L. Langano, and L. Abiyata) is given by STREET (1980). Most of the equations proposed on table 1 are, however, hypothetical. These equations indicate the components which are thought to be the dominant factors affecting the water balance. Seven major types of water balance appear on table 1, but these are, of course, points on a continuum.

Open systems, having a surface outlet

— WB 1: $P \simeq R_o$, or $P + R_i \simeq R_o$.

Ethiopian peat bogs having an outflow, and small montane lakes probably belong to this type.

— WB 2: $P \simeq E$ (atmosphere-controlled lakes) (STREET, 1980).

P and E are very large compared with R_i and R_o. L. Victoria and L. Malawi are classic examples. L. Tana may also be of this type.

— WB 3: $P + R_i \simeq E + R_o$ (WB 3a).

Tropical swamps and associated lakes cover very great areas and are situated in relatively humid zones (e.g. L. Bangweulu, Kagera river-lakes, and their great expanse of associated swamps). These waterbodies are drained by rivers, and R_i and R_o are probably large enough to be considered in the water balance.

In the case of the Gawani swamps (Afar), the equation $R_i + G_i \simeq R_o + E$ (WB 3b) can tentatively be applied.

— WB 4: $R_i \simeq R_o$. Rivers and river-lakes.

L. Mobutu, a flow-dominated reservoir on the White Nile, is an example (STREET, 1980). The

TABLE 1

Location of the diatom sampling points and main characteristics of the corresponding environments.
— *Sample number* : * only qualitative diatom analysis was done.
— *Biotope type* : L : lake ; W : well ; S : swamp, pond ; P : peat-bog ; R : river ; Hsp : hot spring.
— Type of water balance : only the components which are thought to be the dominant factors affecting the water balance are indicated. Inflow : P : direct precipitation on the lake ; R_i : surface runoff ; G_i : groundwater inflow.
Outflow : E : evaporation from the lake ; R_o : surface outflow ; G_o : groundwater outflow (seepage).
— *Sample type* : a : aerophilous ; e : epiphytic ; lm : littoral mud ; ofs : offshore mud ; m : mud ; p : plankton.
Sample collector : C. B. : C. Barton ; R. M. B. : R. M. Baxter ; F. G. : F. Gasse ; J. G. : J. Green ; R. E. H. : R. E. Hecky ; D. A. L. : D. A. Livingstone ; J. K. : J. Kalff ; H. L. : H. Löffler ; P. K. : P. Kilham ; J. M. : J. Melack ; T. M. : T. Monod ; F. A. P. : F. A. Perrott ; J. L. R. : J. L. Richardson ; J. F. T. : J. F. Talling ; P. D. W. : P. D. Weigl ; R. B. W. : R. B. Wood.
— *References* : a : T. Monod (pers. comm.) ; b : Morandini (1940) ; c : Bini (1940) ; d : Talling (1976) ; e : Gasse (1975) ; f : Prosser *et al.* (1968) ; g : Baxter *et al.* (1965) ; h : Talling and Talling (1965) ; i : Makin *et al.* (1976) ; j : Italconsult (1970) ; k : Vatova (1940) ; l : United Nations (1973) ; m : Baumann *et al.* (1976) ; n : Gasse *et al.* (1980) ; 0 : unpublished (field measurements : F. Gasse ; chemical analyses : L. Labeyrie, CFR, Gif-sur-Yvette) ; p : Tiercelin (1981) ; q : Kilham (1971 a) ; r : Talling (unpublished) ; s : Litterick *et al.* (1979) ; t : Talling (1966) ; u : Welcomme (1972) ; v : Melack (1976) ; w : Löffler (1978).

Locality	Sample No.	Latitude	Longitude (°E)	Altitude (m)	Biotope type	Type of water balance (dominant components)	Sample type	Sample collector	Sampling date	Surface water temperature (°C)	Conductivity (µS cm^{-1})	pH	Alkalinity ($HCO_3^-+CO_3^{2-}$) meq. l^{-1}	Na^+/Cl^- (in meq. l^{-1})	$(Na^++K^+)/(Ca^{2+}+Mg^{2+})$ (in meq. l^{-1})	Si O_2 (mg. l^{-1})	References	Diatom assemblage
SUDAN																		
- Nukheila oasis	1	19°03'50"N	26°18'40"		L		lm	T.M.	18.02.1981			9.76		1.71	241	30	a	IV D
- "	2	"	"		W		s	T.M.	"					"	"	"	"	IV D
- El Malka Crater	3	15°8'N	26°12'		L		lm	T.M.	24.02.1981					35.19	49.7		a	IV D
- "	4	"	"		L		p	T.M.	"					"	"		"	IV D
- Mellit	5	14°7'N	25°32'		S		lm	T.M.	25.03.1981									II C
ETHIOPIAN HIGHLANDS AND RIFT LAKES																		
- Lake Tana	6	12°40'-11°30'N	37°00'-35°05'	1,829	L	P≈E	p	J.T.	12.03.1964	19.0.21.8	137-240	7.5 8.4	1.5-1.9	2.1-60	0.2	11-22	b,c,d,e	III C
- "	7	"	"	"	L	"	p	J.T.	12.03.1964	"	"	"	"	"	"	"	"	III C
- "	8	"	"	"	L	"	p	F.G.	21.11.1971	21.0	"	8	"	"	"	"	"	III C
- "	9	"	"	"	L	"	e	F.G.	23.11.1971	21.8	"	"	"	"	"	"	"	II B
- "	10a	"	"	"	L	"	e	F.G.	23.11.1971	21.8	"	"	"	"	"	"	"	II B
- "	10b	"	"	"	L	"	lm	F.G.	23.11.1971	21.8	"	"	"	"	"	"	"	II B
- Lake Kilotes	11				L	$R_i{\approx}E$	p	B.W.	30.03.1980	22-23	5,000	9.6	63.4	5.19		55	f	IV C
- "	12				L		lm	B.W.	"	"	"	"	"	"		"	"	IV D
- "	13				L		s	B.W.	"	"	"	"	"	"		"	"	IV D
- Lake Biete Mengest	14			1,850	L	$R_i{\approx}E$	p	B.W.	09.04.1980	22.4	2,500	9,2	26.8	4.22	5.8	55	f	IV A
- "	15	"	"	"	L		s	B.W.	"	"	"	"	"	"	"	"	"	IV A
- Lake Ziway	16	7°51'-8°07'N	38°42'-38°52'	1,636	L	$R_i{\approx}E+R_o$	ofm	B.W.	08.04.1980	23.7	370	7.9-8.7	3.7	5.45	2.36	47	g,h,i	III D
- "	17	"	"	"	L	"	lm	B.W.	"	"	"	"	"	"	"	"	"	II C
- "	18	"	"	"	L	"	lm	J.T.	. . 1964	21.5-27	"	"	"	"	"	"	"	II C
- "	19	"	"	"	L	"	lm	F.G.	10.12.1971	"	"	"	"	"	"	"	"	II C
- Lake langano	20	7°32'-7°43'N	38°50'	1,582	L	$R_i{\approx}E$	p	J.T.	10.01.1964	22.5-26.2	1,900	9,1	14.6	3.58	70	54	g,h,i,j	IV A
- "	21	"	"	"	L	"	p	B.W.	. 04.1980	"	"	"	"	"	"	"	"	IV B
- Lake Abiyata	22	7°33'-7°43'N	38°27'-38°40	1,578	L	$R_i{\approx}E$	p	J.T.	10.01.1964	23-26.8	8,646	9.3-	102.3	3.04-	252-	55-130	k,h,g,i	IV D
- "	23	"	"	"	L	"	p	B.W.	05.04.1964	24.3	30,000	9.5	"	3.09	383.5	"	"	IV D
- "	24	"	"	"	L	"	ofm	B.W.	06.04.1980	"	"	"	"	"	"	"	"	IV D
- "	25	"	"	"	L	"	p	R.B.	. 12.1971	"	"	"	"	"	"	"	"	IV D
- "	27	"	"	"	L	"	lm	F.G.	10.12.1971	"	"	"	"	"	"	"	"	IV D
- Lake Shala	28	7°24'-7°33'N	38°23'-38°39'	1,558	L	$R_i{\approx}E$	lm	J.T.	29.03.1964	21-27	16-770-29,500	9.7-10.1	162.2	2.92	538555	130	k,h,g,m	IV D IV C
- "	29	"	"	"	L	"	ofm	R.B.	. 12.1970	"	"	"	"	"	"	"	"	IV C
- "	30	"	"	"	L	"	s	B.W.	07.04.1980	22.3	"	"	"	"	"	"	"	IV C
- "	31	"	"	"	L	"	lm	F.G.	12.12.1970	27	"	"	"	"	"	"	"	IV C
- Lake Chiltu	32	7°23'N	38°27'	1,500	L	$R_i{\approx}E$	p	B.W.	07.04.1980	21.5	30,000	10.5	22.6	10				IV B
- Lake Awasa	33	6°39-7°09 N	38°22'-38°29'	1,680	L	$R_i{\approx}E$	p	B.W.	07.03.1980	21-25	790-1,050	8.7	8.4	10.7	28.9	72	h,n	IV A
- "	34	"	"	"	L	$R_i{\approx}E+Go$	p	B.W.	"	"	"	"	"	"	"	"	"	IV A
- "	35	"	"	"	L	"	lm	J.T.	28.03.1964	"	"	"	"	"	"	"	"	III D
- Lake Abaya	36	6°02-6°37'N	37°40'-38°06	1,285	L	$R_i{\approx}E$ or	p	J.T.	30.01.1964	22-28	670 -900	8.0	9.2	3.04	1.8	45	h,n	IV A
- "	37	"	"	"	L	$R_i{\approx}E+Go$	p	J.T.	"	"	"	"	"	"	"	"		IV A
- Mt Badda	38	7°56' N	39°23'	4,000	P	$P+R_i{\approx}$	a	A.P.	04.03.1975	≈ 5		≈ 5						I A
- "	39	"	"	"	P	or $P{\approx}R_o$	a	A.P.	"	≈ 5		≈ 5						I A
- "	40	"	"	"	P	$R{\approx}R_o$	a	A.P.	"	≈ 5		≈ 5						I A
- Lake Garba Gurasch	40b	≃ 7° N	≃ 40'	>3,000	L	$R_i+P{\approx}R_o$	m	H.L.		11.0-11.2	131	7.4	0.6	3.1	0.5		w	II B

TABLE 1 (continued)

- Gadeb Plain	41	7°00'-7°10N	39°15'-39°30	2,250-	R	$R_i \simeq R_o$	s	F.G.	05.02.1977	12.5	60	6.5	0.6				o	II A
- "	42	"	"	2,450	R	"	m	F.G.	12.12.1975	"	"	"	"				o	II A
- "	43	"	"	"	R	"	e	F.G.	12.12.1975	"	"	"	"				o	II A
- "	44	"	"	"	R	"	e	F.G.	12.12.1975	18	60	"	"				o	II A
- "	45	"	"	"	R	"	e	F.G.	"	18	"	"	"				o	II A
- "	46	"	"	"	R	"	e	F.G.	"	"	"	"	"				o	II A
- "	47	"	"	"	R	"	m	F.G.	15.02.1975	17	40	6.5	0.5			31	"	II A
- "	48	"	"	"	R	"	e	F.G.	"	"	"	"	"			"	"	II A
- "	49	"	"	"	R	"	e	F.G.	"	"	"	"	"			"	"	II A
- "	50	"	"	"	R	"	e	F.G.	12.12.1975	17	140	6.0	1.5				"	II A
- "	51	"	"	"	R	"	e	F.G.	15.02.1977	22	165	6.0	1.7			53	"	II A
- "	52	"	"	"	R	"	e	F.G.	"	"	"	"	"			"	"	II A
- "	53	"	"	"	R	"	e	F.G.	"	"	"	"	"			"	"	II C
- "	54	"	"	"	S	"	a	F.G.	11.12.1975	20	140	6.0				75	"	II A
- "	55	"	"	"	S	"	m	F.G.	02.02.1977								"	IV B
- "	56	"	"	"	S	"	m	F.G.	"									IV B
- "	57	"	"	"	S	"	m	F.G.	11.12.1975	18		6.0					"	II A
- "	58	"	"	"	S	"	e	F.G.	17.02.1977	14.5	130	6.0				9.9	"	II A
- "	59	"	"	"	S	"	e	F.G.	"	"	"	"				"	"	II A
- "	60	"	"	"	S	"	e	F.G.	"	"	"	"				"	"	II C
AFAR																		
- Gawani Swamp	61	11°40'N	40°40'	625	S	$R_iG_i \simeq R_o+E$	lm	F.G.	25.11.1972	26.7	24,000	9	150	1.74	422	82	e	V A
- Assaita	62	11°34'N	41°28	360	R	$R_i \simeq R_o$	lm	F.G.	27.11.1972	27.9	400	7.5-8		5.56	1.44	32	e	II C
- Lake Gamari	63	11°29'-11°39'N	41°33-41°43'	339	L	$R_i \simeq R_o$ or	lm	F.G.	03.12.1972	29.1	1,100	8.0		2.46	2.7		e	IV A
- "	64	"	"	"	L	$R_i \simeq R_o+G_o$	ofm	F.G.	05.12.1972	27.7	1,300	8.0		3.9	2.25	35	e	IIID
- Wadi Kalou	67	11°35'-11°45N	42°20'	0-50	R	$G_i \simeq R_o$	s	F.G.	27.11.1975	33	1,570	7	20.3	1.41	1.99	62	o	V B
- "	68	"	"	"	R	"	e	F.G.	"	"	"	"	"	"	"	"	"	V B
- "	69	"	"	"	R	"	m	F.G.	"	34	1,540	"	26.1	1.55	2.40	65	"	V B
- "	70	"	"	"	R	"	s	F.G.	"	"	"	"	"	"	"	"	"	V B
- "	71	"	"	"	R	"	s	F.G.	"	"	1,720	7	"	2,5		37	"	V B
- "	72	"	"	"	R	"	m	F.G.	"	"	"	"		"		"	"	V B
- "	73					"	m	F.G.	"	"	"	"		"		"	"	V B
- Abhë	74	11°05N	39°34'	235	HSp	$G_i \simeq E$	m	F.G.	30.11.1973	44		8						V A
- Asal-Korili	75	11°36'N	40°04	-153	"	"	m	F.G.	26.11.1975	34.5	5,500	7	8.0	1.07	21.3		o	V C
- "	76	"	"	"	"	"	m	F.G.	"	53	23,000	7	100	0.82	2.68	46	"	V C
- "	77	"	"	"	"	"	m	F.G.	"	31	31,000	7	123	0.78	3.05	70	"	V C
- "	78	"	"	"	"	"	m	F.G.	"	46		7						V C
- Asal-Doubye	79	11°43'N	40°05'	-155	"	$G_i \simeq E$	m	F.G.	26.11.1975	34	35,00	7	44.0	0.65	1.54	76	n	V C
- Sakallol	80	11°55'N	40°00'	0	"	$G_i \simeq E$	m	F.G.	12.12.1973	33	13,000	7.2	32.0	1.32	14.2	122	n	V C
- Hanlë. Dagguirou	81	11°36'N	39°37'	100	"	$G_i \simeq E$	m	F.G.	03.12.1975	47	5,800	7	12.2	1.56	106	82	n	V A
- "	82	"	"	"	"	"	a	F.G.	"	"	"	"	"	"	"	"	"	V A
- "	83	"	"	"	"	"	m	F.G.	05.12.1975	33.5	"	8.5	30.2					V A
- "	84	"	"	"	"	"	e	F.G.	"	"		"	"					V A
- Hanlë. Agna	85	11°34'N	39°34'	100	"	$G_i \simeq E$	m	F.G.	07.12.1973	33	3,4	8.3	6.0	1.36	34.7	77	n	IV D
- Dobi bridge	86	11°53'N	41°42	100	R	$G_i \simeq E$	m	F.G.	02.12.1972	30.2	36,000	7		0.86	69.7	59	n	V C
- Ouddouda	87	11°50'N	39°28'	100	W	$G_i \simeq E$	s	F.G.	20.11.1973	30	6,500	9		1.16	16.92	82	n	V A
- Abbaitou	88	11°10'N	40°10'	300	R	$G_i \simeq E$	m	F.G.	10.12.1972	30				3.0	141.9	22	n	IV D
KENYA. EAST AFRICAN RIFT																		
- Lake Turkana	89	2°25'-4°33'N	35°50'-36°44'	406	L	$R_i \simeq E$	p	J.G.	02.01.1979	28	2,860-3,300	9.3-	24.5	2.06-2	6.1	4-18	h	IV A
- "	90	"	"	"	L	"	lm	J.G.	"	30	"	9.7	"	2.63	"	"	"	IV A
- "	91	"	"	"	L	"	lm	J.T.	. . 1961	28-30	"	"	"	"	"	"	"	IV A
- "	92	"	"	"	L	"	ofm	C.B.		"	"	"	"	"	"	"	"	IV A
- Lake Baringo	93	0°31'-0°43'N	36°1-36°8'	985	L	$R_i \simeq E$ or	p	F.G.	28.12.1979	25	60	8.14	4.44-	5.9	4.9	15.8-	o,h,r	IIID
"	94	"	"	"	L	$R_i \sim E+G_o$	p	F.G.	"	"	530	8.48	4.93			23.5	"	IIID
- "	95	"	"	"	L	"	p	F.G.	"	26	1,650	8.36					"	IIID
- "	96	"	"	"	L	"	e	F.G.	"	"	"	8.36						II C
- "	97	"	"	"	L	"	e	F.G.	"	"	"	"						II C
- "	98	"	"	"	L	"	lm	F.G.	"	"	"	"						II C
- "	99	"	"	"	L	"	a	F.G.	"	"	"	"						II C

rivers, and some lakes lying on major rivers are placed in this category.

With the exception of the Gawani swamps, these open systems, having a surface outlet, are freshwater biotopes.

Systems without a surface outlet: closed systems and seepage lakes

— WB 5: $P \simeq E$, or $P + R_i \simeq E$.

The closed crater lakes situated in relatively humid regions and having a high mineral content (e.g. the Bishoftu crater lakes) may be of this type.

— WB 6a: $R_i \simeq E + G_o$, or $R_i + P \simeq E + G_o$.

These seepage lakes lose water mainly by evaporation and ground-water outflow. L. Naivasha is a classic case (KILHAM, 1971; GAUDET and MELACK, 1981). A similar equation can probably be applied to the other freshwater rift lakes lying in closed tectonic basins (such as L. Baringo, L. Awasa, L. Abaya, etc.).

— WB 6b: $R_i \simeq E$, or $R_i + G_i \simeq E$.

This group includes the closed basins typical of arid, semi-arid and sub-humid regions. Lakes in the Ziway-Shala basin are included in this category (STREET, 1980). The rift lakes largely

TABLE 1 (continued)

- Molo River	100	0°31'N	35°57	990	R	R≈Ro	m	F.G.	27.12.1979	25.1	172	7.7		2.48	2.76			II C
- Lake Bogoria	101*	0°11'-0°20'N	36°4'-36°7	997	L	Ri+Gi≈E	p	F.G.	25.12.1979	27.2	46,000	10.3	558	6.27	684.5	21.5	h,p	IV C
- "	102*	"	"	"	L	"	p	F.G.	26.12.1979	27.9	>50,000	10.2	"	"	"	"	"	IV C
- "	103*	"	"	"	L	"	p	F.G.	"	29.2	48,000	10.1	"	"	"	"	"	IV C
"	104	"	"	"	L	"	lm	F.G.	25.12.1979	26.5	46,100	10.3	"	"	"	"	"	IV C
- Loburu Geyser	105	"	"	"	Sp	Gi≈E	m	F.G.	27.12.1979	≈50	6,000	9.1	528	1.74	74.6		o	IV C
- Ficus forest geyser	106	"	"	"	"	"	m	F.G.	"	≈50	24,200	9.8		1.77	22.7		o	
- Kiborrit geyser	107	"	"	"	"	"	a	F.G.	26.12.1979	60	9,200	9,5	45	4.89	12.1	54	o	IV C
- "	108	"	"	"	"	"	m	F.G.	"	50	"	"	"	"	"	"	"	IV C
- Lake ol Bolossat	110a	0°09'S	36°25'-36°26	2,420	L	Ri≈E	p	F.G.	03.12.1979	21.5	1,290	8.62	10	1.5	12.0	32	.o	III D
- "	110b*	"	"	"	L	"	ofm	P.K.	31.07.1969		951	7.8	8.95	4.25	8.45	32.1	q	III D
- "	111	"	"	"	L	"	lm	F.G.	03.12.1979	22.5	1,390	8.36	≈10	2.9	14.3		o	III D
- "	112	"	"	"	S	"	m	F.G.	03.12.1979	24	1,500	8.6					"	II C
- Ol Kalou	113	0°15'S	36°22'	≈2,600	L	Ri≈Ro	e	F.G.	03.12.1979	16	70	6.8	0.7				o	I B
- "	114	"	"	"	L		lm	F.G.	"	21	58	7.2					"	I B
- Lake Solaï	115	0°5'N	36°06'	1,750	L	Ri≈E	lm	F.G.	31.12.1979		720							II C
- Lake Nakuru	116	0°18'-024'S	30°03'-36°07'	1,890	L	Ri≈E	lm	J.LR.	30.12.1979		10,500	10-10.9	107.0	3.7	265.8	142	h,r	IV D
- Lake Elmenteita	117	0°25'-0°29'S	36°12'-16°15'	1,880	L	Ri≈E	lm	F.G.	31.12.1979	18.9.21	43,750	10.4-	289	2.63	1941	295	h	IV D
- "	118	"	"	"	L	"	p	J.T.	. 02.1961	".	"	10.9	"	"	"	"	"	IV C
- Lake Naivasha (Main Lake)	119	0°43'-0°50'S	36°17'-36°20'	1,890	L	Ri≈E+Go	p	F.G.	05.12.1979	29	220-353	7.8	2.55	5.7-	33-68	34	h,r,s,o	III B
"	120	"	"	"	L	"	p	J.K.	08.02.1980	19-29	"	7.8-	"	12.2	"	"	"	III B
- "	121	"	"	"	L	"	p	J.K.	13.03.1980	"	"	8.5	"	"	"	"	"	III B
- "	122	"	"	"	L	"	p	J.K.	19.04.1980	"	"	"	"	"	"	"	"	III B
- "	123	"	"	"	L	"	p	J.K.	02.05.1980	"	"	"	"	"	"	"	"	III B
- "	124	"	"	"	L	"	p	J.K.	. 06.1980	"	"	"	"	"	"	"	"	III B
- "	125	"	"	"	L	"	ofm	C.B.		"	"							III D
- "	126	"	"	"	L	"	ofm	C.B.		"								III D
- "	127	"	"	"	L	"	lm	F.G.	05.12.1979	25		8.0						II C
-(Crescent Island)	128	"	"		L	"	p	F.G.	05.12.1979	25	255-438	8.8					s,o	III B
- "	129				L	"	ofm	C.B.	"	"	"	"					"	III D
-(Olodien Lake)	130	"	"	"	L	"	ofm	C.B.	"		626-892	9.1	6.74	9.5	90.8	42.8	s	III D
-Sonachi crater lake	131	0°50'S	36°17'	1,900	L	Ri≈E	p	F.G.	06.12.1979	25-27	5,100	9.9	52.6	11.3	17.9	77	r,q,o	IV B
- "	132	"	"	"	L		lm	F.G.	"	"	"	"	"	"	"	"	"	IV B
- "	133	"	"	"	L		s	F.G.	"	"	"	"	"	"	"	"	"	IV B
-Sacred lake	134*	0°03'N	37°31'	2,440	L		m	LDW.	. . 1964								q	IA-B?
-Lake Narasha	135*	0°03's	35°32'	2,600	L		m	JLR	07.09.1969		37.7	6.2			1.6	13.9	q	
-L.Makat.Ngorongoro	136*	3°11'S	35°32'	1,720	L		m	P.K.	06.07.1969		9.543	9.35	84.1			56	q	IV C
-L. Magad.Serengeti	137*	2°39'	34°45'	≈1,560	L		m	P.K.	30.07.1969								q	IV C?
- Lake Embagai	138	2°56'S	35°49'	2,208	L		m	P.K.	05.07.1969	23.5	13,500	10.1	183	18.5	482	111	q	IV B
- Lake Eyasi	139*	3°40'S	35°05	1,030	L		m	P.K.	08.08.1969		23,500	9.47	116.4	1.56	1,000	18	q	IV C?
- Lake Mikuyu	140*	4°34'S	34°54'	≈1,600	L		m	P.K.	22.08.1969		10,000	8.54	18.9	1.83	16.50	9.4	q	IV C
- Lake Gidabuid	141	4°18'S	35°07'	≈1,610	L		m	P.K.	21.07.1967	20.5	8,070	8.48	27.4	1.38	6.2	40	q	V A
- Lake Gidaburk	142	4°23'S	35°07	≈1,615	L		m	P.K.	22.07.1969	20	11,120	10.35	87.4	2.9	22.6	11.8	q	V A
- Lake Gidamur	143	4°19'S	35°06'	≈1,600	L		m	P.K.	21.07.1969	19.5	7,920	9.36	70	3.46	40	32	q	IV C
- Lake Laja	145*	4°20'S	35°05'	≈1,600	L		m	P.K.	"	20	11,800	9.37	85.2	2.9	33	10.7	q	IV D?
- Lake Basotu	146	4°22'S	35°05'	≈1,600	L		m	P.K.	"	20	592	6.6	4.52	1.46	0.89	18.1	q	III D
- Kenke Swamp	147	4°40'S	34°40'	≈1,640	L	Ri≈E	m	P.K.	22.07.1969	≥20	1,200	8.58	6.35	1.54	3.5	6.4	q	II C
- Lake Kindai	148	4°51'S	34°44'	1,595	L		m	P.K.	"		4,800	8.27	2.58	0.81	4.15	2.3	q	V A
- Lake Chala	150	3°19'S	37°41'	1,070	L		m	P.K.	08.08.1969	23.5	350	6.9	3.52	3.83	0.37	32.1	q	II B
-Lake NgungaMweru	150b	1°43'S	38°43'	≈1,160	L		m	P.D.W									q	I C
WHITE NILE HEAD-WATERS																		
- Lake Victoria		0°26'-3°05'S	31°39-34°53	1,135	L	P≈E				23-28	97-187	7.1-9.0	0.7-1.4				h,t,u,q	III C
(Kasuri)	151	0°26'S	33°-12	"	L	"	m	P.K.	. 10.1969		187	7.4	0.8	1.66	2.34	5.3	q	III C
(Northern station)	152	0°20'S	33°00	"	L	"	p	J.T.	18.10.1960	23-26	97	7.1-8.0	1.0		2.34	6.4-3	h	III C
(Pilkington Bay)	153	0°26'S	33°15	"	L	"	p	J.T.	07.02.1961	"	"	"	"		"	"	"	III C
"	154	"	"	"	L	"	p	J.T.	03.08.1961	"	"	"	"		"	"	"	III C
(Bottom mud)	155	"	"	"	L	"	ofm	C.B.		23-28	97-187	7.1-9.0	0.7-1.4					III C
"	156						ofm	C.B.										III C
"	157						ofm	C.B.										

fed by rivers and having a high mineral content may also be of this type.

— WB 7: $G_i \simeq E$.

Hot springs and spring-fed lakes belong to this type. These waterbodies are mainly found in the most arid zones (Afar desert).

With the exception of the seepage lakes (WB 6b), the waterbodies without any surface outlet have high mineral content, and their conductivity ranges from 2,000 to more than 50,000 μScm^{-1}.

Physico-chemical conditions

The altitudinal and latitudinal contrast also gives rise to a broad range of physico-chemical conditions. In most cases, depth, pH, conductivity and temperature were measured in the field when the water and diatom samples were collected. References concerning the detailed methods and results of used physico-chemical data are indicated on table I.

Water temperature, which is roughly a function of altitude (fig. 3) varied from a few degrees above zero to 35 °C in montainous and low altitude biotopes respectively. It reaches 55 °C for thermal springs. Conductivity ranges from 10 to more than 50,000 μScm^{-1} (25 °C). Alkalinity varied from 0.1 to 968 ($HCO_3^- + CO_3^{2-}$) meq l^{-1} and pH from about 5 to 10.9. The arbitrary classification used in the discussions are indicated on table II.

In order to characterize the various environments,

TABLE 1 (continued)

- Lake Kioga	158	0°36'-2°00S	32°20'-34°20	1,036	L	$R_i \approx R_o$	m	P.K.	10.10.1969	28.5	212	6.6	2.3	6	106-2.0	30	q	I C
- Lake Bisina	159	1°38-S	33°56'	≈1,036	L	$R_i \approx R_o$	m	J.M.M	24.07.1971	30.5	260	6.95	3.1	16.3	1.03	54.3	q	I C
-L.Mobutu Sese Seko	160	1°3'-2°15'S	30°22'-31°24	≈ 619	L	"	ofm	J.T.	. 08.1961	26-29	675-735	8.9-9.5	73-78	3.9	2.25	01-34	q,h	IV A
- "	161	"	"	"	L	"	p	J.T.	"	"	"	"	"	"	"	"	"	IV A
- Lake Edward		0°04-0°39'S	29°30'-30°05	912	L	$R_i \approx R_o$				≈26	520-925	7.9-9.3	474-				h,u,q	
-	162	0°25'S	29°30		L	"	m	R.E.H	. . 1971		520		4.74	4.91	1.23	12.8	q	IV A
-	163				L	"	p	J.T.	. 06.1961		925	9.1	9.85	4.72	1.54	6.5	h	IV A
-	164				L	"	m	J.T.	25.12.1960		"	"	"	"	"	"	"	IV A
-Kasinga Channel	165	0°05'S	30°05-30°02	914	R	$R_i \approx R_o$	m	J.T.	26.12.1960								h	IIICD
- Lake Kirongoro	166	0°00'S	30°01	925	L	$R_i + P \approx E$	m	P.K.	10.11.1969	≈26	16,300	9.39	144.2	2.91	248.1	75	q	IV C
UGANDA S.W.																		
- Lake Kanyangeye	167	0°42'S	30°15	1,520	L	$R_i \approx R_o$	m	JMM	10.05.1971	22-23	456	8.5	6.4			2.3	v	II B
- Lake Saka	168	0°42'S	30°14'	1,520	L	"	m	P.K.	03.11.1969		535	7.2	7.04	26.0	0.31	30	q	IIID
- Saka crater	169	0°42'S	30°14'	1,520	L	"	m	JMM	17.01.1971	22-24	533	≈7					v	IIID
- Lake Nyabikere	170	0°30'S	30°20'	1,400	L	"	m	P.K.	04.11.1969		233	7.2	2.79	0.17	0.11	38.5	q	II B
- Lake Katanga	171	0°29'S	30°16'	1,340	L	"	m	P.K.	04.11.1969	22-23	393	7.9	4.64	3.59	0.28	41.7	q	II B
- Lake Mwamba	172	0°28'S	30°17'	1,220	L	"	m	JMM	15.06.1971		387	8.7	5.6			48.3	v	II C
- Lake Lugembe	173	0°27'S	30°17'	1,300	L	"	m	JMM	14.05.1971	25-26	308	8.7	3.9			31.3	v	II B
- Lake Chibwera	174	0°09'S	30°08'	975	L	"	m	JMM	01.06.1971	26.7	431	7.8	5.9				v	III B
- Lake Kamweru	175	0°15'S	30°07'	1,160	L	"	m	P.K.			136		1.52	1.76	0.13	25.7	q	II B
- Lake Nyungu	176::	0°15'S	30°06	1,220	L	"	m	JMM	28.05.1971	24.5	431	9.2	8.1			51.5	v	II B?
- Lake Luijondo	177	0°16'S	30°05'	1,000	L	"	m	P.K.	01.10.1969		409		4.93	5.60	0.37	27.8	q	II B
- Lake Nyamusigiri	178::	0°17'S	30°02	975	L	"	m	P.K.	31.11.1969		908	8.7	10.08	2.52	0.95	32.1	q	V A?
- Lake Nkugute	179	0°19'S	30°06'	1,220	L	"	m	P.K.	11.11.1969	22-24	82.7	≈8	0.90	2.40	0.21	3.2	q	II C
- Lake Karengye	180	0°54'S	30°08'	1,370	L	"	m	P.K.	11.10.1969		334		1.66	2.07	0.75	31.0	q	III D
KAGERA RIVER LAKES																		
- Lake Tshohoha N	181	2°15'S	30°08'	1,350	L	$R_i \approx R_o$	m	P.K.	21.09.1969	25.5	393	6.9	4.1	5.44	0.89	36.4	q	I C
- Lake Tshohoha S	181::	2°25'3	30°06'	1,350	L	or	m	P.K.	21.09.1969	26.3	210	7.3	1.91	1.78	0.68	24.6	q	I C
- Lake Rugwero	183	2°24'S	30°19'	1,350	L	$P + R_i \approx E + R_o$	m	P.K.	20. . 1969	28.5	116	6.55	1.08	2.87	0.6	19.3	q	IIIAB
- Lake Mugesera	184	2°06'S	30°20'	1,350	L	"	m	P.K.	02.11.1969		212		1.22	0.94	0.72	20.3	q	IIIAB
- Lake Bisongou	185	2°08'S	30°57'	1,250	L	"	m	P.K.	22.11.1969		94.7	6.8	0.84	2.73	0.6	17.1	q	IIIA IC
- Lake Hago	186::	1°41'S	30°43'	1,250	L	"	m	P.K.	15. . 1969	25.2	76.2	6.5	0.74	3.0	0.67	22.5	q	I B?
- Lake Ikimba	187	1°28'S	31°30'	1,173	L	"	m	P.K.	19.11.1969		56.5	6.5	0.41	4.0	0.66	15	q	I C
- Lake Kiwumba	188	1°44'S	30°46'	1,250	L	"	m	P.K.	15.09.1969	25.0	79.5	6.6	0.68	2.50	0.61	17.1	q	I C
- Lake Nabugado	189	0°22'S	31°54'	1,135	L	"	m	JMM	06.06.1971		51.1	7.3	0.16	1.39	1.59	15	q	IIIA
- Lake Rumira	191	2°11'S	30°13'	1,350	L	"	m	P.K.	20.09.1969	26	119	6.6	1.08	2.86	0.61	18.2	q	I C
VIRUNGA AREA																		
- Lake Mutanda	192	1°13'S	29°40'	1,798	L	$R_i \approx R_o$	m	P.K.	29.10.1969		292	6.75	2.1	2.03	0.65	15.0	q	IIIA
- "	193	"	"	"	L	"	m	J.T.	. 06.1961		230-235	7.2-8.1	2.1	2.09	0.7	11	h	IIIA
- Lake Mulehe	194	1°13'S	29°43'	1,803	L	"	m	P.K.	24.10.1969		244	7.25	2.29	1.52	0.2	18.2	q	IIIA
- "	195	"	"	"	L	"	m	J.T.	. 06.1961		255-260	7 4-8.0	2.1	1.38	0.3	27	h	IIIA
- Lake Bunyoni	196::	1°17'S	29°50'	1,974	L	"	m	P.K.	23.09.1971	21.5	248	7.0	1.94			10.7	q	IIB?
- Lake Kayumba	197a	1°20'S	29°47'	1,894	L	"	m	P.K.	24.10.1969	20	174	7.1	1.43	1.05	0.36	7.5	q	IIIA
- Lake Cyahafi	197b	1°21'S	29°47'	1,894	L	"	m	P.K.	24.09.1969		265	8.0	2.51			23.5	q	IIB
- Lake Bulera	198	1°27'S	29°46'	1,863	L	"	m	P.K.	26.10.1969		120	6.7	0.83	2.13	0.6	0	q	IIIA
- Lake Luhondo	199	1°30'S	29°45'	1,764	L	"	m	P.K.	26.10.1969	21	204	6.85	2.31			15	q	IIIA
ZAMBIA - TANZANIA																		
- Lake Tondwa	200	8°39'S	30°08'	1,040	L	$R_i \approx R_o + E$	m	D.A.L	09.08.1969		762		8.3	22.92	76.6	55.6	q	I B
- Lake Mweru		8027'-9°31'S	28°25-29°10'	927	L					19-30	47.7-125	6.4-9.3	0.416				q,h,u	
- (Nchelenge)	201	9°10'S	28°41'		L	"	m	D.A.L	06.08.1969		47.7		0.416	3.40	0.67	13.9	q	I C
-	202	"	"		L	"	m	"	"								q	I C
- Mofwe Lagoon	203	9°39'S	28°43'	922	S	$P + R_i \approx R_o + E$	m	"	06.08.1969		37.7		0.43	5.0	1.18	12.9	q	I B
- Lake Pansewa	204	9°03'S	33°37'	1,550	L	"	m	"	. 08.1969		61.9		0.54	11.15	19	34.2	q	I B
- Lake Tanganyika	205	3°23'-8°50'S	30°	773	L	$P \approx E$	p	J.T.	1961		520-610	7.3-7.8	6.71	3.29	0.82	0.38	h	IV A
- Lake Malawi	206	9°30'-14°40'S	34° - 35°	471	L	$P \approx E$	p	J.T.	. . 1962	23-25	210	7.7-8.5	2.36	2.91	1.14	1.1	h	IIIC

the following major ions were considered with their respective origins:

— Alkaline-earths $Ca^{2+} + Mg^{2+}$: weathering of rock minerals (feldspars, micas, amphiboles, pyroxenes and peridots).

— Alkali-metals $Na^{+} + K^{+}$: meteoric (sea spray), leaching of pre-existing evaporites, weathering of rocks (feldspars).

— $Cl^{-} + SO_4^{2-}$: meteoric (sea spray), leaching of pre-existing evaporites and oxidation of sulphides.

— $HCO_3^{-} + CO_3^{2-}$: buffering of the release of alkaline and earth-alkaline cations in the environment.

Three major chemical water facies can be distinguished by considering different ionic ratios (in meq l^{-1}). Figures 4 to 6 illustrate this chemical diversity.

Facies 1 and facies 2 are those of the carbonate-bicarbonate type. The ratios $(HCO_3^{-} + CO_3^{2-})/(Cl^{-} + SO_4^{2-})$ and Na^{+}/Cl^{-} are above 1 (tab. 1).

— Facies 1 corresponds to sodium carbonate-bicarbonate waters. The ratios $(Na^{+} + K^{+})/(Ca^{2+} + Mg^{2+})$ and Na^{+}/K^{+} are above 1. The factors conductivity, pH and alkalinity are closely and positively correlated (TALLING and TALLING, 1965). 56 % of the investigated biotopes belong to this chemical

TABLE 2

Arbitrary classification of the values of water temperature, conductivity, pH and alkalinity for the studied samples.

Ecological parameter	Class	Ranges	Sample number
Water temperature (°C)	Low	< 12	38-40c
	Medium low	12- <21	6-8,41-50,54-60,117,118,141,148,197a,199
	Medium	21- <27	9-37,61,93-100,104,110-112,119-133,138,150,151-157,160-169,171,173,174,176,180-191,196,206
	High	27- <35	62-64,67-73,75,77,79,80,83-92,101-103,158,159,183,201-202
	Very high	> 35	74,76,78,81,82,105-109
Conductivity ($\mu S.cm^{-1}$)	Very low	< 100	38-40c,41-53,57-60,113,114,135,179,185-189,201-204
	Low	100- <300	6-10b,100,119-127,151-159,170,175,180,182-184,191-199,206
	Medium	300- <1,000	16-19,33-37,62,94,96,99,115,128-130,144,150,160-164,167-169,171-174,176-178,181,200,205
	Medium high	1,000- <3,000	14-15,20,21,33-37,62,94,96-99,63-73,89-92,85,110-112,147
	High	3,000- <10,000	11-13,75,81-85,87,105,107-109,131-133,136,141,143,148
	Very high	⩾10,000	22-32,61,76-80,86,101-104,106,116-118,138-140,142,166
pH	Low	<6	38-40
	Medium low	6- <7	41-60,113,135,14,146,150,158,159,181,183,188,191,192,198,199
	Medium	7- <8.5	6-10b,16-19,36,37,62-67,85,86,93-100,114,119-127,140,141,151-157,168-171,182,189,193-197bn, 205,206
	High	8.5- <9.5	14-15,20,21,33-35,64,83,84,87,110-112,128-130,139,143,145,147,148,160-164,166,167,172,173, 176,178,179
	Very high	⩾9.5	11-13,22-32,89-92,101-104,106-108,116-118,131-133,138,142
Alkalinity ($HCO_3^- + CO_3^{2-}$) ($meq.l^{-1}$)	Very low	<1	38-40,41-60,113-114,151?, 17 , 185-189,198,201-204
	Low	1- <3	6-10b,152-157,180,182-184,191,196,197a,199
	Medium	2- <10	16-19,33-37,75,85,93-99,110b,111,119-130,145-150,158-164,167-176,181,205,206
	High	50- <100	11-13,32,63,64,131-133,136,142,144
	Very high	⩾100	22-32,61,76-78,101-106,116-118,138-139,166

type. This is encountered in most of the Rift lakes and in the desert regions CZ I and CZ II. The water conductivity ranges from 10 to 50,000 μScm^{-1}.

— Facies 2 includes the calcium-magnesium carbonate-bicarbonate waters. The ratio $(Na^+ + K^+)/(Ca^{2+} + Mg^{2+})$ varies from 0.16 to 1. The ratio Ca^{2+}/Mg^{2+} is generally close to 1. This facies is represented by 19 % of the samples (tab. 1). This mainly occurs in montane volcanic lakes (L. Tana and Virunga region) and in lakes situated along the Kagera river draining the Virunga Volcanoes and the Rwanda highlands. These lakes have very low to low conductivity and alkalinity, and medium pH.

— Facies 3 is that of the sodium chloride type. The ratios $(HCO_3^- + CO_3^{2-})/(Cl^- + SO_4^{2-})$ and Na^+/Cl^- are low (typically below 1). The dominant ions are Na^+ and Cl^-. This type corresponds to 18 % of the samples. The water conductivity range from 1,500 to 35,000 μScm^{-1} and the pH from about 7 to 8. This type occurs in few Central African lakes (such as L. Kindai) but the majority of the biotopes are the hot springs or hot spring-fed rivers and lakes from the Afar desert.

Intermediate facies between these three major types are common (figs. 4 to 6).

Most minor constituents, including forms of important plant nutrients such as N and P, are not considered here. An exception is soluble reactive silicon, expressed as the silica (SiO_2) equivalent.

Diatom analyses

When possible, several types of samples were collected at a given localities (phytoplankton, periphyton, mud). In some cases (e.g. L. Naivasha, L. Tana), phytoplankton was sampled at various times. Sampling was performed by several collectors (their names being indicated on tab. 1). More detailed sample descriptions will be given elsewhere (GASSE, 1983). Nets were often used to collect phytoplankton, and their size-selectivity might influence some of the quantitative data.

Diatom samples were subjected to the physico-chemical treatment proposed by GASSE (1975) Microscope slides were mounted in Naphrax. For each sample, the percentage of each taxon was evaluated by counting 300 to 1,000 valves which were distributed on four slides. The list of rare species was established by scanning the slides until no additional taxon appears. The total number of taxa for all the samples came to 579 (species, varieties and forms). The taxonomic check-list and autoecological data will appear elsewhere (GASSE, 1983), with systematic discussion of those taxa which were difficult to identify.

Comments concerning the relative percentages of the taxa are based on the following arbitrary definitions. The dominant species was that having the highest percentage in the sample, and the following classes were distinguished: abundant: $\geqslant 33\%$; common: 5- $< 33\%$; uncommon: 1- $< 5\%$; rare: $< 1\%$.

Definition of the diatom assemblages

Classification of the encountered communities was difficult because of the high number of taxa and samples. It was facilitated by use of Factor Analysis of Correspondence (FAC). The FAC method (Benzecri, 1980) aims at synthesizing the information contained in a data table, and visualizing the relationships between the elements of two sets of data, I (e.g. taxa percentages) and J (samples). Some main properties and examples of the application of FAC diatom assemblages are presented by Gasse and Tekaia (1982, a, b). The presence and absence of the species (FAC-presence-absence) were taken into account, and then the percentages of the taxa (FAC-percentage). In the FAC-presence-absence, the species which were present in less than 3 samples were eliminated. The species which never reached a percentage above 2% in any of the samples were not considered in the FAC-percentage. FAC leads to graphical classification of the samples based on their diatom communities. Fig. 2 shows one graph obtained from FAC-presence-absence. In FAC, species and samples, which are intradependant, are considered as points in geometrical space (the number of dimensions being: number of samples × number of species). These points are located by their coordinates on the different factorial axes (e.g. coordinates on axes 1 and 2, fig. 2). Taking the factorial axes in pairs, the species and the samples points can be projected on one plane (e.g. plane defined by axes 1 and 2, fig. 2). This gives the approximate location of the points in geometrical space. On such graphs, the samples having similar flora are grouped, and the species which are usually associated with each other are also grouped. Each group of samples is characterized by the corresponding group of species. These graphs were interpreted by considering the numerical tables produced by the computer, and

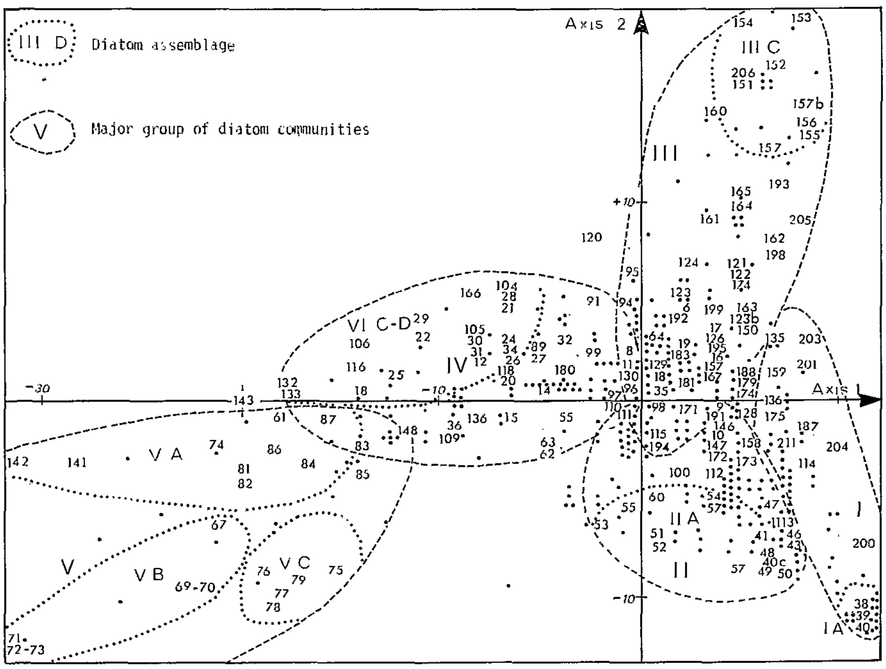


FIG. 2. — Factor Analysis of Correspondence (FAC-presence-absence). Factorial plane 1-2. Dimensions of the analyzed table: 210 samples, 355 species. Projection of the sample points (arabic numbers) and the species points (circles). See explanation in the text. Numerical codes of the species is not given here (see Gasse, 1983). Dashed lines: boundaries between the five major groups of diatom communities. Dotted lines: boundaries between the some diatom assemblages. These boundaries were drawn by taking into account the different FAC-analyses and the successive factorial planes.

TABLE 3

Diatom assemblage definition and distribution.
Sample number : * only qualitative analysis was done. In brackets: intermediate between two assemblages.

Assemblage	Number of taxa	CHARACTERISTIC SPECIES			DISTRIBUTION
		"Species characterized by their percentages"	"Definitive species"	"Cluster of co-occuring species"	
GROUP I		*Eunotia* (1-32%), *Pinnularia*(1-95%) *Eunotia* + *Pinnularia* > 4%	*Eunotia spp.*, *Pinnularia spp.*	*Stauroneis phoenicenteron*, *S. anceps*, *Cymbella ventricosa*, *Neidium iridis*, *N. affine*	Highland peat-bogs and lakes Tropical acid Swamps
ASSEMBLAGE IA	64-92	*Eunotia* (1.5-20%) : *E. praerupta*, *Pinnularia* (15-26%) : *P. microstauron*, *P. subcapitata*, *Navicula tantula*	*Anomoeoneis brachysira*, *Eunotia damasii*, *E. praerupta*, *Cymbella perpusilla*, *Diploneis peterseni* *D. pseudovalis*, *Gomphonema bohemicum*, *Frustulia rhomboides*, *Navicula harbergii*, *N.lapidosa**, *N. margaritacea**, *N.perpusilla**, *N.tantula**, *Pinnularia acoricola*, *P.lata*, *P.lineolata*, *P.scottae**, *P.zanoni*, *Stauroneis acuta*, *S. aerophila*, *S.nana* * : also characteristic of II A	"	Samples 38, 39, 40, 134* From Cholnoky (1960) : Ruwenzori lakes (L. Neuriana, L. Kanganyika, L.Katunda, Muteinda. (1964) : M^t Kenya From Zanon (1938) and Hustedt (1949) : Karimsibi, L. Ilega From Richardson (1968) : L. Irene, L.Mahoma, L.Chiltu (?)
ASSEMBLAGE IB	16-40	*Eunotia* (5-32%) : *E.flexuosa*, *E.lunaris**, *E.pectinalis v.minor**, *Pinnularia* (5-95%) : *P.major**, *P.tropica**, *P.cardinalis*, *Gomphonema parvulum* + *v.micropus*, *G.gracile*, *Synedra rumpens*, *S. ulna*, *Nitzschia palea*. * : also characteristic of IC	*Pinnularia cardinalis*, *P. gracilloides*, *Eunotia veneris*	"	Samples 112, 114, 135*, 200, 203, 204, 186* ? From Cholnoky (1970) :Bangweulu swamps (B1, B3, B5, B8) From Hustedt (1949) : L.Gando
ASSEMBLAGE IC	17-45	*Melosira* (29.5-92.4%) : *M.distans v.africana*, *M.granulata* + *v.* or *M.ambigua*, *Eunotia* (1-5%) : *E. lunaris*, *E.pectinalis v.minor*, *Pinnularia* (1-7%), *Fragilaria*, *Synedra acus*, *S.ulna*	*Melosira distans v.africana*, *v. humilis*, *Eunotia pseudoveneris*, *E.robusta*, *E.valida*	"	Samples 158, 159, 181, 182*, 184, (185), 186* ?, 187, 188, 191, 201, 202, 211 From Cholnoky (1970) : Bangweulu samples (B6) From Richardson (1968) : L.Schiwa-Ngandu
GROUP II		*Achnanthes*, *Amphora ovalis* + *v.* *A.pediculus*, *Cocconeis*, *Cymbella*, *Epithemia*, *Gomphonema*, *Navicula*, *Nitzschia amphibia*, *N.fonticola*, *N.frustulum*, *N.palea*, *N.paleacea*, *N.recta* Cumulative percentage: > 60%	*Amphora ovalis v.tailingii*, *A. pediculus*, *Epithemia*	*Amphora ovalis* + *v.Cocconeis placentula*, *Cymbella affinis*, *C.turgida*, *Epithemia zebra*, *Gomphonema parvulum*, *G.gracile*, *G.clevei*, *Navicula seminulum*, *N.seminuloides*, *N.exiguiformis*, *Nitzschia fonticola*, *Synedra ulna*	Freshwater lake periphyton, Swamps, rivers

Dans la colonne Distribution/Assemblage IC: lire Chiwa au lieu de Schiwa.

giving the relative contribution of each species and each samples to the point patterns for each factorial plane.

Five major sample groups (I-V) corresponding to fice species groups were firstly distinguished. A more sensitive classification was progressively established by considering successively the first three factorial planes obtained from FAC-presence-absence and the first three factorial planes from FAC-percentage. The five major sample-species groups were progressively divided in 17 assemblages which were defined by those species having an important contribution to the point patterns. The continuity observed in the point distribution (fig. 2) can be explained by the continuity of the ecological conditions found in the biotopes.

The assemblages definitions (tab. 3) are based on:

—"*species characterized by their percentages*": species which must be present in relatively high percentages to be characteristic of an assemblage, but which may be ubiquitous;

"*definitive species*": species which are present in very low numbers in particular assemblages and which are characteristic of those associations because of their absence from other assemblages;

—"*cluster of co-occurring species*": also some of the constituent species may be widespread or even ubiquitous, co-occurrence of the entire cluster is characteristic of a particular assemblage.

Taxonomic problems always arise in diatom identification: because these problems have not been yet resolved for East Africa, it seemed preferable to base this work on analyses conducted by a single diatomist. A comparison with the diatom communities known from the literature was however attempted (tab. 3).

DIATOM ASSEMBLAGE STRUCTURE AND DISTRIBUTION

The proposed classification (tab. 3) for the diatom assemblages has the advantage of embracing all the

TABLE 3 (continued)

ASSEMBLAGE IIA	46-119	*Achnanthes lanceolata, Cocconeis placentula, Gomphonema olivaceum, G.parvulum, Navicula salinarum v.intermedia, Nitzschia linearis, Fragilaria construens*	*Achnanthes clevei, A.engelbrechtii, A.lanceolata, A. subhudsonis, Cymbella fonticola C.sinuta, Navicula subtilissima, Surirella angustata, Meridion cicularе, Cymatopleura solea*	*Diploneis elliptica, Gomphonema clevei, Nitzschia recta, N. umbonata*	Samples 41-60
ASSEMBLAGE IIB	12-40	*Cocconeis placentula, Amphora ovalis + v., A.pediculus, Epithemia zebra, Eunotia pectinalis v.minor**, *Melosira distans v.alpigena*+, *Navicula perpusilla* * : also characteristic of group I +:also characteristic of III D	*Amphora ovalis v.tallingii, A.pediculus*	*Navicula exiguiformis, N. seminuloides, Synedra ulna, S.rumpens*	Samples 9, 10a, 10b, 67, 150, 167, 170, 171, 173, 175, 176*, 177, 196*, 197b
ASSEMBLAGE IIC	18-64	*Cocconeis placentula, Gomphonema parvulum + v., Nitzschia fonticola, N.amphibia, Achnanthes minutissima Nitzschia communis*			Samples 5, 17, 18, 19, 54, 62, 90, 96, 97, 98, 99, 100, 112, 115, 127, 147, 172, 179, (199) From Richardson (1968):L.Bukuju
GROUP III		*Melosira, Syndra acus Eunotia + Pinnularia* < 3%			Freshwater lake plankton
ASSEMBLAGE IIIA AA	7-34	*Melosira granulata + v. + Synedra acus + Cyclotella stelligera* >45% *Cyclotella stelligera* (8-32%)	*Cyclotella stelligera, Melosira granulata v.jonensis*	*Melosira granulata, Synedra acus, Cyclotella stelligera*	Samples (185), 192, 193, 198, (199) From Hustedt (1949): L.Ndalaga, L. Bita From Talling (1965): L. Mulehe
AB		*Cyclotella stelligera* < 5%	*Cyclotella stelligera, Melosira granulata v.jonensis*	*Melosira granulata, Synedra acus, Cyclotella stelligera*	Samples (183), 194, 195, 197a From Hustedt (1949) : L.Ndalaga
ASSEMBLAGE IIIB	7-22	*Melosira ambigua + Synedra acus* > 60%			Samples 119-124, 128, 174, (183) From Richardson (1968), Bachmann (1938) : L.Naivasha
IIIC	15-39	*Melosira* (17-98.7%). *Melosira + Fragilaria + Synedra berolinensis* > 50%: *M.agassizii, M.ambigua, M.distans v.alpigena, M.nyassensis + v., Nitzschia fonticola, Stephanodiscus astraea + v., S.hantzschii*	*Surirella nyassaea, S.muelleri, S.engleri, Cymatopleura solea, Synedra berolinensis, Fragilaria pinnata v.trigona*		Samples 6, 7, 8, 151, 152, 153, 154 155, 156, 157, (165), 206. From Brunelli and Cannicci (1940): L.Tana From Ostenfeld (1909), Thomasson (1955), Richardson (1968) : L. Victoria

communities encountered in each lakes. No clear boundaries exist between the major groups or the assemblages, and any classification remains somewhat arbitrary.

Since important ecological conditions are known for each sample, physico-chemical parameters corresponding to a given assemblage can be listed. Because few data are available on light, water transparency trophic conditions and trace elements, the influence of these variables could not be evaluated quantitatively. Relationships between diatom assemblages, macro- and micro-habitats, water temperature, pH, alkalinity and major ionic composition are emphasized.

The results are based on the material analysed in this paper. They are considered as hypotheses which must be tested by further investigation.

Group I : *Eunotia* and *Pinnularia* uncommon to abundant

Group I is defined by the diversity, and the relatively high cumulative percentages, of the genera *Eunotia* and *Pinnularia* (> 3 %), and by a "cluster of co-occurring species" (tab. 3).

ASSEMBLAGE I A

The flora is highly diversified (64-92 taxa per sample) without any abundant species. Twenty-two taxa are "definitive".

Assemblage I A comes from aerophilous or periphytic communities in Afroalpine environments (peat-bogs, ditches, tarns and shallow lakes). In the investigated area, it was only recorded in Ethiopian alpine peat-bogs. Communities described by ZANON (1938), HUSTEDT (1949), RICHARDSON (1968) and CHOLNOKY (1960, 1964) from East African mountain lakes or tarns closely resemble assemblage I A. The communities described by these authors are, however, usually dominated by *Anomoeoneis brachysira*, *Frustulia rhomboides* or *Pinnularia interrupta*, uncommon or rare in the Ethiopian peat-bogs. The Mt Badda communities also differ from those described by the cited authors because of the presence of some species usually regarded as being "polyhalobous"

TABLE 3 (continued)

ASSEMBLAGE IIID	14-95	*Melosira* (24.5-92.4%). *Anomoeoneis sphaerophora* + *Cyclotella meneghiniana* + *Navicula elkab* + *Rhopalodia gibberula* + *N. latens* + *Thalassiosira rudolfi* : 1-13.5%			
DA		*Melosira ambigua*, *Synedra acus*			Samples 125, 126, 129, 130
DB		*Melosira granulata v.angustissima*, *Nitzschia amphibia*, *N.fonticola*, *N. gracilis*			Samples (16), 64, 93, 94, 95, 110a, 110b, 111, 146, 168, 169, 180.
GROUP IV		*Melosira* > 10%, *Anomoeoneis sphaerophora*, *Navicula elkab*, *Nitzschia estohensis*, *N.frustulum*, *N.latens*, *N.pusilla*, *Rhopalodia gibberula*, *Thalassiosira rudolfi*, *Cyclotella meneghiniana**	*Anomoeoneis costata*, *Cyclotella iris*, *Navicula irregularis*, *Nitzschia latens*, *N.pusilla*, *N.estohensis*, *Thalassiosira faurii*, *Navicula elkab*, *Cyclotella meneghiniana**, *Nitzschia sigma**, *Chaetoceros sp.** *also characteristic of Group V.	*Anomoeoneis sphaerophora*, *Navicula elkab*, *Nitzschia latens*	Alkaline rift lakes and crater lakes Hot springs Plankton and periphyton
ASSEMBLAGE IVA		Group IV characteristic species : 2-10%			
	9-56	*Nitzschia* (> 15%): *N.Fonticola*, or *N.communis*, or *N.pseudofonticola*, or *N.amphibia*, or *N.frustulum*, *Fragilaria construens + v*, *Stephanodiscus astraea*, *S.damasii*	*Nitzschia lancettula*, *N.tropica* *Stephanodiscus damasii*		Samples 3,4,14,15,20,33,34,36,38,63, 89,90,91, 92, 160,161,163,164, (205) From Bachmann (1938), Worthington and Ricardo (1936), Rich (1932):L.Turkana From Hustedt (1949) : L. Edward From Degens et al.(1973), Hustedt (1949): L.Kivu. From Talling(1969):L.Mobutu
ASSEMBLAGE IVB		Group IV caracteristic species : 10-40%			
	9-51	*Nitzschia* (> 50%): *N.frustulum*, *N.latens*, *N.pusilla*, *N.estohensis*			Samples 2,21,32,55,131,132,133,138 From Hecky and Kilham (1973): L.Talusia, L.Big Momela, L.Reshitani, L.Gidaburk
ASSEMBLAGE IVC	8-48	Group IV characteristic species : > 40%			
		Nitzschia (> 27%): *N.pusilla*, *N. latens*, *N.frustulum*, *N.estohensis*, *Thalassiosira rudolfi*, *Navicula elkab*			Samples 11,28,29,30,31,101,102,103, 104,107,108,109,118,136,137,140, 146? 166 From Hecky and Kilham (1973) : L. Kirongoro, Small Momela, L.Elkekhotoito

such as *Diploneis smithii* (HUSTEDT, 1957, p. 253). Their presence in such dystrophic habitats could be due to the subaerial conditions which favour the growth of diatoms able to tolerate rather wide fluctuations in osmotic pressure (SIMONSEN, 1962, 1965; FLORIN, 1970).

Few quantitative ecological data are available on these biotopes (tab. 1). The assemblage is associated with low temperature and low pH (figs. 3, 7). The water undoubedly has low mineral content because these habitats are directly fed by an abundant rainfall (WB 1).

ASSEMBLAGE I B

Assemblage I B is not so diversified as assemblage I A (16-40 taxa per sample), and few "definitive" species were found (tab. 3). The communities are dominated by *Pinnularia major* (sample 204: 68 %), or *Gomphonema parvulum* (sample 200: 17.5 %), or *G. javanica* (sample 114: 26.2 %), or *Nitzschia palea* (sample 113: 18.3 %).

Assemblage I B seems to display a preference for environments rich in hydrophytes. It occurs in L. L. Tondwa, L. Pansewa, Mofwe Lagoon (WB 4) and in a small man-made lake in Kenya (Ol Kalou) (WB 3). Close analogies were found with the flora of the Bangweulu swamps (CHONOKY, 1970: samples B1, B3, B4, B5, B6) where the percentages of *Eunotia* ranges between 26.9 and 69.5 %, and that of *Pinnularia* between 0 and 8.2 %. The water temperature was not measured in the Zambian and Tanzanian lakes, but taking into account the geographical situation, it was probably above 25 °C: assemblage I B appears to be eurythermal (fig. 7).

Except for L. Tondwa, this assemblage is found in carbonate-bicarbonate waters of very low conductivity and very low to low alkalinity. The measured pH ranges from 6.1 to 7.0. Na^{+} is the dominant cation but K^{+} represents 10.7 % and 3.7 % of the ionic sum in samples 204 and 200 respectively. The water of Mofwe Lagoon (sample 203) is relatively rich in Ca^{2+} (14.2 %) and Mg^{2+} (6.7 %) (fig. 4, 5). The wide range of the silica content (fig. 7) may indicate that this variable is not a determining factor.

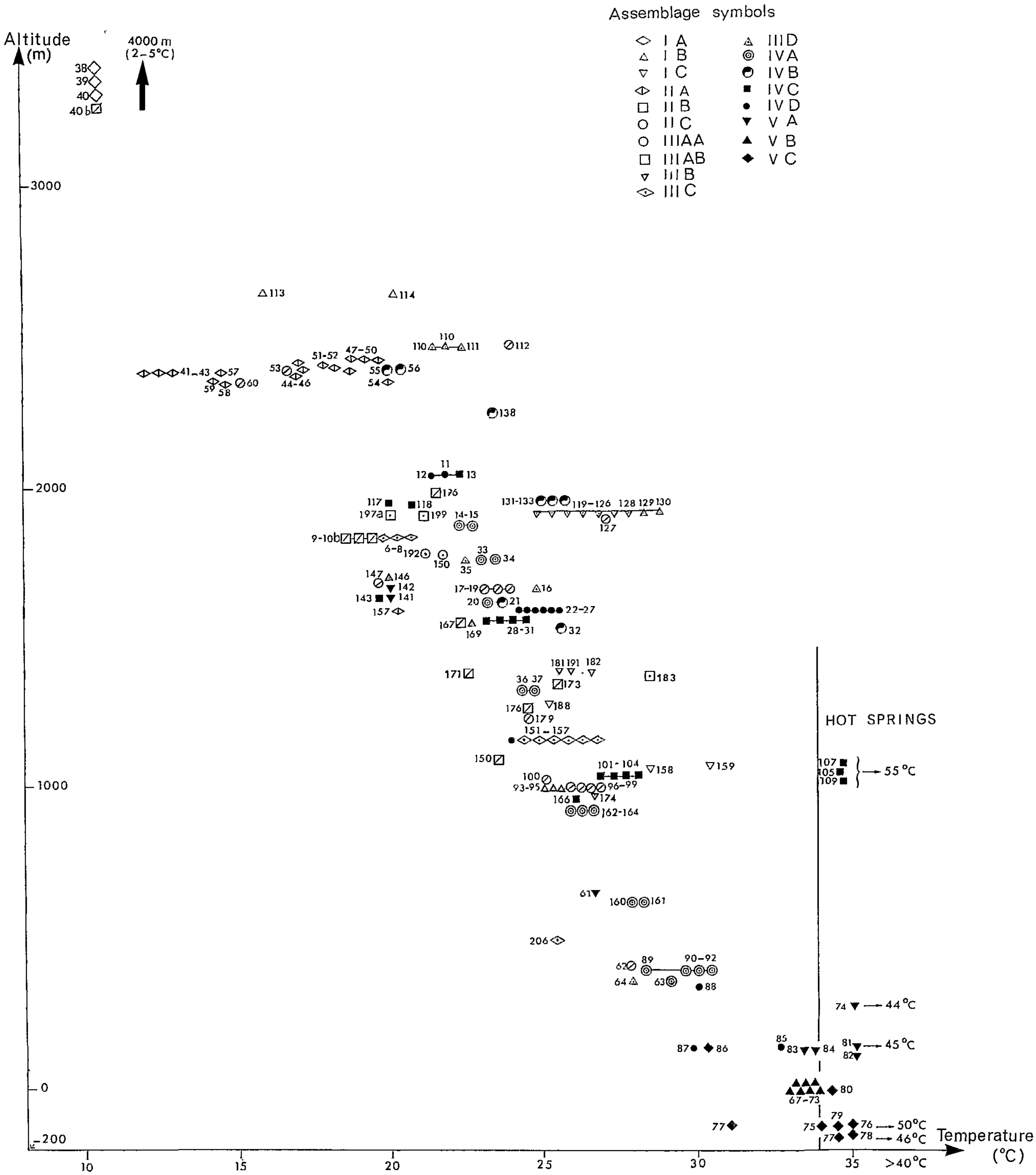


FIG. 3. — Sample and diatom assemblage distribution as a function of water temperature and altitude. Each assemblage is represented by a symbol. Each sample belongs to one assemblage. Each sample is indicated by the sample number (arabic number) and the symbol of the corresponding assemblage. For example, ▲ 72: sample N° 72 belonging to assemblage V B.

TABLE 3 (continued)

ASSEMBLAGE IVD	21-49	Group IV characteristic species : > 40%			Samples 1,12,13,22,23,24,25,26,27,88, 116,117,136,145? From Hecky and Kilham (1973): L. Lgarya, L.Gidamur, L.Magad, L. Lekandiro, Olodian Bay, L.El Rekkotoito
		Nitzschia (> 20%), *Anomoeoneis sphaerophora*, *Navicula elkab*, *Rhopalodia gibberula*			
GROUP V		*Amphora acutiuscula*, *A.coffaeformis* + v., *A.tenerrima*, *Cymbella pusilla*, *Mastogloia elliptica*, *Navicula ammophila*, *N.salinicola*, *Nitzschia elegantula*, *N.punctata*, *Cyclotella meneghiniana**	*Amphora rognonii*, *Chaetoceros mulleri**, *Campylodiscus clypeus*, *Diploneis subovalis*, *Gyrosigma spenceri*, *Mastogloia aquilegiae*, *Navicula iranensis*, *Nitzschia obtusa*, *N. scalaris*, *N.Sigma**, *N.stompsii*, *N. tryblionella*, *N.vivax*, *Hantzschia virgata*, *Stauroneis legleri*, *Synedra affinis* *:also characteristic of groupIV		Closed tectonic or volcanic lakes, Hot springs Planktonic or periphytic
ASSEMBLAGE VA		Group V characteristic species : 2.5-30%			
AA	9-44	*Cyclotella meneghiniana*, *Anomoeoneis sphaerophora*, *Nitzschia elegantula*, *Campylodiscus clypeus*			Samples 61,148,178? From Hecky and Kilham (1973): L. Singida, L.Silversea
AB		*Nitzschia fonticola*, *N.frustulum*, *N.elegantula*, *N.punctata*, *N.latens*, *Rhopalodia gibberula*			Samples 74,81,82,83,84,87,141,142 From Hecky and Kilham (1973): L.Ghama, L.Gidaburk
ASSEMBLAGE VB		Group V characteristic species : 10-60%			
	9-17	*Cymbella affinis* v.*afarensis*, *Gomphonema gracile*, *Nitzschia palea*, *Amphora coffaeformis* + v., *Nitzschia elegantula*, *N.obtusa*	*Cymbella affinis* v.*afarensis*		Samples 67,68,69,70,71,72
ASSEMBLAGE VC		Group V characteristic species : 30-98%			
	7-32	*Nitzschia frustulum*, *Amphora tenerrima*, *A.coffaeformis*, *Navicula ammophila*	*Amphora tenerrima*, *A.rognonii*		Samples 75,76,77,78,79,80,86

ASSEMBLAGE I C

The genera *Eunotia* (1-5 %) and *Pinnularia* (1-7 %) are still well-represented but this assemblage is dominated by *Melosira* (tab. 3).

Variations are observed depending on which taxa reaching the highest percentages.

Melosira granulata v. *jonensis* is common to abundant in samples 201, 202 (27-90 %), 185 (45 %), 187 (14 %), 188 (14 %) and 191 (10 %). Sample 159 contains 26 % of *M. granulata* v. *granulata*. The high percentage of *M. distans* v. *africana* and v. *humilis* characterize samples 158 (75 %), 211 (24.0 %) and 188 (10 %). *M. ambigua* dominates sample 187 (63 %), 181 (80 %) and 182. *Fragilaria* reaches significant percentages in samples 201 (3.5-38 %) and 159 (23 %) with *F. construens* and varieties, *F. brevistriata*, *F. leptostauron*, *F. africana*, *F. lapponica*, and *F. pinnata*. *Synedra acus* and/or *S. ulna* represent 12 % of the population in sample 182, and 11 % in 191. The flora of samples 181 and 202 resembles assemblage III A since the percentage of *Eunotia* + *Pinnularia* only reaches 1.5 %.

Diatoms from L. Chiwa-Ngandu (RICHARDSON, 1968) and some diatom communities from the Bangweulu swamps also belong to assemblage I C. At Twingi, the dominant species is *Melosira italica* and the total percentage of *Eunotia* is 39.3 % (CHOLNOKY, 1970: sample B 6).

Assemblage I C occurs in shallow river-lakes or swamps, most of the waterbodies receiving inflow from swampy areas (WB 3) (Kagera river-lakes, Mweru and Bangweulu systems). It develops under warm conditions, in waters of very low to low conductivity, very low to medium alkalinity and medium low pH (fig. 7). It seems to be linked to chemical facies 2 (figs. 4, 5) since the ratio $(Na^+ + K^+)/(Ca^{2+} + Mg^{2+})$ varies from 0.6 to 1.06 with an average of 0.76 (fig. 7). The silica content of these waters is high ($SiO_2 \geqslant 13.9$ mg.l^{-1}).

ECOLOGICAL OCCURRENCE AND SIGNIFICANCE OF GROUP I

Assemblages characterized by the relative percentages of *Eunotia* and *Pinnularia* are linked to the following environmental conditions:

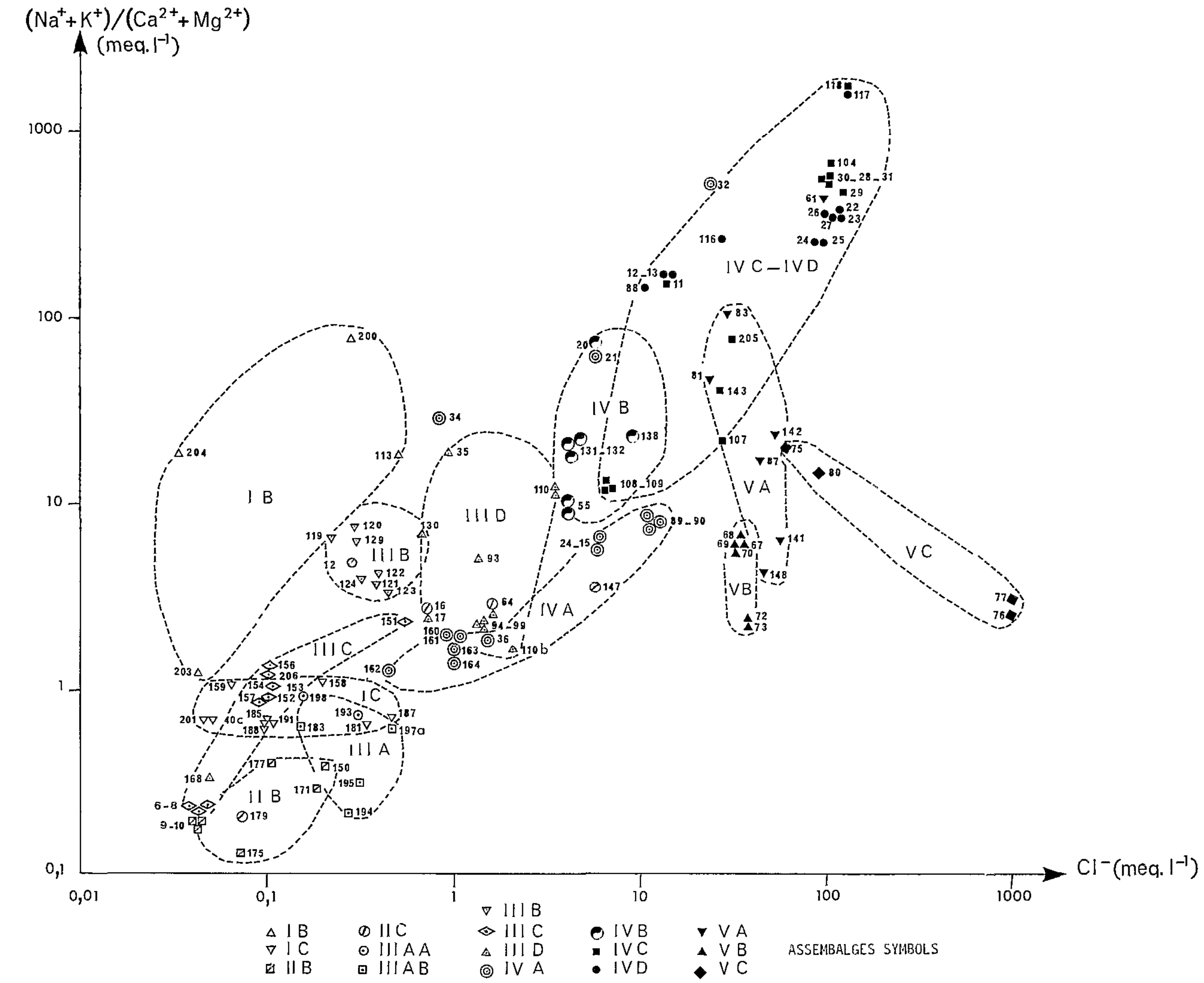


FIG. 4. — Sample and diatom assemblage distribution as a function of the ratio ($Na^+ + K^+$)/$Ca^{2+} + Mg^{2+}$) (in meql⁻¹) and Cl^- (in meql⁻¹). Each assemblage is represented by a symbol. Each sample belongs to one assemblage. Each sample is indicated by the sample number (arabic number) and the symbol of the corresponding assemblage. For example: ▲ 72: sample N° 72 belonging to assemblage V B. The dashed lines group the samples belonging to a given assemblage.

— They occur in peat-bogs, ditches, swamps or shallow lakes receiving considerable amounts of rainfall as a result of their high altitude or their latitude. These biotopes are fed directly by rain, or by rivers draining rainy and swampy catchment areas.

— Except for L. Tondwa, the waters have a low conductivity (< 260 and usually < 100 μScm⁻¹), very low to low alkalinity (<3.1 and generally < 1 meql⁻¹) and medium low to medium pH (< 7.9 and usually < 7).

These carbonate-bicarbonate waters are dominated by $Na^+ + K^+$ (assemblage I B), or $Ca^{2+} + Mg^{2+}$ (assemblage I C). The silica content ranges from 2.4 to 55.6 mgl⁻¹ SiO_2. The water temperature varies from 2.5 to 30.5 °C.

The dilute, acid conditions which prevail when *Eunotia-Pinnularia* assemblages develop are encountered in two main types of biotopes:

— The first one is represented by small lakes or *Sphagnum* bogs lying in high mountains, and populated by assemblage I A (WB 1). In the present survey, this assemblage corresponds to cold water. A low temperature, however, does not seem to be the determining factor since the diatom communities from some other high mountain lakes belong to

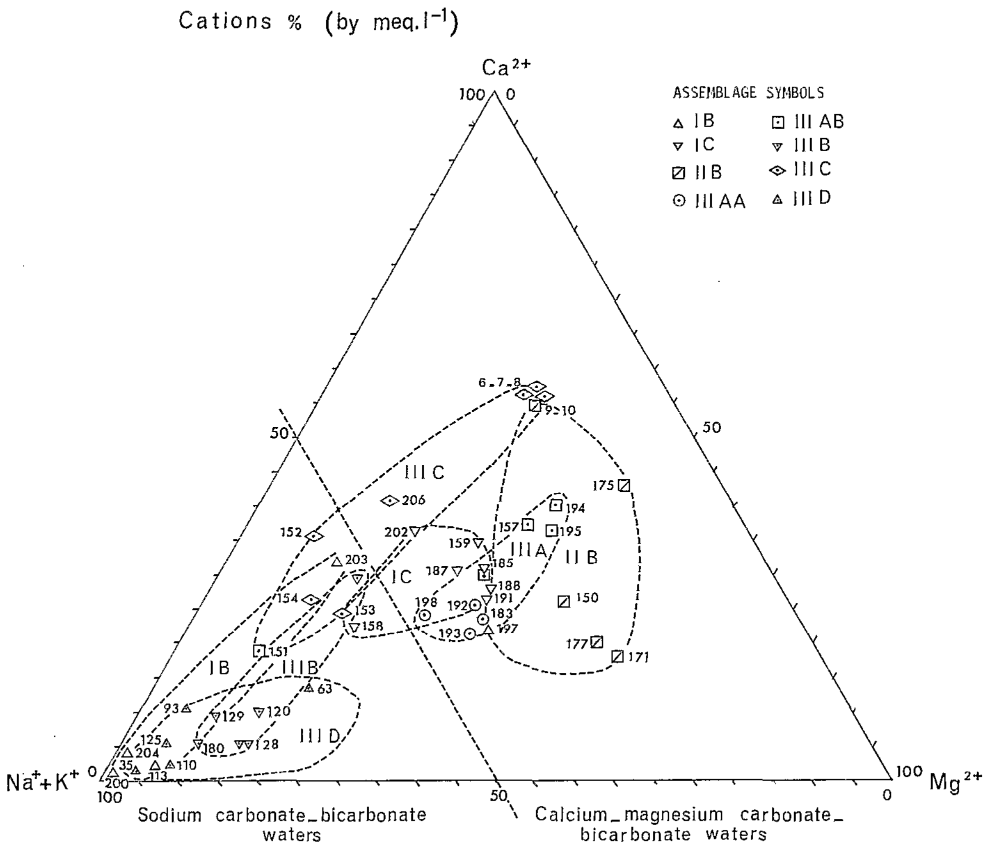


FIG. 5. — Sample and diatom assemblage distribution as a function of the water cationic composition for carbonate-bicarbonate water type waters (assemblages I B to III D are considered). Each assemblage is represented by a symbol. Each sample belongs to one assemblage. Each sample is indicated by the sample number (arabic number) and the symbol of the corresponding assemblage. For example, ☒ 175: sample N° 175 belonging to assemblage II B. The dashed lines group the samples belonging to a given assemblage.

group II (sample 40 b: assemblage II B). In order to verify the major influence of the chemical factors, a study of the diatom population of tropical *Sphagnum* bogs would be necessary. In Africa, such *Sphagnum* swamps occur in the crater of Mgahinga volcano on the Uganda-Zaire border, and on the east side of L. Nabugabo in the Katonda River system. The TDS (Total Dissolved Solids) under the *Sphagnum* is very low and waters are very acid (pH: 3.5-4.0) (BEADLE, 1974, p. 245), but are warm.

— The second type of biotopes includes tropical-equatorial swamps, swampy lakes populated by different emergent plants, and lakes draining swampy areas (WB 3). Some characteristics of the African tropical swamps are discussed by BEADLE (1974), and the water chemistry of the Bangweulu swamps was studied by SYMOENS (1968). The waters have a low TDS. Because of the oxygen consumption, the water logged mat and bottom peat are poor in oxygen and highly reducing. The pH of the papyrus swamp water is usually between 6.0 and 6.5. "Though some organic acids are present, the acidity seems to be mainly due to carbon dioxide from organic decomposition" (BEADLE, 1974, p. 248).

A number of species characteristic of Group I are commonly regarded as being cold or cool water forms, such as *Pinnularia cardinalis* (6 % in L. Tondwa), *Eunotia valida* (PATRICK and REIMER, 1966, p. 639, p. 192) and *E. pectinalis* (PATRICK and REIMER, 1966, p. 205) (WHITFORD and SHUMACHER, 1968). From the present survey, it appears that they are actually linked to very low to low salinity, pH and alkalinity, but not to low temperature because they develop in equatorial swamps under rather warm conditions.

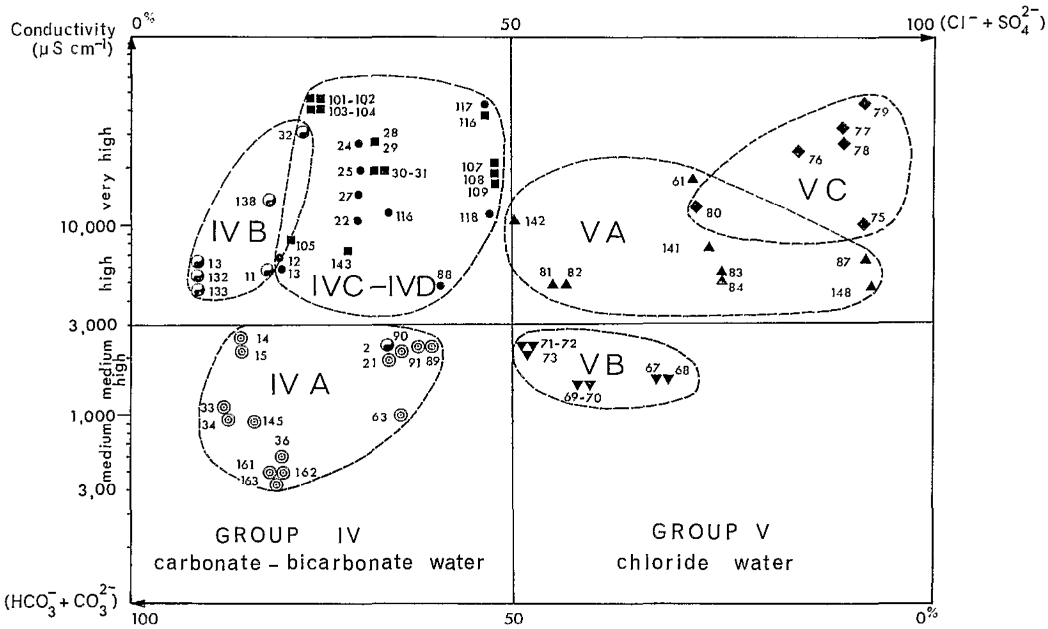


FIG. 6. — Sample and diatom assemblage distribution as a function of water anionic composition and conductivity. Assemblages IV A to V C are considered. Each assemblage is represented by a symbol. Each sample belongs to one assemblage. Each sample is represented by the sample number (arabic number) and the symbol of the corresponding assemblage. For exemple: ▲ 72: sample N° 72 belonging to assemblage V B. Assemblage symbols as for fig. 4.

Group II : *Achnanthes, Amphora, Cocconeis, Cymbella, Gomphonema, Navicula, Nitzschia* **abundant**

Group II is defined by the high percentages of freshwater species belonging to the genera *Achnanthes, Amphora (A. ovalis* and v., *A. pediculus). Cocconeis, Cymbella, Epithemia, Gomphonema, Navicula, Nitzschia (N. amphibia, N. fonticola, N. frustulum, N. palea, N. paleacea, N. recta)*, the total percentage of these taxa being above 60 %.

The most widely distributed species are *Amphora ovalis* and v., *Cocconeis placentula, Cymbella affinis, C. turgida, c. ventricosa, Epithemia zebra, Gomphonema parvulum* and v., *G. clevei, G. gracile, Navicula seminulum, N. seminuloides, N. exiguiformis, Nitzschia fonticola* and *Synedra ulna*.

This group corresponds to numerous periphytic samples from freshwater lakes and rivers. In such biotopes, the diatom communities are highly dependent on the substratum. Thus changes in community structure over very short distances are commonly observed at a given locality. Samples 41, 42, 43, for example, were collected from the same station in the Webi Shebelle river. Sample 41 is a rock scraping: it is dominated by *Cymbella affinis* (55.4 %) and *Navicula bryophila* (11 %). Sample 42 is the bottom mud; *Cocconeis placentula* (12.4 %) and *Nitzschia amphibia* (11.0 %) are the dominant species. Sample 43 is the epiphytic flora on a *Scirpus* stem; the best developed species are *Gomphonema olivaceum* v. *minutissima* (12 %), *Nitzschia linearis* (11.4 %), and *Navicula salinarum* v. *intermedia* (11.2 %). Marked differences are even observed between the stem and the floating leaves of the same aquatic plant. Sample 45 was taken from *Potamogeton* leaves : *Cymbella fonticola* reaches a percentage of 24, *Navicula salinarum* v. *intermedia* (18.4 %) and *Nitzschia linearis* (10.2 %) are common. Sample 46 was collected from the submerged stem and it contains 29.2 % of *N. salinarum* v. *intermedia*, 18 % of *Nitzschia amphibia*; *Cymbella fonticola* is absent. In Lake Tana, sample 9 collected on *Ceratophyllum* is dominated by *C. placentula* whereas *Nitzschia amphibia* is the best developed in the bottom mud (sample 10 b) taken about 10 cm from sample 9.

Few species however exhibit a clear habitat preference. *Cocconeis placentula* or *Cymbella fonticola* seem to favour epiphytic habitats. Of particular note is the development of *Achnanthes hungarica* on *Lemna* in samples 53 and 54, this affinity having been previously observed by HUSTEDT (1927-1966, II, p. 384). The flora' heterogeneity at a given locality makes any subdivision of Group II difficult, and the association of "definitive" or "co-occurring" species is more important than the common or abundant species in the assemblage definitions.

Assemblage II A

The flora is highly diversified (46-119 taxa), the assemblage being mainly defined by the "definitive" and the "cluster of co-occurring" species (tab. 3). Only three species are abundant in a few samples (*Achnanthes minutissima* in samples 52, 53), *Cymbella affinis* in sample 41, and *Fragilaria construens* in sample 54). Many species have percentages ranging from 3 to 20 %. The dominant species is one of the following taxa: *Achnanthes minutissima* (samples 51, 52, 53), *A. lanceolata* (sample 47), *Cocconeis placentula* (samples 42, 49), *Cymbella affinis* (sample 41), *Fragilaria construens* (samples 55, 54), *Gomphonema olivaceum* (samples 43, 48), *Navicula salinarum* v. *intermedia* (samples 44, 45, 46), *Nitzschia recta* (sample 58).

Assemblage II A is linked to low to medium low temperatures since it occurs in the Ethiopian highlands. These biotopes are fed mainly by turbid waters descending from the neighbouring high Balé mountains (Gadeb plain) (WB 4). The waters have low to very low TDS, medium low pH, very low alkalinity and belong to the sodium carbonate-bicarbonate type (chemical facies 1).

Assemblage II B

At least two of the following taxa, characteristic because of their percentages (tab. 3) are associated: *Amphora ovalis* and v., *A. pediculus*, *Cocconeis placentula*, *Epithemia zebra*, *E. sorex*, *Eunotia pectinalis* v. *minor*, *Melosira distans* v. *alpigena*, *Navicula perpusilla*. The total percentage of these taxa varies from 12 to 80 %. *E. pectinalis* v. *minor* and *N. perpusilla* also characterize Group I. *M. distans* v. *alpigena* is also found in assemblage III D.

The dominant taxa are *Cocconeis placentula* (samples 10, 171, 173), *Fragilaria construens* v. *venter* (sample 197 b). *Gomphonema parvulum* and v. *micropus* (sample 175), *Nitzschia amphibia* (sample 9), *N. fonticola* (sample 177), *N. frustulum* (sample 150). "Definitive" and "co-occurring species" are indicated in tab. 3.

Assemblage II B is typical of mud or epiphytic samples. It is a periphytic association found in small shallow lakes or in the littoral zone of large lakes such as L. Tana. These lakes of high to medium altitude have low to medium water temperatures. They are mainly fed by direct rainfall over the lake (WB 2: L. Tana) or by runoff from high mountains (Kivu area, Ruwenzori, Kilimanjaro: WB 3). The waters have a low conductivity, a medium pH, and a low to medium alkalinity. This assemblage seems to be linked to chemical facies 2 (figs 4, 5, 7) and is found in waters which are rather rich in silica (figs 3, 4, 5, 7).

Assemblage II C

Assemblage II C satisfies the structure definition of Group II, but is heterogeneous and badly defined since no "definitive" or "cluster of co-occurring species" can be discerned. The dominant taxa are:

— *Achnanthes minutissima* (44-50.5 %) and *Nitzschia communis* (16.5-34.6) in samples 96, 97, 98, 99.

— *Cocconeis placentula* (35 %) associated with *Navicula mutica* (18 %) and *Epithemia zebra* (14 %) in sample 147.

— *Gomphonema parvulum* (57.0 and 17.8 % in samples 179 and 60 respectively) associated with numerous *Nitzschia*, especially *N. fonticola* (26 % in sample 179, 5.5 % in sample 60), *N. frustulum* and *N. paleacea* (17.5 and 8.5 % respectively in sample 60).

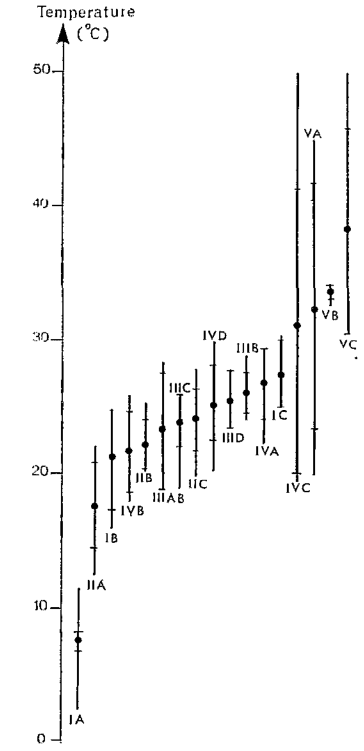
— *Nitzschia fonticola* (90 % in 172, 32.5 % in sample 62).

— *Nitzschia amphibia* in samples 17, 18, 19 associated with common *Fragilaria intermedia*, *Cymbella microcephala*, *C. ventricosa*, *Anomoeoneis exilis*, *Cyclotella pseudostelligera*.

Assemblage II C is a littoral association found in shallow lake periphyton, swamps and rivers, in waters of low to medium high conductivity. As regards the water temperature and chemical facies, it is eurytopic (tab. 1, fig. 7). This assemblage is typical of biotopes of various hydrological types (WB 2, 3, 4, 6) and of various chemistry. Samples 17, 19, 60, 62 are taken from sodium carbonate-bicarbonate waters, whereas the dominant cations are Ca^{2+} and Mg^{2+} in 197, 167 and 179. Waters from Kenke swamp (147) are dominated by sodium ($Na^{+} \geqslant 37.9$ %); Cl^{-} is the dominant anion and the ratio $(Cl^{-} + SO_4^{2-})/(HCO_3^{-} + CO_3^{2-})$ reaches 1.1. The imprecise definition of assemblage II C could explain the ecological diversity of the corresponding environments.

Ecological occurrence and significance of Group II

Group II represents the periphytic assemblages of numerous freshwater biotopes including lakes, rivers and swamps. Most of these biotopes are populated by abundant aquatic macrophytes on which epiphytic diatoms developed. The diatom assemblages seem to depend on several ecological factors.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IIA
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IVB
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IIID
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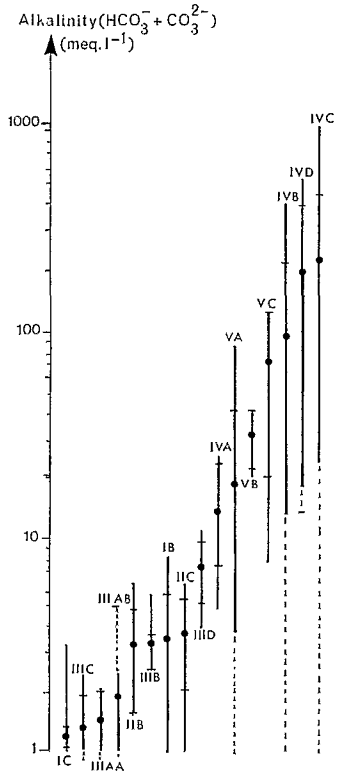
IVC
VA
VB
VC

7a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($meq.l^{-1}$)
1000
100
10
1
IC
IIIC
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IIID
IVA
VA
VB
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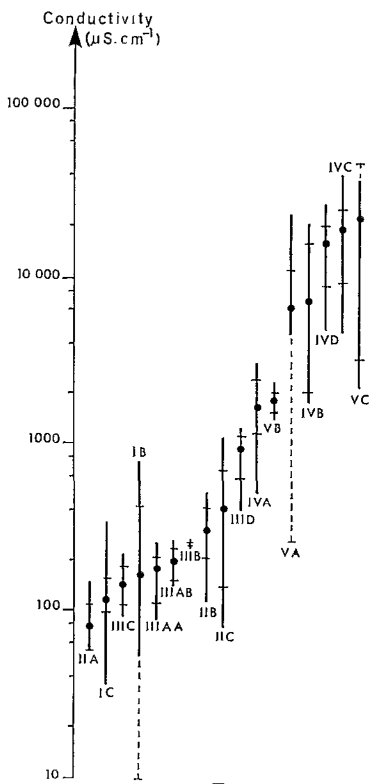
IVB
IVD
IVC

7b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($\mu S.cm^{-1}$)
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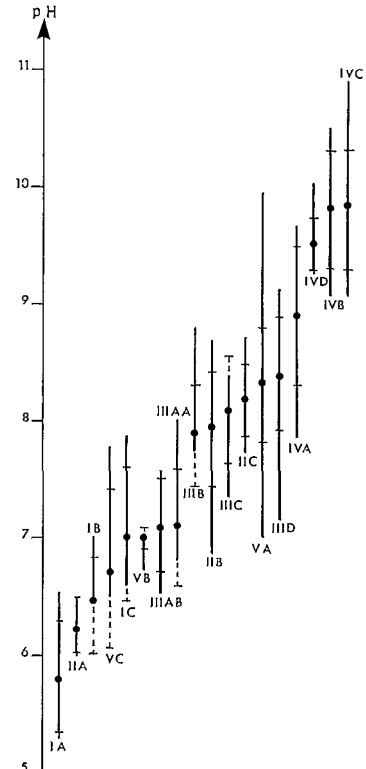
IVD
IVC
VC

7c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IVC

7d

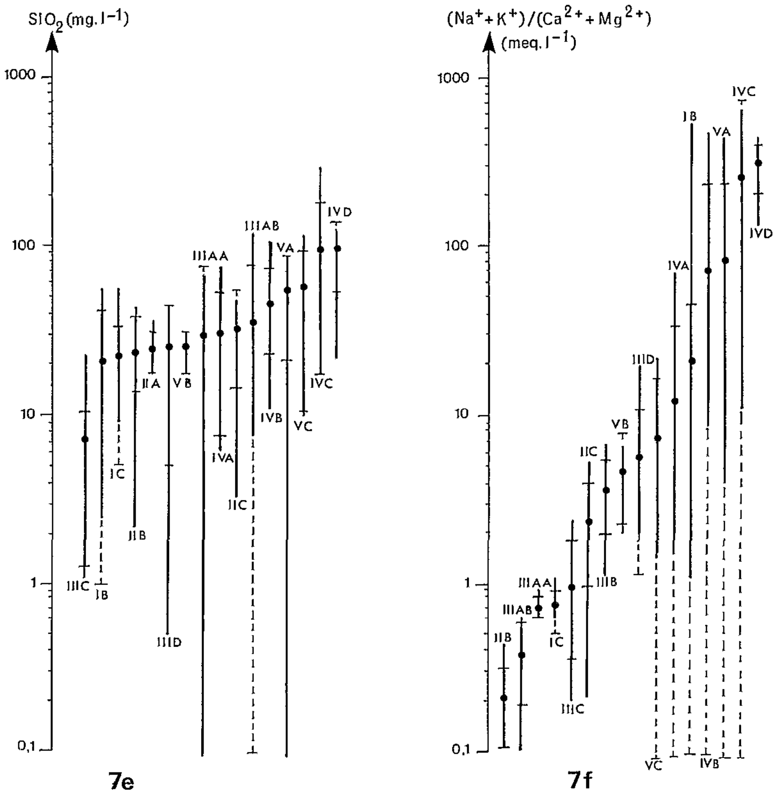

FIG. 7. — Diatom assemblage distribution as a function of: a: water temperature; b: conductivity; c: pH; d: alkalinity; e: $(Na^+ + K^+)/(Ca^{2+} + Mg^{2+})$ (in $meql^{-1}$); f: Na^+/Cl^-(in $meql^{-1}$); g: SiO_2 (in mgl^{-1}). For each of these individual variables, and for each assemblage, the mean, the range and the standard deviation were calculated. The assemblages are ordered in function of the increasing mean value of the individual variables. Circles indicate means; solid lines, ranges; transverse bars and dashed lines, standard deviations.

— The microhabitat is of major importance. At a given locality, it is responsable for variations in community structure and for species diversity.

— Assemblages II A and II B seem to be associated with certain chemical conditions in terms of conductivity, pH, alkalinity and ionic ratios (figs. 4, 5, 7).

— Assemblage II A could be an indicator of low to medium low water temperature whereas assemblage II B occurs in mesothermic biotopes (fig. 7).

The localities where assemblages II A and II B develop are mainly fed directly by rainfall, or indirectly by runoff, from highland precipitation. Assemblage II A is found in biotopes hydrologically dependant on the Balé mountains. Most of the lakes corresponding to assemblage II B are fed by small rivers descending from high equatorial mountains. Local precipitation would represent the major water input in L. Tana.

Group III : *Melosira* spp. and / or *Synedra acus* abundant

Group III includes the planktonic communities of many East African lakes and is dominated by the genera *Melosira* or *Synedra*. In contrast to assemblage I C, the total percentage of *Eunotia* + *Pinnularia* is below 3 %. According to HUSTEDT (1949) and RICHARDSON *et al.* (1978), the prominence of the genera *Melosira* and/or *Synedra* is, in itself, an indication of relatively dilute conditions. A more sensitive interpretation can, however, be attempted by taking into account the whole community rather than just the abundant taxa, and by recording changes in the dominant species and in their environments.

ASSEMBLAGE III A

Assemblage III A is defined by the high percentages of *Melosira granulata* and varieties (especially v.

jonensis), *Synedra acus*, *Cyclotella stelligera*. At least two of these taxa are common to abundant, their total percentage being > 45 %.

This assemblage can be subdivided on the basis of the development of *Cyclotella stelligera*.

Assemblage III AA: *Cyclotella stelligera* is common (8.2-31.4 %). The dominant taxa are *C. stelligera* in sample 192 (31.4 %), *Melosira granulata* and varieties (86.6 % in sample 193), or *Synedra acus* (52 % in sample 198). The community of L. Bisongou (sample 185) is intermediate between assemblages I C and III A because of the relative percentages of *Eunotia* (1 %) and *Pinnularia* (3 %). This lake, however, presents the ecological conditions required for the growth of the *Synedra acus* — *Melosira granulata*— *Cyclotella stelligera* assemblage.

From the semi-quantitative analyses conducted by HUSTEDT (1949), the deep water (20 m) of L. Ndalaga (Kalondo station) appears to belong to assemblage III AA. The diatom flora from L. Bita (HUSTEDT, 1949) also resembles assemblage III AA in its abundance of *Cyclotella stelligera* v. *tenuis* (which may not be separated from the type: GASSE, 1983), although this species is associated here with abundant and dominant *Melosira ambigua*.

— *Assemblage III AB* is dominated by *M. granulata* and its varieties in samples 197 a, 194, 195. This species and its varieties represent 37.8 % of the population in sample 183, where *M. ambigua* reaches the percentage of 50.0 %. As a result of the dominant species and the rather low percentage of *Synedra acus* (4.2 %), sample 183 is intermediate between assemblages III AB and III B. In assemblage III AB, the percentage of *Synedra acus* varies between 4.2 and 20 %, and is often associated with *S. ulna*. A number of other species are occasionally common such as *Fragilaria construens*, *Melosira agassizii*, *Cocconeis placentula*, *Nitzschia fonticola*, *N. paleacea*. *Cyclotella stelligera* is rare to uncommon. Most of the samples from L. Ndalaga (HUSTEDT, 1949) have to be included in this assemblage.

Assemblages III AA and III AB are typical of the plankton and bottom mud samples of small shallow equatorial lakes, situated around the Virunga area (L. Mutanda, L. Muleha, L. Bulera, L. Ndalaga, L. Bita) or belonging to the Kagera river system (L. Bisongou, L. Rugwero). The water temperature is medium or medium-low as a result of their altitude. These open lakes are mainly fed by runoff from small mountainous catchment areas (WB 1 or 3). Assemblages III A are linked to low conductivity, medium or medium low pH and very low to low alkalinity. They occur in calcium-magnesium carbonate-bicarbonate waters of various silica content (fig. 7). The chemical composition differs slightly between assemblage III AA and III AB. Although the ratio $(Na^+ + K^+)/Ca^{2+} + Mg^{2+})$ is below 1 in all cases, it is lower for assemblage III AB than for assemblage III AA (mean values: 0.37 and 0.71 respectively). Ca^{2+}/Mg^{2+} (by $meq\,l^{-1}$) is > 1 in the case of assemblage III AB whereas it ranges between 0.5 and 0.8 for assemblage III AA (fig. 5). The development of *C. stelligera* may be favoured in Mg^{2+} rich waters. The silica content varies widely from lake to lake (fig. 7).

ASSEMBLAGE III B

Assemblage III B is defined by the high percentages of *Melosira ambigua* (> 10 %) and *Synedra acus* (> 12 %), one of these species being dominant, and their total percentage being above 60 %.

This assemblage was found in only two lakes, and its real value must be tested by further investigation. It is recorded from L. Naivasha (samples 117-124) and L. Chibwera (sample 174). The diatom community of L. Rugwero (sample 183) is similar to assemblage III B since *M. ambigua* dominates and *S. acus* represents 4.2 % of the diatom population. According to BACHMAN (1938) and RICHARDSON (1968), the flora from L. Narawska would belong to this assemblage. In L. Naivasha, 7 samples, collected at different times between December 1979 and May 1980, show the fluctuations indicated on tab. 4.

Assemblage III B is a planktonic association found in small shallow equatorial lakes having medium temperatures as a result of their altitude. By contrast with the nearest lakes L. Elmenteita and L. Nakuru, which are hyperalkaline (WB 6b), L. Naivasha is a freshwater lake, its water chemistry being controlled by groundwater seepage (KILHAM 1971 a; GAUDET and MELACK, 1981) (WB 6a). This assemblage occurs in waters of low to medium conductivity, medium pH, medium alkalinity, which are of sodium carbonate-bicarbonate type (figs. 3, 4, 5, 7).

ASSEMBLAGE III C

The cumulative percentage of *Melosira*, *Fragilaria* and *Synedra berolinensis* is above 50 % with the genus *Melosira* representing between 17.3 and 98.7 % of the population. *Nitzchia fonticola* is widely distributed and sometimes abundant. *Stephanodiscus astraea* and its v. *minutula* + *S. hantzschii* are often uncommon to abundant. To be noted is the presence of a number of "definitive" species which are generally regarded as being endemic in the great East African lakes (tab. 3), including some in the genera *Surirella* and *Cymatopleura*.

TABLE 4

Seasonal fluctuations of the most abundant diatoms in the plankton of Lake Naivasha.

Best developed taxa	Sample number						
	Main Lake						Crescent Island L.
	119 (5.12.79)	120 (8.2.80)	121 (13.3.80)	122 (19.4.80)	123 (2.5.80)	124 (6.80)	128 (5.12.79)
Synedra acus and v. (%)..	16.2	17.0	31.5	71.0	80.0	21.0	91.4
Synedra ulna and v. (%)..	0.0	9.0	5.0	0.5	0.5	0.0	
Melosira ambigua (%)....	61.2	62.0	59.0	22.5	17.5	75.7	6.6
Melosira granulata v. *angustissima*............	16.0	8.0	2.5	3.5	0.5	0.5	1.5

Changes in the community structure were observed between the different lakes, and the different samples of a given lake.

— *Melosira distans* v. *alpigena*, *M. italica* v. *bacilligera* and *M. agassizii* achieve dominance in L. Tana (samples 6, 7, 8).

Minor differences are observed between samples taken from L. Victoria and L. Malawi.

— *Melosira nyassensis* with its variety *victoriae* dominate samples 206 (L. Malawi), 153 and 154 (L. Victoria). They are associated with *Stephanodiscus astraea* which is common to abundant and, in the case of L. Victoria, with *Nitzschia fonticola*, *Fragilaria (F. construens, F. leptostauron, F. pinnata* and its variety *trigona)*.

— *Melosira ambigua* (84.6 %), *M. agassizii* (8.9 %) and *M. nyassensis* v. *victoriae* (5.2 %) represent 98.7 % of the community in sample 152 (L. Victoria).

— *Nitzschia fonticola* is the dominant species in samples 155, 157 (L. Victoria). It is associated with *Melosira agassizii*, *Synedra berolinensis* and *Fragilaria* spp. which are common. The diatom community from the Kasinga Channel (sample 165) closely resembles that from sample 157 although *Melosira granulata* v. *angustissima* replaces *M. agassizii*.

Diatom communities previously described from L. Tana (BRUNELLI and CANNICCI, 1940), and L. Victoria (OSTENFELD, 1909; HUSTEDT, 1922; THOMASSON, 1955; RICHARDSON, 1968) appear to satisfy the definition of assemblage III C. Ross (1952), and TALLING found *Nitzschia acicularis* to be the commonest *Nitzschia* in phytoplankton samples of L. Victoria.

Assemblage III C is a typical planktonic assemblage of great East African lakes, L. Tana, L. Malawi and L. Victoria having an area ranging between 3,500 and 70,000 km². In such lakes, local precipitation and evaporation (on the lakes themselves) are probably important components of the water budget (WB 2) (STREET, 1980). Their waters have a low to very low conductivity, medium pH, very low to low alkalinity. They are carbonate-bicarbonate lakes with the exception of one sample from L. Victoria (151) where $(Cl^- + SO_4^{2-}) = (HCO_3^-) + CO_3^{2-})$. The ratio $(Na^+ + K^+)/(Ca^{2+} + Mg^{2+}) = 0.2$ in L. Tana, 0.8 in L. Malawi. This ratio varies from 0.9 to 2.3 in L. Victoria samples. Silica content ranges from 1.1 to 22 $mg.l^{-1}$ (figs. 4, 5, 7). Variations observed in the species representation could be due to these chemical differences, but the habitat must also be considered. Samples from open water are mainly colonized by the euplanktonic *Melosira*, whereas the shallow marginal areas of L. Victoria seem to be favoured by *Fragilaria* spp., *Nitzschia fonticola* and *Synedra berolinensis*.

ASSEMBLAGE III D

The genus *Melosira* (24.5-92.4 %) prevails in this assemblage. It is often associated with common *Stephanodiscus (S. hantzschii + S. astraea)*, or *Nitzschia* (especially *N. amphibia*, *N. fonticola*, *N. frustulum*, *N. gracilis*, *N. palea)* in samples 16, 35, 63, 111 and 168. Several species absent in previous groups appear, such as *Anomoeoneis sphaerophora*, *Cyclotella meneghiniana*, *Navicula elkab*, *Rhopalodia gibberula*, *Thalassiosira rudolfi*, *Nitzschia latens*, *N. pusilla*. These species are characteristic by their percentages when common or uncommon, or by their presence when several of them are associated together.

The assemblage can be subdivided on the basis of the *Melosira* species which reach the highest percentages.

— Assemblage III DA: *M. ambigua* dominates, as in the bottom mud samples of L. Naivasha (125, 126, 129, 130) where the communities resemble assemblage III B (*Synedra acus* uncommon to common). These bottom samples differ from the living plankton in the percentages of *Cyclotella meneghiniana*, *Thalassiosira rudolfi* and *Navicula elkab*, which are uncommon to common. This difference could be due to the lake-level fluctuations involving changes in water conductivity during the past few years. L. Naivasha experienced a low lake-level from about 1940 to 1961 (Vincent *et al.*, 1979, fig. 3): the species cited above could developed at this time, but this is purely hypothetical. Sample 35 is transitional between assemblage III D and IV A because it is rich in planktonic *Nitzschia* (40.6 %).

— Assemblage III DB (samples 93, 94, 95, 110a, 110b, 168, 146, 64) is mainly composed of *M. granulata* v. *angustissima* and *M. granulata* v. *angustissima f. curvata*. The community of sample 16 is rich in *M. granulata* v. *granulata* and resembles assemblage II C because of the abundance of periphytic freshwater species.

Assemblages III D are planktonic associations which populate numerous rift lakes situated in semi-arid or arid zones. Assemblages III DA and III DB occur in L. Gamari, a river-lake of the Afar desert (WB 4), and in lakes without surface outlet (L. Baringo, L. Ol Bolossat, L. Naivasha, L. Awasa) where the relatively low salinity is probably due to groundwater seepage (WB 6a) (as in L. Naivasha: Gaudet and Melack, 1981). These small shallow lakes have usually low transparency. L. Naivasha and L. Baringo are daily mixed (Howard-Williams and Ganf, 1981, p. 105). Such a diurnal, wind-induced water mixing, which characterizes most of the African shallow lakes, probably also occurs in the three other lakes and may influence the plankton composition.

Assemblage III D develops in waters of medium high conductivity and alkalinity, medium to high pH and varying silica content (fig. 7). All the biotopes have carbonate-bicarbonate water (figs. 4, 5). Na^+ is the dominant cation in assemblages III DA and III DB samples (facies 1) except in L. Saka (facies 2).

Ecological occurrence and significance of Group III

Group III includes planktonic assemblages from numerous East African lakes, most of them being characterized by the prominence of the genus *Melosira*.

Changes in the dominant species of *Melosira* provide some information on the general habitats of these lakes. *M. agassizii* and *M. nyassensis* tend to develop in large lakes whereas *M. granulata* and its varieties, or *M. ambigua*, tend to prefer small shallow and turbid lakes, or the littoral areas of the bigger lakes. *M. granulata* var. *angustissima* appears to be particularly abundant in very turbid waters.

Assemblage III A is found in lakes which depend hydrologically on abundant rainfall from the neighbouring high mountains. The water budget of the lakes which are populated by assemblage III C depends largely on local precipitation and evaporation. Assemblages III B and III D develop mainly in rift lakes.

All the biotopes have waters which are fresh, with conductivities between 96 and 1,360 μScm^{-1}. Group III also reflects low to moderate alkalinity (0.8-12 $meql^{-1}$), circumneutral to high pH, and occurs in carbonate-bicarbonate waters. *M. granulata* v. *jonensis* and *M. distans* v. *alpigena* developed mainly in waters with very low salt contents belonging to chemical facies 2. The highest percentages of *M. granulata* v. *angustissima* are observed in Na^+ rich waters whereas *M. ambigua* seems to be indifferent to the cationic ratios. Assemblage III A is associated with facies 2. Assemblages III C, III B, and III D, occurring in sodium-dominated waters (facies 1), seem to replace each other as the conductivity, pH and alkalinity increase.

According to Kilham (1971b), *Melosira granulata* is rarely a dominant species in waters having low silica concentration (< 1.0 $mg.l^{-1}$). These observations are widely misinterpreted to mean that *M. granulata* is particularly successful at high silica concentrations. Physiological work on a clone of *M. granulata* from L. Mulehe (= sample 194) shows that this species has a high growth requirement for silica compared to other diatom species (S. Kilham, pers. comm.). This means that *M. granulata* would be a poor competitor for silica under Si-limitating conditions, and therefore is particularly unsuccessful when silica levels are low. It should also recognized that correlations of diatom relative abundances determined from sediment samples with nutrient chemistry determined usually from single water samples are particularly prone to error.

Group IV : *Nitzschia* **spp.** *Thalassiosira rudolfi*, *Anomoeoneis sphaerophora*, *Rhopalodia gibberula* **common to abundant**

Group IV is in sharp contrast to Group III because of the poor development of *Melosira* (< 10 %), the diversity of the genus *Nitzschia*, and the high cumulative percentage of *Anomoeoneis sphaerophora*, *Navi-*

cula elkab, *Nitzschia estohensis*, *N. latens*, *N. pusilla*, *Rhopalodia gibberula*, and *Thalassiosira rudolfi*. These species are characteristic because of their frequencies. Group IV is also defined by a number of "definitive" species indicated in table 3.

Assemblage IV A

The genus *Nitzschia* represents 15 to 99 % of the population. The cumulative percentage of the species, cited above ranges from 2 to 10 %. The genus *Stephanodiscus* is often common or abundant, forming a transition between assemblage III D and IV A. Samples 160, 161 (L. Mobutu Sese Seko), 162, 163, 164 (L. Edward) are rich in *Stephanodiscus damasii*. *S. astraea* occur in sample 63. In the most dilute lakes, *Fragilaria construens* v. *venter* is sometimes abundant.

Assemblage IV A is found in the plankton or the periphyton of numerous lakes (samples 3, 4, 14, 15, 20, 33, 34, 36, 37, 63, 89, 91, 92, 160, 161, 162, 163, 164). The relatively high percentages of *Stephanodiscus* are observed in the river-lakes L. Mobutu Sese Seko, L. Edward and L. Gamari (WB 3). The other lakes are endorheic (WB 6a, b). The water temperature is medium to high (fig. 3). All the biotopes have medium to high conductivity, medium to high pH, medium to high alkalinity and belong to the chemical facies 1 (figs. 5, 6, 7). The high percentages of *Stephanodiscus damasii* in L. Mobutu Sese Seko and L. Edward are associated to relatively high concentrations and proportions of K^+ and Mg^{2+}, which represent 8.1 to 9.8 %, and 14; 6 to 16.8 % of the ionic sum respectively. High proportions or concentrations of these cations may favour the growth of *Stephanodiscus damasii*.

Plankton from L. Tanganyika may also belong to this association. Sample 205 is mainly composed of *Nitzschia spp* (*N. spiculum* dominant), but *Stephanodiscus damasii* is commonly found in this lake (C. Haberyan, pers. comm.; J. L. Richardson, pers. comm.). Diatom communities previously described in L. Mobutu Sese Seko (Bachmann, 1933; Talling, 1963), L. Edward (Hustedt, 1949), L. Kivu (Hustedt, 1949; Degens *et al.*, 1973) seem to satisfy the definition of assemblage IV A.

Assemblage IV B

The percentage of the genus *Nitzschia* exceeds 50 % in this assemblage, and the species characterizing Group IV represent between 10 and 40 % of the population. The dominant species is one of the following: *Nitzschia frustulum*, *N. latens*, *N. pusilla*, *N. estohensis*.

Assemblage IV B is found in plankton, periphyton and offshore samples from closed lakes (12, 20, 32, 131, 132, 133, 138) (WB 5 or 6b), and in a small pond on the Gadeb plain (samples 55, 56). A number of lakes studied by Hecky and Kilham (1973) have a similar flora (L. Tulusia, L. Big Momela, L. Reshitani, L. Gidaburk). The water temperature varies from 18 to 26 °C. This assemblage occurs in sodium-bicarbonate waters having medium high to very high conductivity, high to very high pH, medium high to very high alkalinity and a high silica content (> 10 $mg.l^{-1}$). ($HCO_3^- + CO_3^{2-}$) represents more than 75 % of the anions (except for sample 20) (figs. 4, 6, 7).

Assemblage IV C

Nitzschia is common to abundant in this assemblage (> 27 %). The dominant species are *Nitzschia latens* + *N. pusilla* (samples 30, 101, 102, 104, 107, 108, 109, 118, 143), or *N. frustulum* + *N. subrostrata* (samples 28, 31), or *Thalassiosira rudolfi* (samples 29, 166, 121). The cumulative percentage of the species characteristic of Group IV is above 40 %. The diatom community from Small Momela lake (Hecky and Kilham, 1973) meets this definition.

Assemblage IV C is encountered in the plankton, littoral or bottom mud samples of closed lakes (WB 6b) and in alkaline hot springs (WB 7). Water temperatures range from 19.5 to 55 °C. In all cases, the conductivity is > 6,000 μScm^{-1}, pH is > 9.1, alkalinity is > 25 $meql^{-1}$, SiO_2 content is > 17 $mg.l^{-1}$. ($Na^+ + K^+$)/($Ca^{2+} + Mg^{2+}$) varies from 1.16 to 1941 (figs. 4, 7), and ($HCO_3^- + CO_3^{2-}$) represents between 50 % and 80 % of the anions (fig. 5). It does not appear possible to provide a more sensitive classification using the dominant taxa. In a given lake, the dominant species changes as a function of the sampling date and of the sample type. No relationship between the various dominant species and the water composition could be detected.

Assemblage IV D

Assemblage IV D differs from assemblage IV C in its dominant species which include *Anomoeoneis sphaerophora* (samples 1, 2, 5, 22, 116), *Navicula elkab* (samples 23, 88, 117), and *Rhopalodia gibberula* (sample 24), all of which are usually regarded as being periphytic.

This association can be compared with the communities from L. Small Momela and El Kekhotoito (*N. elkab* dominant), L. Lgarya and L. Gidamur (*A. sphaerophora* dominant), described by Hecky and Kilham (1973).

Assemblage IV D occurs in closed lakes or hot spring (sample 88) (WB 6, WB 7) as a planktonic or benthic association. When planktonic, however, it occurs in shallow lakes (L. Abiyata) which exhibit frequent water mixing, thus allowing the littoral species to enter the plankton. There were no clearly defined differences between the chemical composition of the habitats of assemblages IV C and IV D (fig. 5).

Ecological occurrence and significance of Group IV

Group IV includes planktonic and periphytic assemblages from weakly to strongly alkaline, silica-rich, waters of the sodium carbonate-bicarbonate type. Assemblages IV B, IV C and IV D can be compared with the diatom communities studied by Hecky and Kilham (1973) from 23 East African lakes, with alkalinity ranging from 14.0 to 965 $meql^{-1}$ and pH between 9.1 and 10.6. According to these authors, there is a pronounced tendency for the species to replace each other as alkalinity increases. *Cyclotella meneghiniana* is most abundant in the most dilute lakes whereas *Nitzschia frustulum* is clearly favoured as the alkalinity exceeds 80 $meql^{-1}$. *Thalassiosira rudolfi* (referred to as *Coscinodiscus rudolfi*) and *Navicula elkab* would fall between *C. meneghiniana* and *N. frustulum*. From the present investigation, the status of *N. frustulum* in the alkalinity gradient is not clear since it prevails in waters of medium to medium high alkalinity in the plankton of L. Langano and in some assemblages from Groups II and V. *N. frustulum*, however, has often been misidentified and is largely polymorphic (Lange-Bertalot, 1976; Lange-Bertalot and Simonsen, 1978). Further examination would be necessary in order to interpret the relationships between the morphological types and the water chemistry satisfactorily, but the dominant taxon is not sufficient to define an assemblage and all the characteristic taxa have to be considered.

Group V : *Amphora coffeaeformis*, *A. tenerrima*, *Campylodiscus clypeus*, *Mastogloia* spp., *Nitzschia punctata* common to abundant

Group V is defined by a list of species which are characteristic because of their high percentages or because of their presence (tab. 3). *A. coffeaeformis* and v., *A. acustiuscula*, *A. tenerrima*, *Nitzschia punctata*, *N. elegantula*, *Navicula ammophila*, *N. salinicola* often reach percentages above 10 %. *Mastogloia elliptica*, *Campylodiscus clypeus*, *Nitzschia obtusa*, *N. hungarica*, *N. tryblionella* and v., *Cymbella pusilla*. *Diploneis subovalis* are the most widely distributed.

A number of species are only found in one or several samples belonging to Group V; these include, for example, *Amphora rognoni*, *Gyrosigma spenceri*, *Mastogloia aquilegiae*, *Navicula iranensis*, *Nitzchia scalaris*, *N. stompsii*, *Hantzschia virgata*, *Stauroneis legleri*, *Synedra affinis*.

Most of these characteristic species usually inhabit littoral marine environments.

In spite of the numerous characteristic species, the number of taxa encountered in each sample is generally low (7-47 taxa per sample).

Assemblage V A

This assemblage is intermediate between Groups IV and V. The species found exclusively in Group V are present and sometimes common, their cumulative percentage ranging between 2.5 and 30 %. One also notes, however, the development of *Anomoeoneis sphaerophora*, *Rhopalodia gibberula*, *Nitzschia latens*, *Cyclotella meneghiniana*, *N. pusilla* which, when abundant, are otherwise regarded as being characteristic of Group IV.

Subdivisions can be formulated on the basis of the dominant taxa.

— Assemblage V AA: *Cyclotella meneghiniana* is dominant in samples 61 and 148. Their flora is comparable with that of L. Singida and Silver Sea (Hecky and Kilham, 1973).

— Assemblage V AB: Genus *Nitzschia* is the best represented. The dominant species are *N. latens* (sample 87), *N. frustulum* (samples 141, 142), *N. punctata* (sample 82), *N. elegantula* (sample 83), *N. fonticola* (samples 81, 84), or *Rhopalodia gibberula* (sample 74).

Diatom communities from L. Ghama and L. Gidaburk (Hecky and Kilham, 1973) resemble assemblage V AB.

Assemblage V A is encountered in closed lakes, spring-fed swamps and hot springs (WB 4b, 5, 6b and 7). The water temperatures range from 20 to 45 °C. The conductivity is high, pH varies from 7.5 and 10.3 and alkalinity from 2.58 to 87.4 $meql^{-1}$. The Na^+/Cl^- ratio is rather low (0.81-2.9) and ($Cl^- + SO_4^{2-}$) represent more than 50 % of the anions (fig. 6).

Assemblage V B

Assemblage V B is similar to assemblage II C since it is rich in freshwater periphytic and eurytopic diatoms. The dominant taxa are *Cymbella affinis* v. *afarensis*, *Gomphonema gracile*, or *Nitzschia palea*. *Amphora coffeaeformis* and varieties, + *Amphora acustiuscula*, reach percentages of 3 to 42 %, and

Nitzschia elegantula represents 4 to 14 % of the population. *N. obtusa* and *Mastogloia elliptica* are uncommon.

This assemblage is found in 6 samples from Wadi Kalou, a perennial spring-fed biotope (WB 7). It develops as an epiphytic, epipelic, epilithic or aerophilous community in clear running water. The dominant species changes rapidly depending on the microhabitat. Water temperatures are high. The water has a medium high conductivity, circumneutral pH, and medium high alkalinity. The Na^+/Cl^- ratio is about 1.5; ($Cl^- + SO_4^{2-}$) represent between 50 and 75 % of the anions (fig. 6).

Assemblage V C

The species characterizing Group V have a cumulative percentage ranging between 30 and 98 %, the dominant species belonging to the genera *Nitzschia* or *Amphora*. *Nitzschia* dominates samples 79, 96 *(N. frustulum)*, 75 *(N. punctata* and *N. af. kutzingiana)*, and 77 *(N. sigma)*. *Amphora* prevails in samples 76, 78 *(A. tenerrima)* and 80 *(A. coffeaeformis, A. acutiuscula, A. rognonii)*.

Assemblage V C is recorded from biotopes fed by hot springs (WB 7) having the following characteristics: high to very high temperature, high to very high conductivity, circumneutral pH, medium alkalinity. Na^+/Cl^- ranges between 0.65 and 1.32 ($Cl^- + SO_4^{2-}$) represents more than 70 % of the anions (fig. 6).

Ecological occurrence and significance of Group V

Assemblages belonging to Group V are found in saline lakes and hot springs having abundant sodium chloride. Chemical facies 3 is clearly reflected by the diatom flora. The characteristic species of Group V appear when the ratio ($Cl^- + SO_4^{2-}$)/($HCO_3^- + CO_3^{2-}$) reaches 1. Their percentage increases with this ratio and with the conductivity.

GENERAL DISCUSSION AND CONCLUSIONS

This work aims to compare the diatom communities from diversified East African biotopes, and to arrange them in phytosociological groups or assemblages. Each assemblage is found in a number of samples for which certain ecological conditions are known. Relationships between these diatom assemblages and their habitats, water temperature and water chemical composition are described. For each assemblage, the range, the mean value and the standard deviation were calculated for the following variables: water temperature, alkalinity, conductivity, pH, silica content, the ionic ratio ($Na^+ + K^+$)/($Ca^{2+} + Mg^{2+}$). On figure 7, the assemblages are ordered as a function of the increasing mean value of each of these individual variables.

Some general conclusions can be proposed based on the interpretation of the data obtained from the material studied here.

— Diatom assemblages appear to be clearly linked to the major ionic composition. Relationships between alkalinity and the dominant species or genus has been previously established for the sodium carbonate-bicarbonate, and saline lakes (Richardson *et al.*, 1978) (Hecky and Kilham, 1973). This work provides more sensitive results by taking into account the whole assemblage and the cationic and anionic ratios. Figure 4 shows the assemblage distribution as a function of the ratios ($Na^+ + K^+$)/($Ca^{2+} + Mg^{2+}$) and Na^+/Cl^-. The mean value of the ratio ($Na^+ + K^+$)/($Ca^{2+} + Mg^{2+}$) is below 1 for assemblages I C, II B and III A, which characterize the calcium-magnesium carbonate-bicarbonate waters (fig. 5). It is about 1 for assemblage III C. It is low (4.7-8) for assemblages III B and III D (fresh sodium carbonate-bicarbonate waters), and V B and V C (sodium chloride waters). It increases from 13 to 2,000 between assemblages IV A and IV D occurring in alkaline waters and reaches 85 for assemblage V A, which is intermediate between Groups IV and V.

The sodium carbonate-bicarbonate waters have a ratio ($Na^+ + K^+$)/($Ca^{2+} + Mg^{2+}$) ranging from 1 to 2,000; Na^+/Cl^- is above 2. These waters are populated by assemblages I B, III B to III D, IV A to IV D. These assemblages replace each other when the pH, conductivity and alkalinity increase.

The ratio Na^+/Cl^- is relatively low (about 2) for assemblage III A occurring in calcium-magnesium waters. Lower values are observed for assemblages V A, V B and V C (1.8, 1.5 and 0.9 respectively) (fig. 7) for which the ionic percentage of Cl^- ranges from 16 to 47 % (fig. 6). The ratio Na^+/Cl^- is above 3 for other assemblages.

— Poor correlations between the diatom assemblages and the silica content (SiO_2 mg.l^{-1}) are found. The best correlation is observed for assemblage III C for which the calculated mean, range, and standard deviation are 7.1, 1.1-23 and 5.7 SiO_2 mg.l^{-1} respectively.

— Information about the thermal requirements of the diatom communities is difficult to establish, probably because temperature varies diurnally through a wide range in most African tropical lakes, even in high mountains (Löffler, 1978). Correlations between the diatom assemblages and the water temperature are not clear (figs. 3, 7a). Standard deviations < 2 °C are only observed for assemblages I A, II B, III B and V B. In freshwater biotopes, low pH, alkalinity and conductivity appear to be more important than water temperatures for assemblages I B, I C and III A. In lakes having high mineral contents, the standard deviation calculated for the water temperature is high, and ranges from 7.8 to 10.8 °C for assemblages IV C, V A and V C; the direct effects of the temperature seem to disappear when the conductivity increases.

— The diatom flora reflects the types of habitats to varying degrees. In the freshwater biotopes (populated by assemblages I A to IV A), the planktonic, periphytic and aerophilous communities differ markedly in terms of their species composition and percentages. Changes in the dominant species of *Melosira* in the planktonic assemblages III A to III D seem to depend on lake size and depth, on the shore proximity and on the water turbidity. In contrast, in the alkaline and saline environments littoral and planktonic flora are often identical.

From the present investigation, the chemical factors appear to be clearly reflected in the diatom flora. The water chemistry is linked to climatic factors, geology and vegetation of the catchment area, type of water budget, and to chemical and biological cycles within the lakes themselves. An exhaustive classification of the biotopes would be impossible; but the diatom flora, however, allows some major groups of environments to be distinguished in relation to their geographical setting and/or their water budget.

— The alpine biotopes are situated above the timberline (in CZ IV). The dystrophic bogs, ditches and small acid lakes are fed mainly by direct rainfall over the highlands (WB 1). Their water has low temperature, very low pH and conductivity. They are populated by assemblage I A. Some alpine lakes having higher conductivity and water of the calcium-magnesium carbonate-bicarbonate type, are colonized by assemblage II B. The low temperature is not responsible for this assemblage distribution since assemblage II B is also found in warm environments.

— Between the Western Rift and L. Victoria (CZ VI), numerous small equatorial lakes are situated at medium altitude (900-1,900 m) in a rather humid region. Their small catchment areas are covered by different vegetation types ranging from tropical montane forest to grassy steppe. These open lakes present a certain homogeneity in terms of water chemistry and are characterized by a low $(Na^{+} + K^{+})/(Ca^{2+} + Mg^{2+})$ ratio. The highest lakes extend to the base of the Virunga volcanoes: they have medium low to medium pH, low conductivity and alkalinity, and their plankton belongs to assemblage III A. A continuum is observed between these highest lakes and the Kagera river-lakes with regard to their water chemistry and diatom flora. The Kagera river receives large quantities of water from th Virunga volcanoes ans the Rwanda highlands. The Kagera valley is, however, choked with swamp vegetation, and most of the Kagera river-lakes have the specific characteristics of tropical-equatorial swamps. Such environments are also represented by L. Kioga and L. Bisina belonging to the Victoria system. Their calcium-magnesium carbonate-bicarbonate waters are populated by assemblage I C. This chemical facies is also found in the small lakes situated on the Eastern side of L. Edward; they are more concentrated and populated by assemblages II B or II C.

— The group of the Southern shallow lakes and swamps also present some common characteristics. They are situated in a sub-humid region where a tropical evergreen and dediduous forest prevails (CZ VII). The waters are of carbonate-bicarbonate type, and usually have a very low conductivity and alkalinity. Assemblage I C occurs in the big L. Mweru, in its calcium-magnesium rich water. In the other lakes and swamps, Na^{+} is the dominant cation, but the proportions of K^{+}, Ca^{2+} and Mg^{2+} are often relatively high. These biotopes, rich in hydrophytes, are populated by assemblage I B.

— Planktonic flora from the large African lakes (L. Victoria, L. Malawi, L. Tana) (WB 2) can be recognized because of the presence and the quantitative development of several species, which are regarded as endemic to this lake region (especially a number of *Surirella*). Such a speciation phenomen could be due to the size of these lakes and to their long history.

— The Eastern Rift and the Ethiopian Rift lakes lie in semi-arid to sub-humid regions (CZ II, III, V) covered by thorn trees and grass savanna. Most of them have sodium carbonate-bicarbonate waters. Their conductivity ranges from 250 to 50,000 μScm^{-1}. There is a clear tendency for the diatom assemblages III B, and III D to IV D to replace each other as the total ionic content increases. The most dilute rift lakes are either river-lakes (such as L. Gamari, WB 4), or those having significant losses of salts as a result of seepage (such as L. Naivasha, Wb 6a). Such lakes are populated by the assemblages III B, III D and IV A. Assemblages IV B to IV D develop in the closed alkaline rift lakes (WB 6b).

— A similar chemical and floristic gradient is observed in the other alkaline biotopes in closed crater lakes (WB 5) or thermal springs (WB 7), independently of their geographical region and water temperature.

— Many hot spring-fed environments from the Afar desert (CZ I, II) and some closed lakes of volcanic or tectonic origin are characterized by their sodium chloride waters. Several diatom species are exclusively linked to such facies and define assemblages V A, V B, and V C.

This study shows the statistically derived relationships between the composition of living diatom communities and some environmental variables. The data at our disposal, however, still do not allow a full understanding of the controlling factors involved in the diatom assemblage distribution. Firstly, this would imply a thorough knowledge of the interrelations between the different ecological variables, as linkages may arise from secondary correlations as well as causal relationships. The significance of ionic ratio is often difficult to distinguish from that of individual ion concentrations. Secondly, more efforts are needed on the investigation of some additional and possibly critical factors, such as N and P sources, water transparency and movements, organic matter and trace elements. A biological consideration is that environmental factors may influence diatom communities indirectly by their effects on other accompanying algae, such as the *Microcystis* spp. abundant in such lakes as Baringo, George, and Abaya. Thirdly (as suggested by TILMAN 1977 and KILHAM and KILHAM, 1980) experimental studies must be done to determine the relationships which might exist between field observations and the causative mechanisms controlling the algal community composition.

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