HISTORY OF AN AFRICAN RIFT LAKE AND ITS CLIMATIC IMPLICATIONS[1]

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TABLE OF CONTENTS

ABSTRACT 499
INTRODUCTION 500
MODERN LAKE NAIVASHA AND ITS NEIGHBORS 500
THE CORE AND ITS GROSS STRATIGRAPHY 503
CHEMISTRY AND MINERALOGY OF THE CORE 504
  Methods 504
  Results and interpretation 505
    Moisture and organic matter 505
    Extractable cations 506
    Minerals 508
    Chemical and mineralogical conclusions 510
MICROFOSSIL STRATIGRAPHY 512
  Methods for study of diatoms 512
  Results 513
    Frequently occurring assemblages 513
    Infrequent or sporadic assemblages 513
INTERPRETATION OF STRATIGRAPHY 515
  Modern analogues of the fossil communities 516
  Lake depth and area 517
  Water temperature and chemistry 518
  Productivity 521
LAKE NAIVASHA AS A DEVELOPING ECOSYSTEM 522
  Hydrarch succession 522
  Productivity 522
  Diversity of diatom assemblages 523
  Paleochemistry and the lake's present freshness 524
PALEOCLIMATIC RECONSTRUCTION 525
  Chronology 525
  The Gamblian climate 527
  Climate of the post-Gamblian "interpluvial" 529
  Comparisons and conclusion 530
ACKNOWLEDGMENTS 532
LITERATURE CITED 532
APPENDIX I: DIATOM ASSEMBLAGES

ABSTRACT

Analysis of a 28-m core from a relict fresh-water lake in Kenya has provided a detailed limnologic and climatic history covering 9,200 years. The core is an incomplete section through the sediments of a submerged crater near the eastern shore of Lake Naivasha. The overall sedimentation rate, 0.33 cm wet sediment per year, is the most rapid on record for a lake whose sediments are essentially autochthonous and organic. A three-stage limnologic history is inferred from the microfossils (particularly diatoms), chemistry, and mineralogy of the core: (A) From before 9,200 B.P. until about 5,650 B.P. a lake significantly larger than the present one existed in the basin. Algal productivity was high, and the water temperature was probably above the present average. The surface waters of this lake were evidently depleted in silica, suggesting some stratification, but the total ion content was not far below today's. (B) Between 5,650 B.P. and 3,040 B.P. the lake shrank, aquatic macrophytes increased in abundance near the core site, and the water grew more dilute. The crater became isolated from the main lake and finally dried briefly. (C) For the past 3,000 years a small lake has existed in the basin. It has been frequently smaller and its water sometimes much more concentrated than that of the modern lake. The lake discharged through a southern outlet prior to 5,650 B.P., but since that time has had no surface outlet. Various freshening mechanisms have operated during the past 5,000 years, probably including deflation, burial of alkaline layers, underground seepage, and perhaps ion removal by aquatic plants.

The climate during the period of the large lake (Leakey's Gamblian Pluvial period) was much wetter and probably warmer than today, and rainfall at Naivasha was more seasonal. Rainfall was perhaps 65% above the modern average. We find no convincing evidence for an early post-Gamblian wet phase, the Makalian, proposed by earlier workers for this region. A later wet phase, the Nakuran, may be represented by the small, fluctuating lake of the past 3,000 years, but this lake probably never stood as high as the strandline previously assigned to the Nakuran. The climatic inferences from this study are in substantial agreement, but provide interesting points of contrast, with those from other recent investigations in sub-Saharan Africa.

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Introduction

The lakes of East Africa, fascinating in their modern variety, beckon also to the paleoecologist. Many are old, and their basins contain the most detailed guides available to the Pleistocene climatic history of the region. The evolution, preservation, and present distribution of Africa's magnificent biota are interwoven with this climatic history; so, too, is the story of man's origins and evolution on this continent.

To the paleolimnologist these lakes are attractive for an additional reason. The histories of many temperate lakes, from their postglacial beginnings to the present, have been uncovered in detail through core studies of their sediments. The developmental record is better documented for this ecosystem type than for any other. Some ecologists have been tempted to suggest that common patterns exist—in changing productivity and species diversity, for example, and that these can be extrapolated from temperate lakes to quite different types of ecosystem, such as forests, whose own developmental histories can be less fully known. Tropical lakes offer the possibility of testing the limnological universality, at least, of the "temperate lake model" of ecosystem development. They possess equally well-preserved stratigraphic records, yet are unlike temperate lakes in age and conditions of origin. It would be interesting to discover if they nevertheless show similar developmental patterns.

This paper presents the chemical and microfossil record of a 28-m sediment core from Lake Naivasha, Kenya. It has proved difficult to compare the history of this lake with the "temperate lake model," partly because our record does not reach to the beginnings of Naivasha; but the changes in our core are nevertheless of limnological as well as climatic interest. The climatic aspects of the core study have been treated briefly in an earlier paper (Richardson 1966) and are expanded here.

This history adds another link to an 850-km paleoclimatic transect across equatorial Africa, from the Ruwenzori Range to Mt. Kenya (Bakker 1964, Coetzee 1967, Livingstone 1967, Kendall 1969). Based on sediment cores, this series constitutes the most detailed climatic record for any part of the tropics. The subjects of the present inquiry, Lake Naivasha and its small neighbors in the Kenya Rift, are relict lakes whose basins contain evidence that water levels were once much higher. Early workers such as Leakey (1931) and Nilsson (1931, 1940; see Fig. 1) recognized this evidence, and it played a formative role in the development of the pluvial-interpluvial hypothesis of sub-Saharan climates during the Pleistocene. Widely accepted and applied by archeologists, this theory envisioned a series of pluvial (wet) periods in Africa coinciding with temperate glacial periods, and of African interpluvials coinciding with temperate interglacials. Especially in recent years, however, much of the evidence for this paleoclimatic sequence has been questioned (Solomon 1939, Cooke 1958, Flint 1959, Washbourn 1967). Our reinvestigation of the history of Lake Naivasha was prompted partly by this controversy.

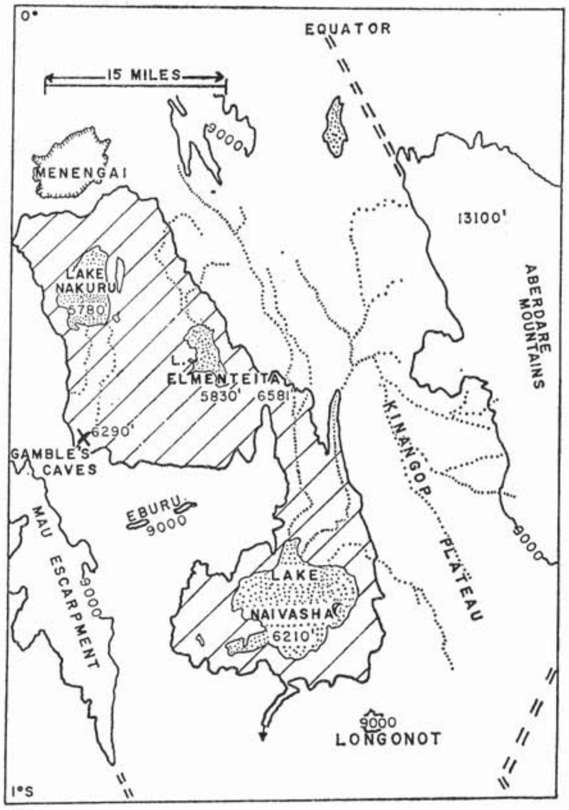
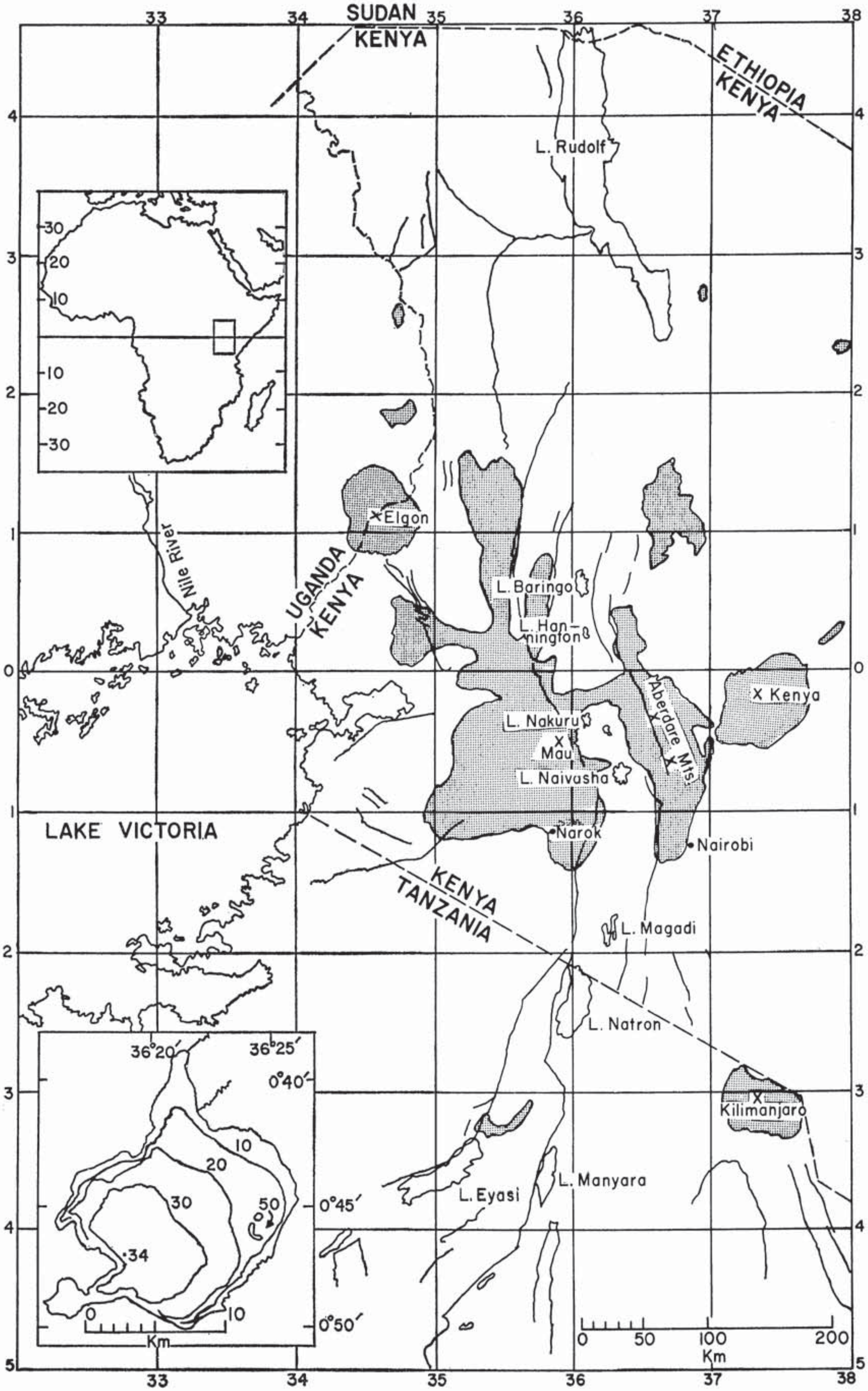


FIG. 1. The Naivasha–Nakuru region, showing the lakes ca. 1927 (stippled) and the extent of the largest Pleistocene lake recognized by Nilsson (hatched). Double broken lines indicate extensions of Rift escarpments. (Redrawn from Nilsson 1931.)

Modern Lake Naivasha and Its Neighbors

The three lakes linked in this study—Naivasha, Elmenteita, and Nakuru—are the central and most elevated members of a chain of lakes scattered within the Eastern Rift Valley from Ethiopia to Tanzania (Fig. 1, 2). Most of the lakes are small and lack outlets, and the valley is now a region of internal drainage. However, biogeographic evidence suggests that at least the northern part formerly drained into

FIG. 2. The region of the Eastern Rift. Lakes, fault lines, mountains (X), and areas of montane forest (stippled) are indicated. Unshaded land areas are mostly savannah or grassland, or both. Lower inset: Depth contours in feet of Lake Naivasha in 1927. Deep hole on east side is Crescent Island crater. (After P. W. D. drawing No. 4930, reproduced in Thompson and Dodson 1963.)


SUDAN
KENYA
ETHIOPIA
KENYA
UGANDA
KENYA
KENYA
TANZANIA
L. Rudolf
Elgon
Nile River
L. Baringo
L. Hannington
Aberdare Mts.
X Kenya
L. Nakuru
Mau
L. Naivasha
LAKE VICTORIA
Narok
Nairobi
L. Magadi
L. Natron
Kilimanjaro
L. Eyasi
L. Manyara
36°20′
36°25′
0°40′
0°45′
0°50′
Km
Km

the Nile. Lake Rudolf, for example, harbors species with nilotic affinities such as the Nile perch (*Lates nilotica*).

Although situated within one degree of the equator, the three lakes of this study are relatively cool. Naivasha, the highest, is about 1,890 m (6,200 ft) above sea level and presently supports a thriving population of American largemouth bass. Introduced trout flourish in many of the streams feeding these lakes, and temperate crops are grown in their basins. Fertile volcanic soils and a long growing season allow as many as seven crops of alfalfa to be grown annually at Naivasha (Thompson and Dodson 1963). Lake Naivasha receives drainage from the highest parts of the valley floor and also from the highest parts of the flanking escarpments. These are elevated to over 3,960 m (13,000 ft) on the east, as the Aberdare Mountains, and to over 3,000 m (10,000 ft) on the west, as the Mau Escarpment. The Kinangop Plateau forms a broad step between the Aberdares and the valley floor east of Naivasha. The breadth of the valley in this region is between 45 and 70 km.

The valley floor is broken by subsidiary faulting and volcanic activity. Three major volcanoes—Longonot, Eburu, and Menengai—help to define the lake basins (Fig. 1). Longonot and smaller volcanoes form a barrier to the south of Lake Naivasha which is breached by Njorowa Gorge, a former outlet of the lake. Eburu partially separates Naivasha from the Nakuru–Elmenteita basin, and Menengai bounds that basin to the north. Lakes Nakuru and Elmenteita once drained northwards around the shoulder of Menengai (Washbourn 1967), but like Naivasha, they are presently without surface outlet.

Rainfall in the basins varies markedly with altitude. The wettest western slopes of the Aberdares probably receive as much as 1,525 mm (60 inches) annually, whereas Naivasha, in the rain shadow of these mountains, receives but 610 mm (24 inches) (East African Meteorological Department 1963). Evaporation at Naivasha is some 1,360 mm (53.5 inches) annually, so the lake clearly depends heavily on rainfall at higher elevations for its existence. Lakes Elmenteita and Nakuru, though receiving greater direct precipitation than Naivasha, occupy smaller watersheds with less reliable surface influents and have been virtually dry within living memory. Rainfall is distributed fairly evenly throughout the year, with maxima at Naivasha in April and November (Fig. 17). The natural vegetation of the basins ranges from acacia and grass scrubland on the valley floor to montane forest and bamboo at higher elevations.

The lakes themselves are shallow and productive. Lake Naivasha is far more dilute than its neighbors (Table 1), but the ionic composition of all three reflects the basic, soda-rich volcanic rocks of the region. Elmenteita and Nakuru, which are fed by alkaline springs, deposit trona ($Na_2CO_3NaHCO_3 \cdot H_2O$) during periods of low water. The water of these lakes is pea-green, and the flora and fauna are quite restricted. Especially at Nakuru great flocks of flamingoes strain the rich mixture of water and soft mud for nutriment. Lake Naivasha is essentially a fresh-water habitat and has a much greater variety of aquatic life. The most thorough accounts of its biology are by Beadle (1932*a, b*) and Jenkin (1936). The phytoplankton is diverse; *Botryococcus*, diatoms, desmids, and blue-green algae have all been reported as common (Rich 1932, 1933, Ross 1955, Richardson 1964*a*). Lind (1965, 1968) has recently recorded interesting spatial and seasonal variations in the phytoplankton. Rotifers and copepods are common in the zooplankton. Naivasha has one indigenous species of fish, the other lakes none.

TABLE 1. Chemical analyses of modern lake waters

Item	Naivasha (1)[a]	Naivasha (2)[a]	Elmenteita (2)	Nakuru (1)	Nakuru (2)
Conductivity (µmho)		335	43,750		162,500
Na (mg/liter)	41	41	9,450	5,550	38,000
K (mg/liter)	19	21.6	381	256	1,312
Ca (mg/liter)	16	21.9	<10	10	<10
Mg (mg/liter)	7	6.9	<30	0	<30
Fe + Al (mg/liter)	6			6	
$HCO_3 + CO_3$ (meq/liter)	3.0	3.43	289	205	1,440
Cl (mg/liter)	10	16	5,200	1,375	13,000
SO_4 (mg/liter)	17	8.4	2,200	253	4,270
SIO_2 (mg/liter)		31.5	295		730
NO_3 . N (µg/liter)		32			
Total P (µg/liter)		58	2,000		12,200

[a](1) Beadle 1932 (analyses 1930-31).
(2) Talling and Talling 1965 (analyses 1961).

The striking chemical and biological differences between Naivasha and the other two lakes have led to suggestions that Naivasha has underground drainage to the south which prevents concentration of its salts by evaporation (Gregory 1921, Baker 1958, Thompson and Dodson 1963). Whether or not this is true, the lake has fluctuated considerably during historic times, after the fashion of a closed lake (Fig. 3). In the 1920's it was nearly twice as extensive as it was in 1960–61, when we took our core. At the latter time its surface area was 113 km^2 (44 square miles), its average depth only 2–3 m, and its maximum depth (in the submerged crater on the east side) 14 m. The 30- to 40-year trend of declining levels reflects a slight trend of decreasing rainfall during this period, averaging 5 mm/year over the basin between 1920 and 1949 (Sansome 1952). Perhaps increasing human consumption from river influents and boreholes contributed to the lake's decline. The wetter years beginning in 1961 saw a

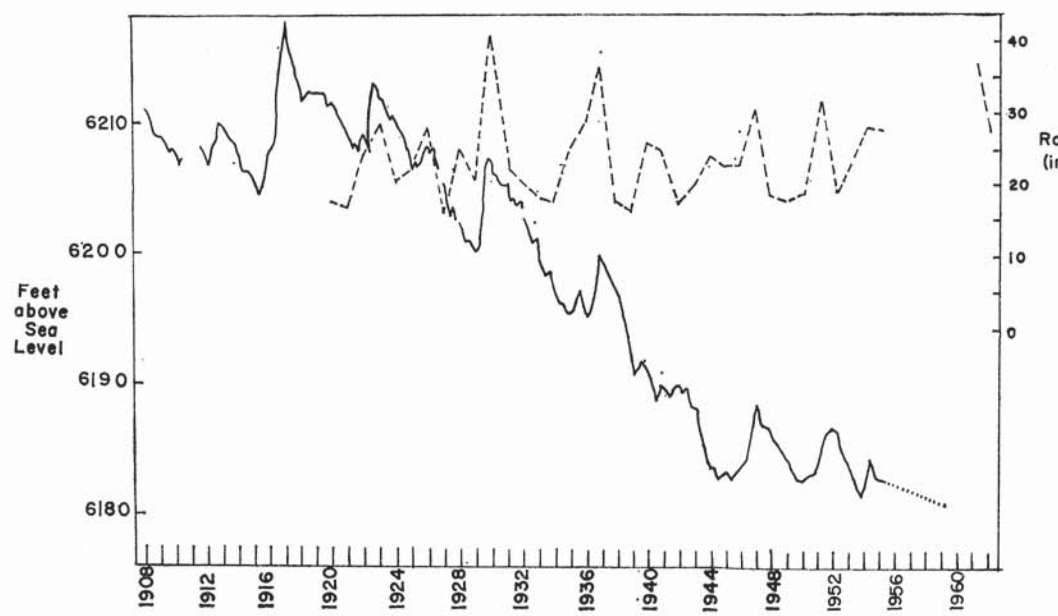


FIG. 3. Trends of yearly rainfall (broken line) and lake level (solid line) at Naivasha. (Redrawn from Nilsson 1940 and Thompson and Dodson 1963).

sharp rise in the level of Naivasha, as well as of Elmenteita and Nakuru.

THE CORE AND ITS GROSS STRATIGRAPHY

Our sediment core was obtained near the center of the submerged crater on the east side of Lake Naivasha (Fig. 4). Coring took place in 13 m of water and lasted 3 days, Dec. 30, 1960–Jan. 2, 1961. Crescent Island, the highest part of the crater rim, was actually a peninsula at the time of our visit, and the crater made connection to the main lake only through a shallow swamp to the north of the "island."

We used a light-weight Livingstone piston sampler of the type described by Walker (1964). The sampler was operated from a rubber raft through casing which extended from the water surface to the bottom. (During later stages of drilling, the casing was pushed several meters into the mud.) This type of sampler collects sediment in 1-m lengths, in aluminum tubes of 3.8 cm internal diameter. The tubes were corked for transport to the United States. Recovery of sediment ranged from an apparent 29% in the uppermost, very fluid meter to nearly 100% in some of the lower, more compact meters. Failure to obtain a full tube may have been due to (1) frictional compaction of sediment within the tube during sampling, in which case none was actually lost; or (2) a true failure to collect sediment during part of the sampling drive. This might occur if a plug of sediment blocked the lower part of the tube, resulting in the forcing aside of the deeper part of each meter's drive. It has been convenient to construct all graphs as if the second explanation were correct,

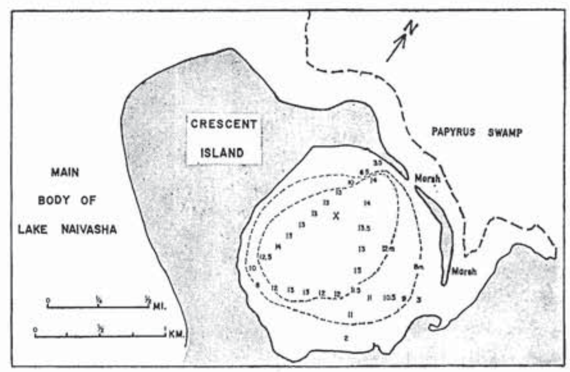


FIG. 4. The Crescent Island crater in December 1960, showing core site (X).

i.e., as if the sediment actually obtained in any meter was the uncompacted upper portion of that meter. For example, the diatom samples from the uppermost meter's drive, which collected only 29 cm of sediment, are graphed at the 0- and 20-cm levels, and the uppermost sample from the second meter's drive is graphed at the 100-cm level.

Drilling difficulties were experienced with a hard, sandy layer in meter 9, and the core was obtained in several segments. Distinctive layers could be matched from the bottom of an 11-m upper segment (a) and the top of an 18-m lower segment (c) to obtain a continuous 28-m profile. Part of a third segment (b) was also analyzed and appears in some graphs.

Our core probably contains only a small fraction of the history of Lake Naivasha. We did not reach the base of the lacustrine sediments, and the whole section represents postglacial time. The bottom of the core has been dated by C^{14} at 9,200 ± 160 years before 1950 (hereafter designated B.P., "before the present"). The overall sedimentation rate during this period, 0.33 cm of wet sediment per year, appears to exceed that recorded for any lake not forming extensive evaporite deposits.

When first extruded, the upper 10 m of the core were highly variable in color and texture. The uppermost sediment was light brown and fluid, becoming gelatinous after partial drying. Meters 2 through 10 were generally moist, with the exception of the hard layer in the upper part of the ninth meter; this was very dry and composed of layered sand, beneath which was finer sediment partially weathered into a soil. Colorful bands and zones characterized many parts of meters 2 through 10. These included numerous reddish areas containing white flecks of $CaCO_3$, several regions of very smooth gray-brown or gray-black sediment, and a number of whitish, flocculent zones. In the lower part of the ninth meter and in meter 10, the sediment was generally dark and fine, but included several thin bands of sand, sometimes associated with yellowish- to reddish-brown layers of finer sediment. Two carbon dates have been obtained for the upper third of the core; these bracket the hard layer and indicate that the crater dried completely, but very briefly, about 3,000 years ago.

The lower 18 m of the core were much more homogeneous than the upper portion, being brown or greenish-brown gyttja. The major contrasts evident when the sediment was extruded were light-colored layers of volcanic ash in meters 17, 23, 24, and 26. None of these layers was more than 4 cm thick. Cinders were found at several levels, the uppermost being in meter 11. Several regions lower in the core were rather sticky, smelled of organic decay, and contained gas bubbles.

Although tightly wrapped in Saran-wrap during the period of analysis, the extruded core dried gradually, and thin white laminae became evident in part of the eighth meter and through much of meters 11 to 28. They were especially regular and well developed in the lowermost 8 meters. Suspecting that these laminae were seasonal bands, we measured their thickness wherever possible, and the widths were compared with average rates of wet sedimentation derived from carbon dates. Only in the lower half of the core were the laminae sufficiently widespread and discrete to permit confident comparison of rates. Here, 149 measured pairs of light and dark bands averaged 0.283 cm in thickness. Over this same interval the deposition of wet sediment as calculated from carbon dates averaged 0.376 cm/year.

The most reasonable explanation of these data is that one pair of laminae was laid down per year. If so, the rate of sedimentation based on laminae is only 75% of the rate calculated from carbon dates. In view of probable compaction of the sediment during coring, drying after collection, and irregular additions to the sediment by ashfalls and perhaps floods, a discrepancy of this sort is not unexpected. Nilsson (1931), who found layered sediments in a dry exposure near Naivasha, concluded reasonably that two pairs of laminae had been formed per year, since two rainy and two dry seasons now characterize the climate at Naivasha. However, if Nilsson's conclusion is applied to our data, the rate calculated from laminae is half again as fast as that calculated from carbon dates, and we can think of no explanation for a discrepancy in this direction. We therefore interpret the banding in the Naivasha core to mean that between 9,200 and about 2,500 years ago the characteristic pattern of annual precipitation in the Naivasha basin was a single rainy season and a single dry season per year. The gently bimodal modern rainfall pattern at Naivasha is perhaps reflected by the absence of obvious laminae in the upper 7 m of the core.

Chemistry and Mineralogy of the Core

The Naivasha core was analyzed at 20-cm intervals for moisture and organic matter and 50-cm intervals for extractable cations. Qualitative X-ray analysis of minerals was performed at nine levels, and quantitative or semiquantitative measurement of certain minerals at 23 levels. Black pyrite spheres, recorded during microfossil examinations, will be discussed later.

Methods

Moisture was determined as the difference in weight between freshly extruded samples of 0.4–1 cc volume before and after drying for 12 hr at 80° C. To determine organic matter the dried samples were ignited in a muffle furnace for 5 hr at 400° C, cooled in a desiccator, and reweighed.

A Beckman DU spectrophotometer with flame attachment and photomultiplier tube was used for cation analyses. One-centimeter samples of sediment were mixed with 1 N ammonium acetate and made up to 25 ml. Five milliliters of this slurry were dried and weighed; the remainder was covered and left to extract for 17–19 hr, after which it was filtered, washed in demineralized water, and evaporated to dryness on a hotplate. This residue was ignited for 45 min in a muffle furnace at 600° C, and the ash was redissolved in 10 ml hot 0.2 N HCl. Five-tenths milliliter of 0.1 N $FeCl_2$ was added to precipitate phosphate, after which enough NH_4OH was added to bring the mixture to neutrality and precipitate the iron. The sample was then cooled, made up to 10 ml, mixed well, and centrifuged; the supernatant was removed for analysis.

A Norelco diffractometer equipped with scintillation counter and automatic strip-chart recorder, and using a cooper K-α radiation source at 40 kv and 20 ma, was used in the X-ray studies. Scanning speed was 1°/min for quantitative studies and usually 2°/min for qualitative studies. Most qualitative samples were dried at 80° C, ground to a 325-mesh powder, and mounted in aluminum frames for analysis. At three levels wet slurry suspensions were dried on glass slides for more accurate determination of clays. The Fink Index (American Society for Testing and Materials 1963) was used for identification of all minerals.

Quantitative mineralogical analyses were made by the internal standard technique (Klug and Alexander 1954). Standards and samples were separately ground to a 325-mesh powder, then mixed for approximately 15 min in an automatic ball-and-mill grinding machine and mounted in aluminum frames. Approximately half the samples were dried at 80° C before grinding; duplicates of these were treated with HCl for removal of $CaCO_3$ and heated for 4 hr at 900° C to enable determination of diatomaceous opal, after the method of Goldberg (1958). This procedure converts the amorphous opal into cristobalite, a crystalline silicate measurable by X-ray methods. In our samples, however, feldspar minerals and perhaps also native cristobalite masked the peaks of opaline cristobalite, and we were unable to measure opal quantitatively. Nevertheless, the heated samples were useful in conjunction with the "unheated" (80°) duplicates in discriminating between volcanic ash shards and opal. Both ash and opal caused a disordered doming in unheated samples, but doming due to opal disappeared in the samples heated to 900°. Doming was measured in the manner indicated in Fig. 8, and the measurements for heated and unheated samples were plotted together (Fig. 9).

Quantitative determinations of calcite and quartz were made on the unheated samples. Known mixtures were mounted in aluminum frames with reversible glass backing and were scanned three times on each side. Peak heights from these tracings were used to construct standard curves of peak height to concentration. The core samples themselves were scanned three times on one side, and the mean of the three ratios was determined. Quantitative samples were ordinarily scanned only between 4.5 Å and 3.2 Å; X-ray traces over this distance included the desired peaks and enough area free of peaks to establish a baseline for measurement of peak heights.

The relative abundance of feldspar could be estimated because all the important feldspar minerals in the core possess marked intensity peaks in the 3.75–3.79 Å region and also in the 3.26–3.22 Å region. Feldspar peaks in both these regions were measured relative to the peak height of the standard, and the curves were plotted independently.

Results and interpretation

Moisture and organic matter (Fig. 5).—Moisture decreased fairly steadily with depth, but even toward the bottom of the core it remained as high as 80%. Except for a few sharp decreases which obviously reflect changes in the nature of the sediment, most of the irregularities in the moisture curve can be attributed to drying at the ends of each meter section after collection. This is especially true of the uppermost samples in meters 10, 13, 15, and 17, which may have been contaminated during collection by loose material falling into the drilling hole from the sandy layer in meter 9. (This sand would have dried more quickly than gyttja between the time of collection and the time of analysis.) The top of the core yielded the highest moisture value, 96.5%. The hard, weathered layer of meter 9 had a moisture content of only 10–12%, but there was a rapid rise in moisture above and beneath this layer. The low moisture value in meter 26 was recorded from a layer of fine volcanic ash.

Organic content fluctuated widely in the upper part of the core, but was relatively low and constant (8–17%) in the lower 14 meters. Some of the jaggedness of the curve in meters 10 through 13 may result from contamination with sand from the hard layer, as mentioned above. A sharp minimum of organic matter was recorded from this layer.

Stratigraphic variations in organic content presumably reflect changes in any or all of the following: (1) the biological productivity of the lake; (2) the amount of terrestrial organic matter entering the lake; (3) the degree of preservation of organic matter; and (4) the concentration of inorganic materials. Because of the rich concentration of aquatic microfossils, we believe that terrestrial organic matter formed only a small fraction of the organic matter in the core at any level, and that once organic material was incorporated into the sediment, differential preservation was a factor only when the lake dried or became sufficiently shallow for waves to resuspend the surface sediment. Hence it may be possible, with caution, to infer levels of past lacustrine productivity from the organic matter changes in the core, after converting these to absolute rates of organic sedimentation. Such biological products as diatom frustules and sponge spicules are inorganic, however, and high concentrations of remains such as these could blur any relationship between organic sedimentation rate and past productivity.

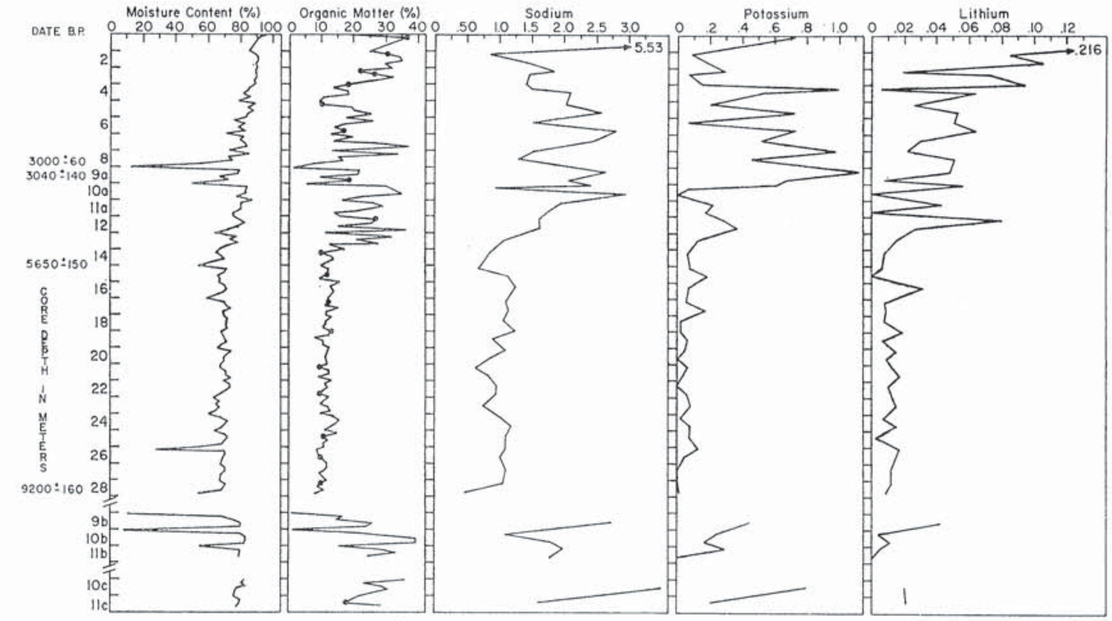


FIG. 5. Naivasha core stratigraphy: moisture (% of wet weight), organic matter (% of dry weight), and extractable alkali metals (mg/g dry weight).

TABLE 2. Rates of deposition of wet and dry sediment and organic matter in different parts of the core

Core interval (m below mud surface)	Depth of wet sediment deposited per year (cm)	Average dry weight of 1 cc of wet sediment (g)	Dry sediment deposited per year (g/cm²)	Average organic content (%)	Organic matter deposited per year (g/cm²)
0.0 − 7.67	0.256	0.1350	0.0346	22.6	0.0078
7.67− 8.32	1.625	0.5838	0.949	9.7	0.0920
8.32−14.20	0.225	0.2444	0.0550	20.5	0.0113
		(0.2295)[a]	(0.0516)		(0.0106)
14.20−27.57	0.376	0.3023	0.1131	11.4	0.0130
		(0.2895)	(0.1089)		(0.0124)

[a]Rates in parentheses are recalculations which exclude samples from a few levels that may have been altered before analysis by contamination or drying.

Table 2 presents sedimentation rates for the four carbon-dated intervals of the core. The margin of error (± 200 years) of the dates bracketing the interval 7.67–8.32 exceeds the difference between the two dates themselves, so sedimentation rates for this interval are only rough approximations. It seems reasonable to believe the rapid rate of inorganic sedimentation in this sandy part of the core; but we suspect that the apparently rapid rate of organic sedimentation here is a calculation artefact, ascribable to the combination of high organic content in the dated material just above and below the sand and rapid deposition of the sand itself.

More meaningful are the rates of sedimentation for the three larger core intervals. During the past 3,000 years the average rate of deposition, both of dry sediment in toto and of organic matter, has been significantly lower than during the preceding 6,200 years (represented by the two lower intervals). The low organic percentages recorded for the bottom half of the core are not indicative of low organic productivity or poor preservation, but merely reflect the rapid sedimentation rate. It will be useful to keep these rate changes in mind when considering all the stratigraphic diagrams.

Changes through time in the lake's productivity will be discussed further when the microfossil evidence has been presented.

Extractable cations.—Two series of spectophotometric emission analyses showed the same general trends. The second, and more accurate, series is presented in Fig. 5 and 6. Each point is the mean of three determinations on the same sample. Potassium and magnesium determinations are less accurate than those of sodium and calcium because of narrower spectral emission bands. Lithium determinations are probably quite reliable despite the small amounts involved; those of strontium are less accurate.

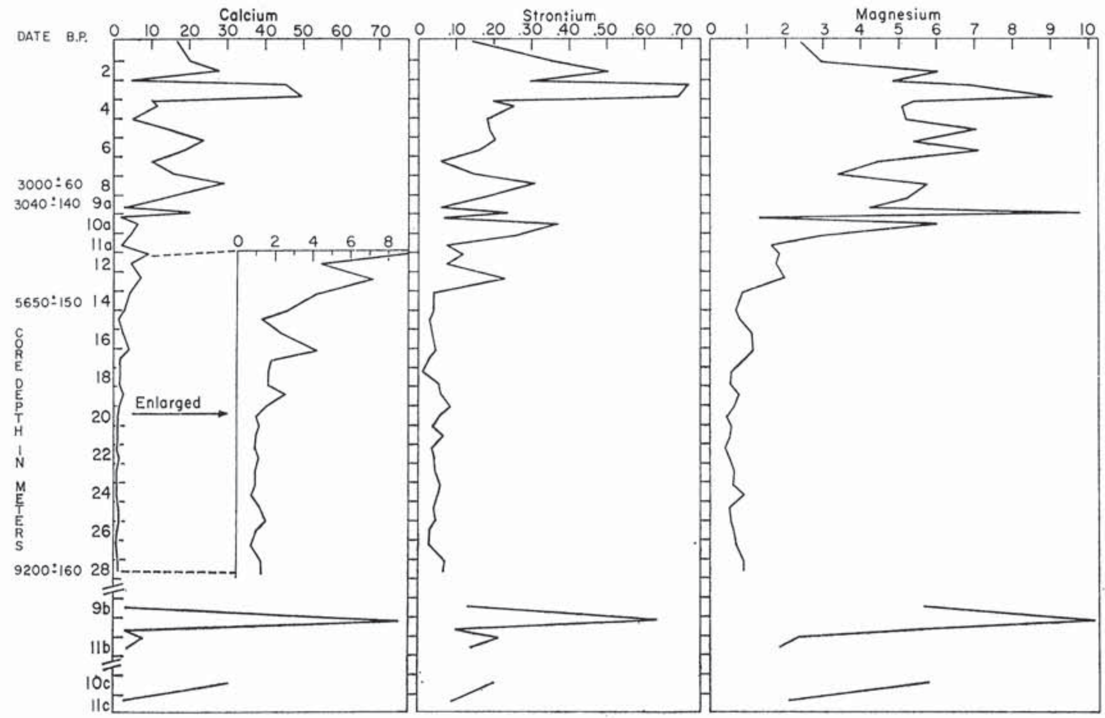


FIG. 6. Core stratigraphy: extractable alkaline earth metals (mg/g dry weight).

The three alkaline earths fluctuated stratigraphically in generally parallel fashion, although divergent trends characterized Ca and Mg at several levels. Strontium determinations were too inaccurate to permit ecological inferences from changing Sr:Ca ratios (Odum 1957). Relationships among the three alkali metals, and between these and the alkaline earths, were much more complicated, but the enrichment of Na and Li in the uppermost sample is noteworthy. Sodium is the predominant dissolved cation in the present lake (Table 1).

The cation curves are difficult to interpret. In part, they undoubtedly reflect stratigraphic differences in exchange capacity. Hutchinson and Cowgill (1963) recorded a dramatic increase of exchangeable cations in a peaty layer sandwiched between less organic sediments of a lacustrine core, and organic content generally influences exchangeability in soils. To explore the possible influence of organic content on cation levels in our core, we plotted four important cations against organic matter, using the 19 levels in the core from which samples were taken for both types of determination (Fig. 7). In only two small regions, meters 5–7 and 12–14, do trends for all four cations coincide with that for organic matter. In other parts of the core, certain ions seem related to organic matter, others not; in particular, changes of Na nearly parallel those of organic matter through the whole of meters 12–28. Altogether, however, the influence of sedimentary organic content on the levels of extractable cations seems slight.

One of the greatest influences on the cation curves may be the presence of carbonates and other salts at some levels of the core. (The ammonium acetate extractant probably dissolved precipitates in the sediment to at least some degree.) This is most likely to affect the curves for alkaline earths, since carbonates of these would easily have been precipitated had the lake become concentrated through evaporation. There are general similarities between the distribution of $CaCO_3$ in the core (Fig. 9) and the levels of extractable Ca. The X-ray studies revealed no other carbonates or salts in the core, but it is possible that extractable Mg and Sr, as well as Ca, were stratigraphically enriched by precipitation. Extractable Ca and Mg were generally much higher in the core than extractable Na and K, a situation contrasting markedly with the relative abundance of these ions in the present lake.

The degree to which the cation curves may reflect pore water concentrations, rather than ions actually bound to the sediment, must also be considered. Solubilities are important here. Pore water saturated with brine or trona would contain more than enough Na to account for the extractable amounts of this ion found in the core. However, we believe that pore water was not the source of most of the recorded Na; pore water in the surface sediments, if ionically iden-

TABLE 3. Summary of qualitative mineralogical analyses (X = abundance)

Lake and level (m below mud surface)	Quartz minerals	Feldspars	Clays	$CaCO_3$	Other
Naivasha					
27.60	X (T, C)[a]	X (NaS, S)[a]	Low	—	XXX (O)
18.40	X (C, Q)	XXX (NaS, S, An?)	Low	—	
11.40	XX (Q, T, C)	X (S, An?)	Low	—	XXX (O)
8.06	X (C)	XXXX (NaS, S, Or, An)	Very low	—	$FeCO_3$?
7.40	X? (C)	XX (NaS, An)	Low	—	
7.30	X (C)	XX ½ (NaS, An?, Al?)	Low	X?	XX (O) FeS_2
6.70/6.82	X? (C)	XX (NaS, S, An)	Low	XXXX (25%)	
3.12	Very low	Low	Very low	XXXX (20%)	
0.01– .05	XX (Q, C, T)	X (NaS, An, Al?)	Low	XX (c. 4%)	
Rukwa					
0.01– .02	X? (Q)	Very low	XX	X	
Pilkington					
0.01– .05	XXXX (Q)	Almost none	X	—	
Chila					
0.01– .02	XXX (Q, T?)	Very low	X	—	X (O?)

[a]Minerals in each category listed in order of abundance.

Key to Minerals

Al — Albite; An — Anorthoclase; C — Cristobalite?; $FeCO_3$ — Siderite; FeS_2 — Pyrite; NaS — Na-Sanidine; O — Opal; Or — Orthoclase; Q — Quartz; S — Sanidine; T — Tridymite?

Cristobalite and tridymite in samples may really be ordered opal.

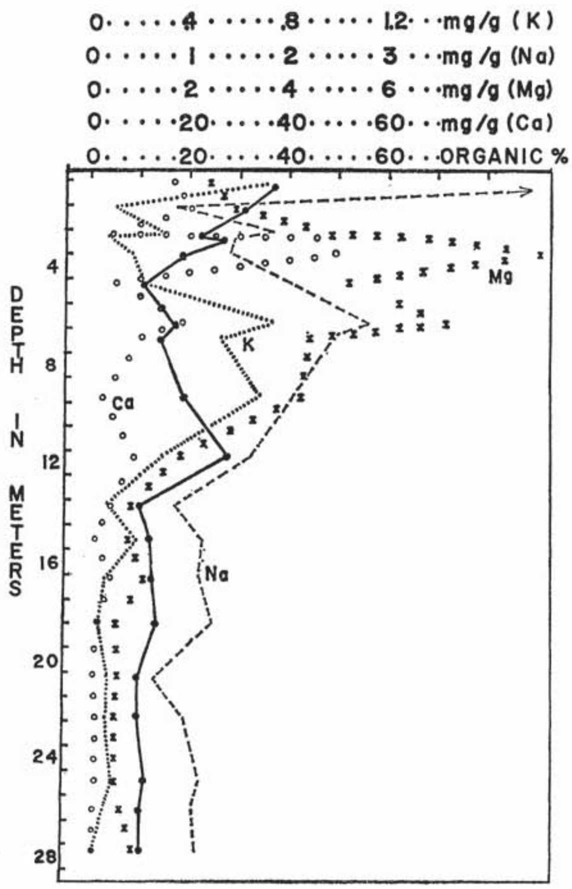


FIG. 7. Core stratigraphy: changes in organic matter (solid line) compared to changes in major extractable cations.

tical to modern lake water, can account for only 20% of the Na found at the top of the core. In the case of less soluble ions, pore water is even less of a factor. For Ca, it could account for only 1–4% of the amounts actually found.

Minerals.—Qualitative X-ray analyses of Naivasha sediment are summarized in Table 3; the surface sediment mineralogy of three other African lakes is given for comparison. Differences among the surface spectra clearly reflect differences in the water chemistry and geological setting, and probably also differences in size, of the four water bodies. Lake Chila and the crater portion of Naivasha are of comparable size (ca. 2 km^2) and morphometry; Pilkington Bay of Lake Victoria is considerably larger (32 km^2), and Lake Rukwa is a broad sheet some 750 km^2 in area and 2.5 m deep. Since the sediment samples were collected near the center of each water body, the proportions of coarse and fine terrigenous mineral matter should roughly reflect the size differences among the lakes. This relationship prevails in a very general way. For example, the sample from Lake Rukwa was unusually low in coarser materials such as feldspar and quartz and relatively high in finer clay materials. "Clay" in the Rukwa sample and throughout the Naivasha core, however, was very poorly defined mineralogically (see Fig. 8); there were no sharp clay peaks on the X-ray traces, but rather a general doming in the region where clays such as montmorillonite have their peaks. Rukwa is a rather alkaline lake of the sodium bicarbonate/carbonate type, and Naivasha, although today much fresher than Rukwa, also is of this chemical type.

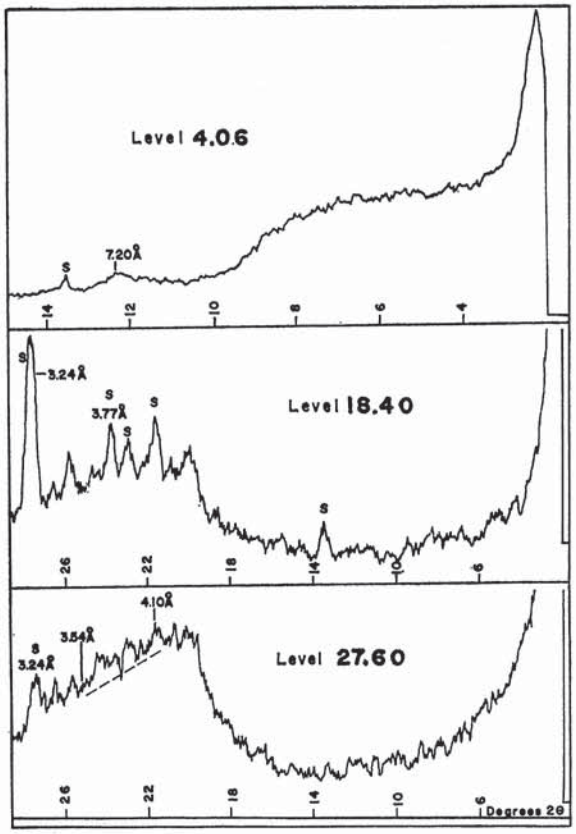


FIG. 8. X-ray traces from three levels in the core. Top: fine, gray sediment with disordered doming in clay mineral region (altered montmorillonite?). Center: gyttja rich in feldspar (S = sanidine). Peaks measured for feldspar graph are marked. Bottom: Gyttja rich in opal, causing massive doming in this unheated sample. Slope of dashed line was used as a measure of the degree of doming. Slope was determined as: (height of 4.10Å baseline — height of 3.54Å baseline) / height of 3.54Å baseline.

Apparently the crystalline clay minerals in Rukwa and at many levels in the Naivasha core (e.g., level 4.06, Fig. 8) have been destroyed or altered. Hay and Moiola (1963), who studied the mineralogy of highly alkaline sediments from the Searles Lake basin in California, concluded that there, also, montmorillonite and chlorite clays had been dissolved or diagenetically changed.

The waters of Pilkington Bay and Lake Chila are much more dilute than those of Rukwa and Naivasha and are not of the sodium bicarbonate/carbonate chemical type. The soils are old and well leached in the drainage basins of these two lakes, whereas soils around Naivasha and Rukwa are at least partly young and volcanic. These differences are reflected by the well-defined peaks of kaolinite and chlorite and larger amounts of quartz in the samples from Pilkington Bay and Lake Chila.

Crystalline minerals in the deeper parts of the Naivasha core were largely feldspars and, in places, calcite. Quartz was a minor constituent at all levels. The feldspars, dominated by sanidine, were most probably derived from volcanic rocks in the basin, although some feldspar may be authigenic, as in Searles Lake (Hay and Moiola 1963). The calcite is certainly a precipitate, deposited either through evaporation or through photosynthetic activity. No other evaporite minerals were found at any level of the core.

The stratigraphic distribution of minerals is shown in Fig. 9. Calcite values above 2% of dry weight were recorded only from the upper 7 m of sediment. Other peaks probably occurred between the levels sampled in this region, since calcite was often visible as white flecks in reddish bands of sediment. Surface sediment from Naivasha contained about 4% calcite, part of which was probably precipitated from the pore water when the sediment was dried before X-ray analysis. However, the data of Talling and Talling (1965) indicate that dissolved Ca and HCO_3 during the year we obtained the core were at least seasonally at saturation levels. The low quantities of $CaCO_3$ recorded below the seventh meter were within the limits of analytical error. Among surface sediments from the three other lakes, $CaCO_3$ appeared only in that of Rukwa, and here in very small quantity. Although more concentrated ionically than Naivasha, Rukwa waters were found by Talling and Talling (1965) to contain very little Ca.

Quartz levels were higher in the surface sediments of the three other lakes than in any part of the Naivasha core. The relative monotony of the Naivasha quartz curve should not obscure the fact that the rate of deposition was actually quite different at different times. The slow sedimentation rate of the upper 8 m, as opposed to the lower 14, means that during the earlier period quartz was being delivered to the lake approximately three times as fast as during the past three millenia.

Slight differences between the two curves for feldspar probably reflect changes in the proportions of different feldspar types, since the relative sizes of the two measured peaks vary among different feldspars. The level richest in feldspar was the hard, sand-silt layer deposited when the crater was dry or nearly dry. Quartz was completely absent in this sample; this contrast, and the scarcity of quartz rocks near the present lake, suggest that the quartz in the core is primarily the product of riverine transport into the lake from some distance, whereas the feldspar represents volcanic valley soils brought to the lake by smaller streams and perhaps by local sheet erosion. The curves for feldspar, like most of those already discussed, are lower and more regular in the lower part of the core than in the upper part. A single peak in meter 19 breaks this pattern; microfossil

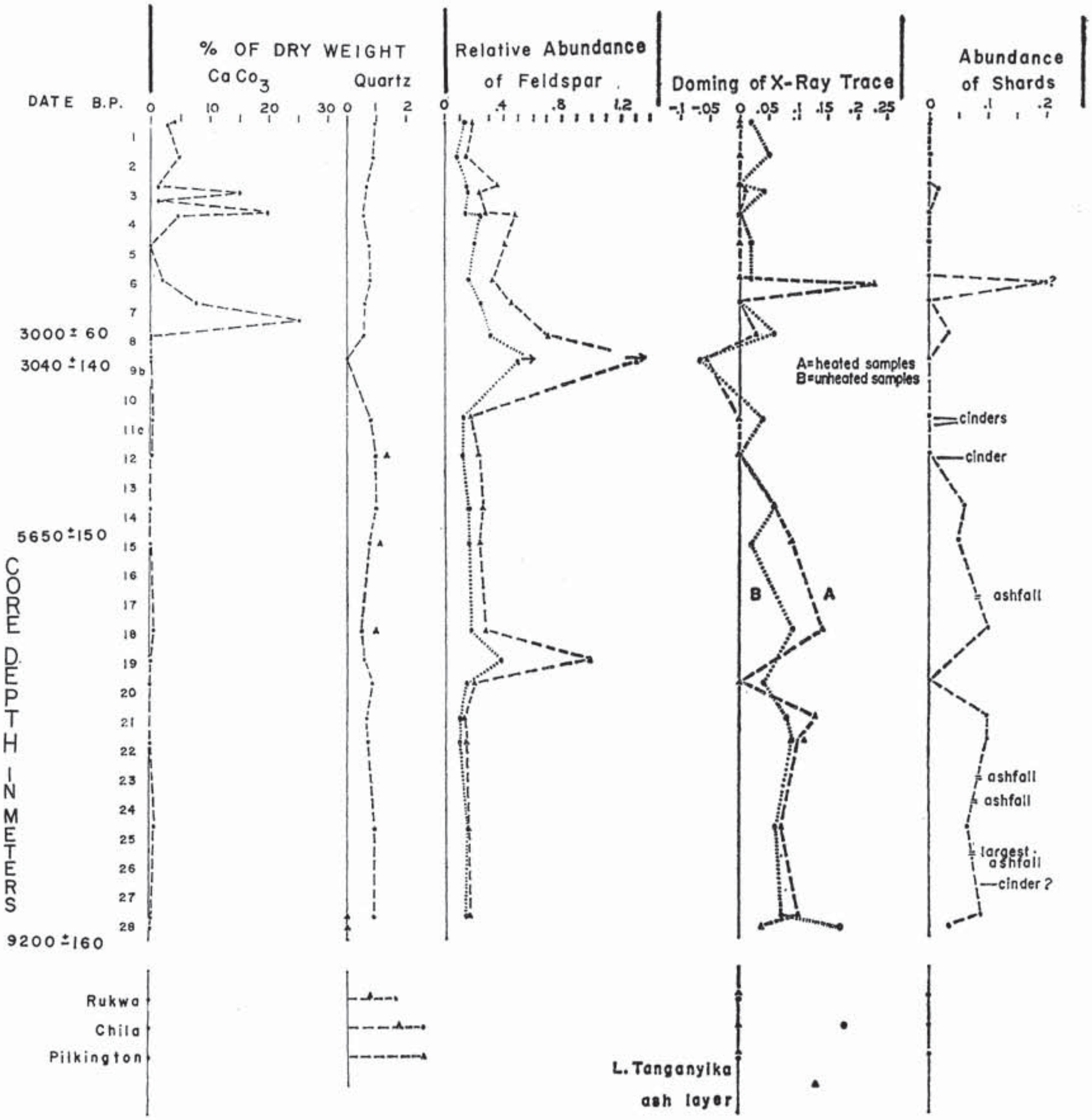
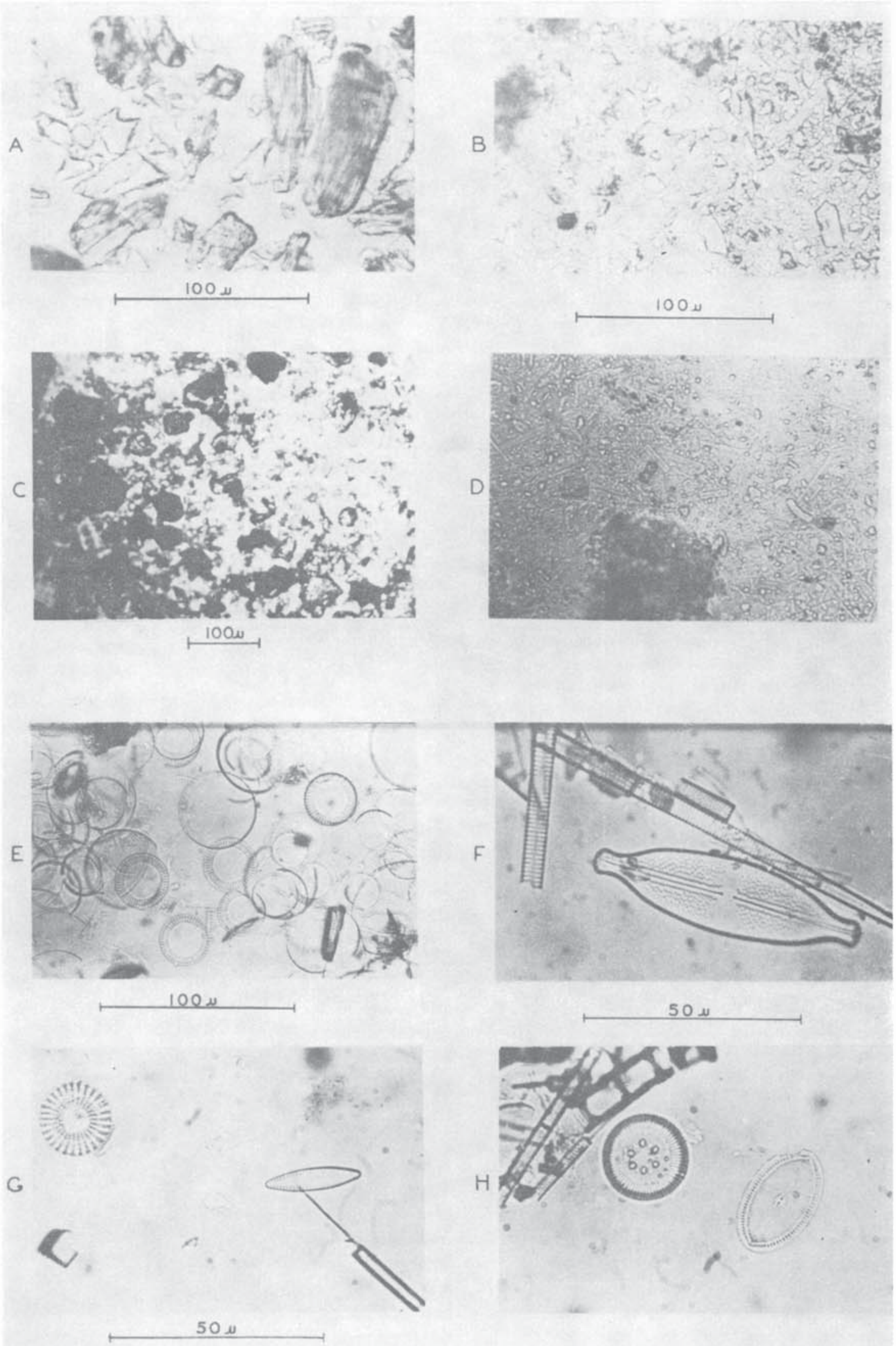


FIG. 9. Core stratigraphy: X-ray mineralogy. Quartz: triangles represent quantities determined from 4.26-Å peak, dots quantities from 3.34-Å peak. Feldspar: dotted line derived from 3.77-Å peaks, broken line from 3.24-Å peaks. Graphs for doming and abundance of shards are explained in text.

peculiarities were also discovered at this level, suggesting possible inwash from a sudden flood.

The curve of volcanic ash (shard) abundance indicates relative amounts, based on the doming remaining in samples after heating. We have added the positions of discrete ash layers and cinders to this diagram. Figure 10 shows photomicrographs of shards from two ashfalls. Shards seen through the microscope appeared fresh and sharp-edged at all levels, suggesting that much ash in the core fell directly on the lake. The record indicates fairly continuous local volcanic activity between 9,000 and 3,000 years ago, followed by significant diminution. The sharp peak in the sixth meter may represent a

FIG. 10. Microscopic aspects of core. A and B: Coarse and fine volcanic ash from layers at 23.36 and 25.20. C: Sand and silt from level of dry period (8.00–8.15). D: Clay-size mineral material and diatoms from stage just prior to dry period. E: Diatom assemblage representing rather alkaline water (level 7.49). Shown are *Cyclotella meneghiniana* (with radial ribs) and *Coscinodiscus rudolfi*. F: Assemblage just prior to dry period (level 8.20). Clockwise from upper left: *Synedra ulna, Melosira granulata* v. *jonensis, Anomoeoneis sphaerophora*. G: Stage of shrinking lake, still rather deep (level 12.40). Left to right: *Stephanodiscus astraea, Fragilaria fonticola, Melosira granulata* v. *angustissima*. H: Large lake phase (level 14.40). Left to right: *Melosira granulata* v. *angustissima, M. ambigua, Cyclotella ocellata, Cocconeis placentula*.


A
100 µ
B
100 µ
C
100µ
D
E
100 µ
F
50 µ
G
50 µ
H

brief resumption of vulcanism, but no unheated sample was analyzed at this level. If local vulcanism has continued almost to the present, as Thompson and Dodson (1963) have suggested, it evidently has been minor or has involved lava rather than ash eruptions.

Chemical and mineralogical conclusions.—The foregoing analyses may be summarized and interpreted as follows. All measured cations, as well as calcium carbonate, occurred in higher but also more variable concentrations in the upper half of the core than in the lower half. Quartz, a mineral probably brought to the lake from some distance away, was deposited most rapidly during the period before 5,650 B.P. This is not true of feldspar, a detrital mineral of more local origin, the concentration of which rose in the more slowly deposited sediments of the upper part of the core. These lines of evidence combine to suggest that the lower half of our record represents a larger lake, more immune to short-term climatic variation and receiving stronger discharge from its main influents; and that the upper half of the core represents a smaller lake, more variable in its chemistry though often more concentrated than earlier, with generally weaker inflow.

Microfossil Stratigraphy

Diatoms were the primary focus of our microscopic studies. Many other microfossils were probably destroyed by the diatom-cleaning procedure, but *Botryococcus, Pediastrum* spp., and sponge spicules survived the treatment, and their stratigraphy was recorded. Also recorded were microscopic black spheres, very probably pyrite nodules. Vallentyne (1961) suggests that these form at the mud-water interface under anaerobic conditions.

The fungi (Wolf 1966) and pollen of the Naivasha core have been studied separately. D. A. Livingstone has kindly let us present his preliminary pollen data for aquatic plants.

Methods for study of diatoms

Samples of sediment (usually ⅛ cc) were cleared of organic matter by the peroxide-dichromate method (Van der Werff 1953), centrifuged, washed, and made up to 20 cc with distilled water. Aliquots representing 0.0004–0.005 cc of sediment were removed by automatic pipette, dried on coverslips, and mounted in Hyrax. The size of the aliquot was varied according to the density of diatoms in the sediment.

Absolute abundance of the larger diatoms was recorded at 20-cm intervals in every third meter. These counts, at 160×, usually covered half a slide. All are probably underestimates of true abundance; our subsampling procedure tended to discriminate against larger diatoms, because of their more rapid settling rate, even when the samples were thoroughly shaken and the aliquots withdrawn as quickly as possible. At levels between those of the absolute counts, abundances of the larger diatoms were estimated by scanning the slides at 160× through 2–2½ sweeps.

Smaller diatoms were counted under oil immersion (1,125×) of a Leitz Ortholux microscope equipped with apochromatic objectives. The sampling interval was 20 cm in the upper half of the core and in meters 18 and 27; 40 cm in meters 15, 21, and 24; and 1 m elsewhere in the lower half of the core. One meter in the lower part of the core represents about 270 years; in the upper 8 m the 20-cm sampling interval represents about 78 years. A closer sampling interval (7 cm) was employed in the second meter, and three laminae of 2.8 mm total thickness were separately sampled in the eighth meter. Additional diatom samples were taken from apparent grey-clay and evaporite levels, from sediment just above ash bands, and from whitish, diatom-rich layers.

Most counts under oil were made by starting at the center of a slide and proceeding toward one edge until 400 diatom valves had been counted. In later counts we continued to the edge of the slide even when a count of 400 valves was exceeded, because of the possibility that nonrandom, radially oriented distribution of species occurred during preparation of the slide. All counts were continued beyond 400 whenever this was insufficient to record at least 100 of the most common species. Counting of sparsely strewn slides was usually halted after one complete sweep, even when 400 frustules had not yet been recorded. Counts of replicate samples were usually very similar (Table 4).

Since most frustules were separated, it was convenient to count each valve as a unit. Every fragment comprising more than half a valve was counted; smaller fragments were ignored. This convention may have led to low counts of the more fragile diatoms, assuming that these were more often broken into several fragments. However, we believe that neither breakage nor nonrandom sorting of species on the slides caused serious errors of interpretation. Such errors, in a study like the present one, are more likely to result from misidentification of species, especially when ecological information about misidentified taxa is drawn from the literature rather than at first hand. Our principal taxonomic and ecologic references have been listed elsewhere (Richardson 1968: 302). Wherever possible, however, ecological interpretations have been based on our own collections and ecological measurements from existing lakes in Africa. A photomicrograph file was used to compare diatoms from these lakes with those in the Naivasha core and to check the consistency of our identifications from level to level in the core.

TABLE 4. Mean (%) and standard deviation (%) of replicate counts at four depths in the core

	Core depth (m)							
	9.80 (n = 2)[a]		18.00 (n = 3)		18.40 (n = 3)		18.80 (n = 3)	
Species	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Cyclotella ocellata	2.3	0.8	2.5	1.1	4.4	1.2	5.6	1.5
Fragilaria spp.	3.3	0.8	11.3	0.6	11.2	2.5	7.1	1.1
Gomphonema spp.	4.3	0.6	0.3	0.2	0.1	0.5	0.0	0.0
Melosira granulata v. *angustissima*	2.9	0.9	9.6	1.1	4.6	1.9	23.0	0.5
Melosira ambigua	47.3	2.6	1.6	1.6	2.5	1.2	5.5	0.8
Melosira agassizii	0.4	0.1	2.3	1.8	1.3	1.9	1.5	0.6
Nitzschia fonticola	0.0	0.0	30.2	10.1	39.2	0.4	30.1	2.8
Stephanodiscus astraea	0.5	0.3	23.5	5.3	20.3	1.4	6.7	0.5
Synedra spp.	26.7	1.0	0.2	0.3	0.2	0.5	0.4	0.1

[a]Number of counts = n. At each level counts were made of two slides prepared from the same sediment sample. Where n = 3, two of the counts were made on different parts of a single slide, to check for nonrandom sorting of frustules. For total species lists from selected levels, see Appendix I.

Results

Percentage frequency diagrams of the smaller diatoms are presented in Fig. 11 and 12. Figure 11 also includes a subjective log of diatom abundance and a graphic measure of community diversity. Figure 13 presents the absolute counts of larger diatoms, supplemented by estimates of their abundance at other levels. Estimates of abundance of nondiatom microfossils also appear in this figure. Figure 14 depicts the close-interval samplings of the second and eighth meters. The stratigraphy of aquatic pollen types appears in Fig. 15.

The microfossil stratigraphy documents a heterogeneous history for the communities of the lake. Rapid and repeated changes, both quantitative and qualitative, were found in the upper part of the core, the same region that was highly varied in its gross and chemical aspects. In the lower half of the core individual taxa fluctuated in abundance, but the same taxa were consistently prominent from level to level; that is, there was an approach toward the homogeneity revealed in this part of the core by the other analyses. The graphs do not make clear the several rather distinct diatom community types that occurred in different parts of the core. These characteristic and often-recurring assemblages are described below. Complete species lists for representative levels appear in Appendix I.

Frequently occurring assemblages.—Two assemblages are included in this category.

(1) *Melosira/Synedra.* These two genera dominated the upper 12 m of the core. The species of *Synedra* were typically long and slender, usually more or less delicate forms (*S. acus* and several very similar types), but occasionally the coarser *S. ulna* occurred. The species of *Melosira* were *M. ambigua*, *M. granulata* (there were several varieties of the latter), and, chiefly in meters 10 to 12, *M. agassizii*. Species of *Nitzschia* and *Gomphonema* were the most frequently occurring minor components of this assemblage.

(2) *Nitzschia fonticola/Melosira/Stephanodiscus.* This was the characteristic assemblage of the lower part of the core. Modifications were introduced from level to level by changes in the proportions of these three components (and in the specific make-up of the *Melosira* fraction), and also by the fluctuations of two important lesser constituents, *Fragilaria* spp. and *Cyclotella ocellata.* We had difficulty separating the various species and forms of *Fragilaria,* and although lumping them may greatly diminish their indicator value (Richardson 1968), we have reluctantly done this in the diagram.

Infrequent or sporadic assemblages.—Three assemblages are included in this category.

(3) *Coscinodiscus rudolfi/Cyclotella meneghiniana.* The occurrence of these two species together was erratic; at times one was very important and the other rather rare or absent. Assemblages dominated by either or both of these species occurred occasionally in the upper 8 m of the core, usually in zones of gray, clayey sediment. *Anomoeoneis sphaerophora* was a frequently associated larger species. Sometimes these assemblages were fairly pure, but elsewhere elements of the *Melosira/Synedra* assemblage were intermixed.

(4) *Navicula "el Kab."* Many of the red, calcite-flecked regions of the upper part of the core were dominated by this species, sometimes overwhelmingly.

(5) *Nitzschia assemblages.* At a few levels in the upper part of the core, a species of *Nitzschia* (or rarely a group of *Nitzschia* species) dominated the sample. *Nitzschia amphibia, N. palea,* and *N.* "sp. A" were the most prominent types; the latter two may be conspecific. All three tended to reach their individual peaks of importance at levels that were rather

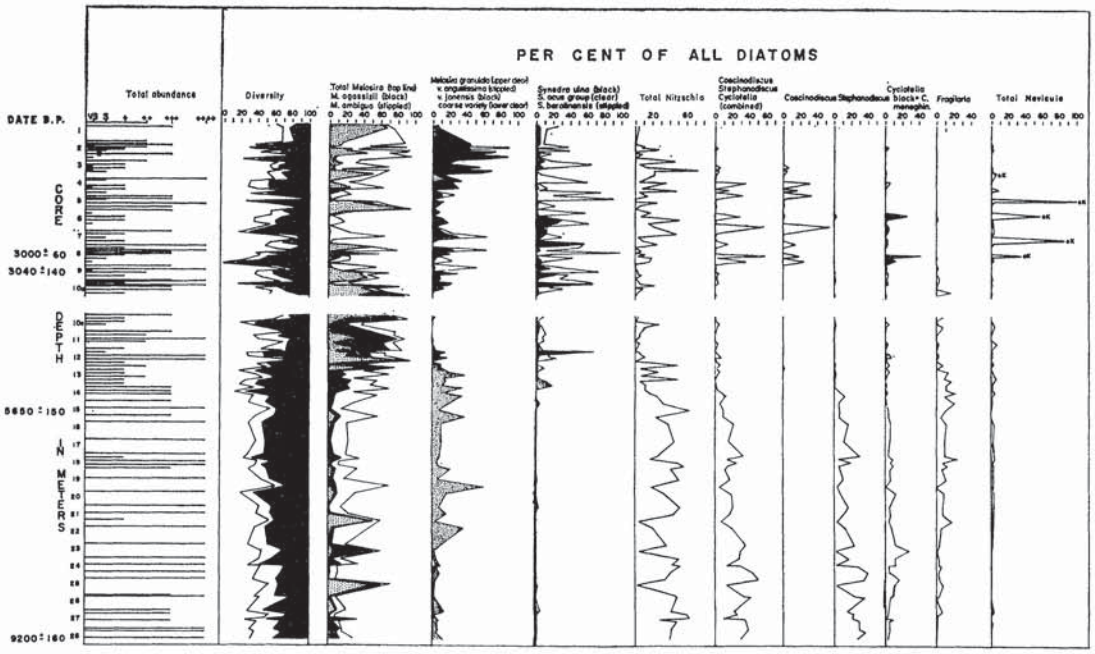


FIG. 11. Core stratigraphy: most abundant species and genera of diatoms. Diversity diagram: The composition of assemblages is shown as the percentage abundance of the two most common species (clear areas) and of all other species combined (black). In *Navicula* stratigraphy, "eK" indicates peaks due almost solely to *Navicula el Kab*.

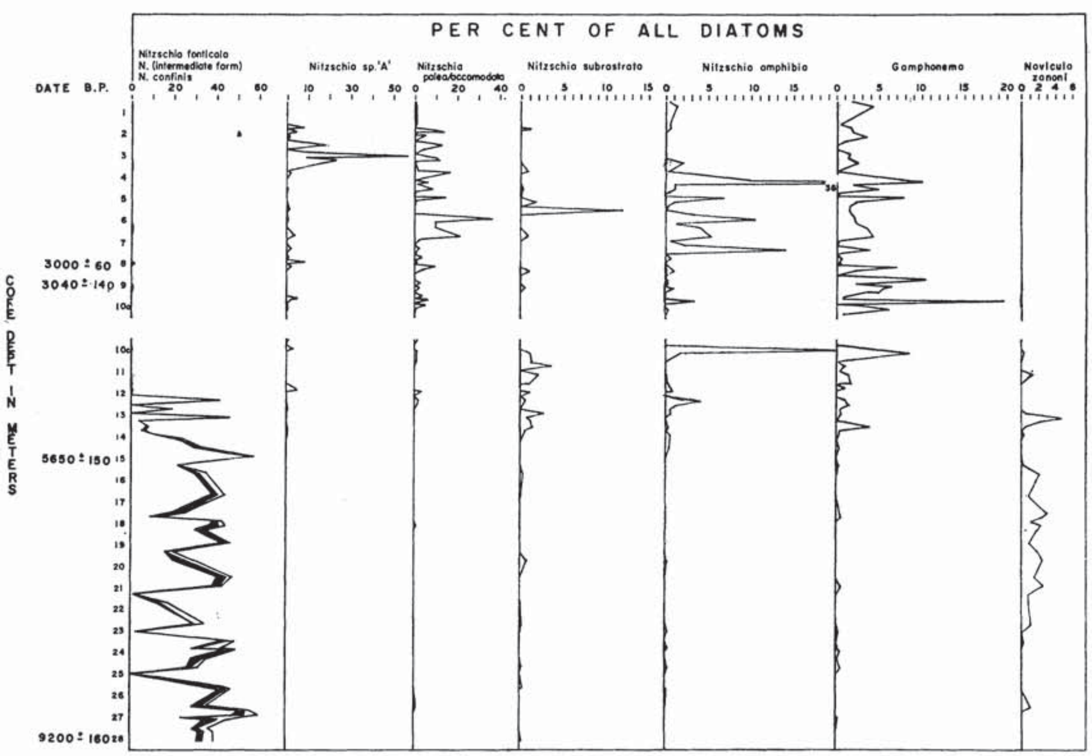


FIG. 12. Core stratigraphy. Distribution of three apparent forms of *Nitzschia fonticola* is at left; *N. confinis* is represented by enclosed area (where one exists) to right of shading, *N. fonticola* by clear area to left of shading, and morphological intergrades by the shaded area. Other diagrams show distribution of taxa that were sporadically prominent.

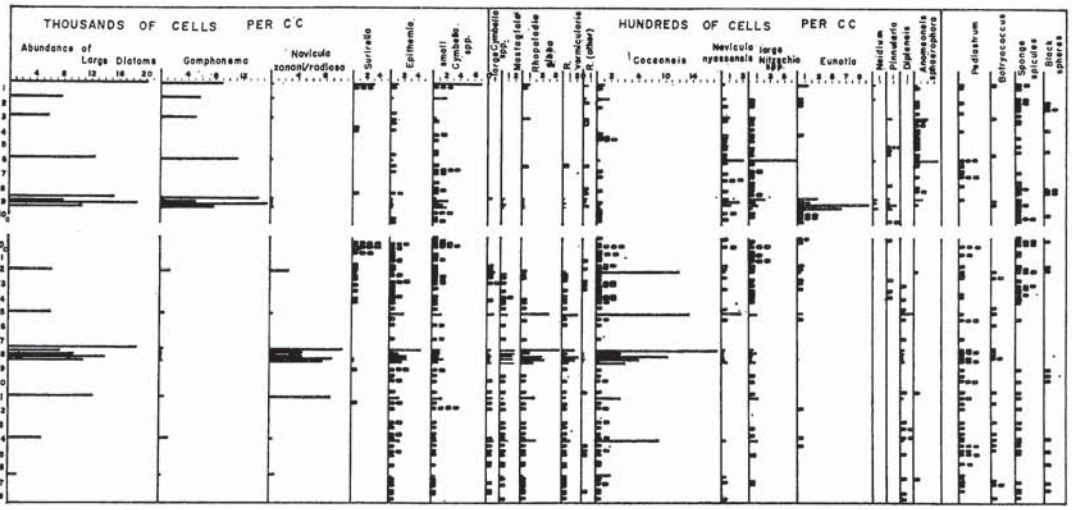


FIG. 13. Stratigraphy of larger diatoms and other microscopic objects. For the diatoms, absolute counts (in cells/cc of wet sediment) are represented by narrow solid lines. Estimates of abundance at uncounted levels are represented by broken lines. Interpret these as follows: Four segments—very prominent; three segments—prominent; two segments—not uncommon; one segment—present.

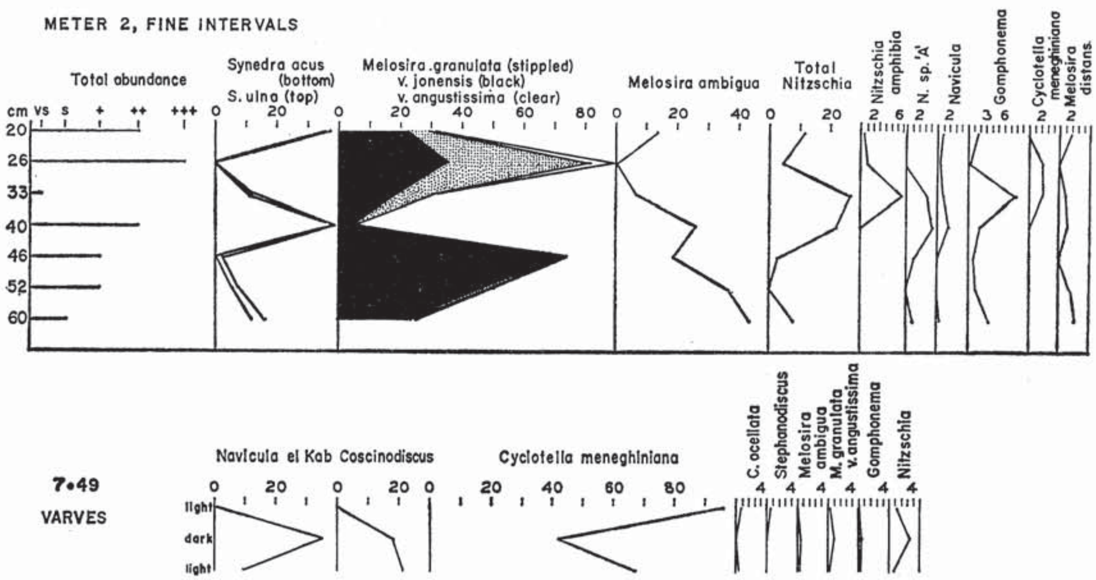


FIG. 14. Narrow-interval stratigraphy, illustrating rapid changes in diatom communities in the upper part of the core. Total thickness of the three varved layers is 2.8 mm. vs—very sparse; s—sparse.

sparsely populated, although the zones of mixed-*Nitzschia* dominance had large diatom populations. The *Nitzschia* assemblages sometimes contained elements of either the *Melosira*/*Synedra* or the *Coscinodiscus* assemblages.

All these assemblages seemed to represent situations more permanent than transitory blooms, in spite of their rapid fluctuations.

INTERPRETATION OF STRATIGRAPHY

The history of the diatom communities of Lake Naivasha reveals a great deal about the history of the lake. The lower 16 m are dominated by a single, distinctive diatom community. In the upper part of the core this is replaced by a group of new community types. Not only do the dominant species change, but a great many of the important species are found only in the upper or the lower part of the core, not both. Our interpretations (Table 5) are based largely on comparisons of the diatom communities in the core with those of modern lakes in Africa and other parts of the tropics (Hustedt 1949, Richardson 1968 (and references contained therein), 1969), and partly on the indicator value of individual taxa. The interpretations are explained below.

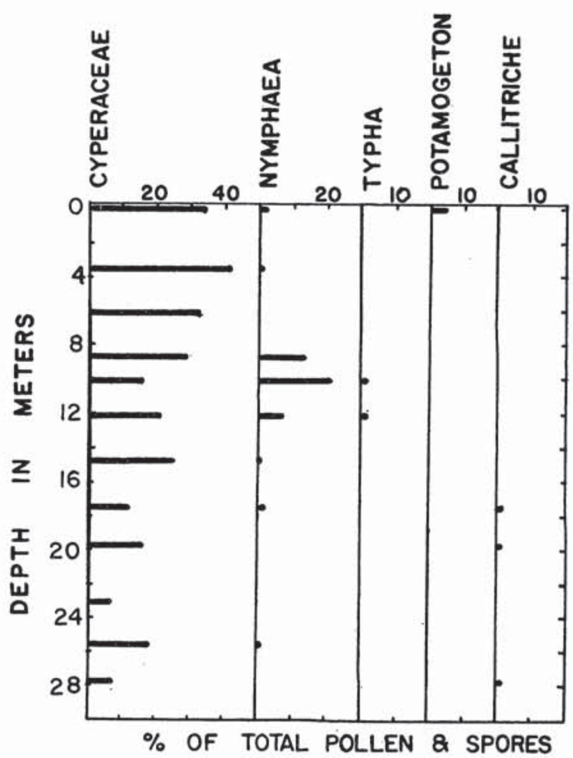


FIG. 15. Pollen stratigraphy of aquatic plants (data of D. A. Livingstone). As indicated, total pollen and spores (terrestrial as well as aquatic) is the basis for calculating these percentages.

Modern analogues of the fossil communities

Strong similarities exist between the diatom flora dominating the lower half of the core and that of present-day Lake Victoria (see Appendix I). *Stephanodiscus astraea, Nitzschia fonticola,* and *Melosira granulata* v. *angustissima,* the primary species low in the core, all occur today in Lake Victoria, although *N. fonticola* is a relatively minor species in that lake and *M. granulata* v. *angustissima* is quite uncommon. Of the second-rank diatoms in the early Naivasha assemblages, *Melosira agassizii, M. ambigua,* and *Fragilaria construens* are prominent in Lake Victoria, and only *Cyclotella ocellata* is absent. Another noteworthy similarity is the prominence in both floras of *Pediastrum simplex,* which was abundant only in Lake Victoria among the 11 East African lakes studied by Richardson (1968).

Meters 14–12 of the core contain diatom communities that appear transitional between the dominant community types of the lower and upper parts of the core. *Synedra berolinensis* assumes importance here. *Melosira agassizii* becomes more prominent than at most lower levels, and *Stephanodiscus astraea* virtually disappears. *Melosira granulata* v. *angustissima* and *Nitzschia fonticola* remain prominent through the top of the twelfth meter, but the latter species, particularly, fluctuates markedly in importance from level to level. The diatom communities of this transitional part of the core bear a resemblance to those presently found in Lake George in the Western Rift Valley (Appendix I; also Elizabeth Haworth, unpublished core study). The dominant diatom in samples of surface sediment from Lake George is a small species of *Nitzschia,* believed by J. F. Talling (*personal communication*) to live epiphytically on blue-green algae in the plankton. This diatom is very similar but probably not identical to *N. fonticola* of the Naivasha core (the two may be varieties of the same species). Second in abundance in Lake George is *Synedra berolinensis;* and several small species and varieties of *Fragilaria* are prominent both in Lake George and in this part of the core. However, *Melosira* is less well represented in Lake George than in its counterpart Naivasha assemblages, and in Lake George there is also a comparative paucity of large species having benthic or tychopelagic habits.

The most prominent community of the upper part of the core (*Melosira*/*Synedra*) appears in the most recent sediments of Lake Naivasha, but was found by Richardson (1968) in none of the other lakes he studied. *Melosira* and *Synedra* do appear as codominants in several lakes in western Uganda and Rwanda (Hustedt 1949) that do not differ markedly from modern Naivasha in size or chemistry.

The sporadically prominent diatom communities of the upper part of the core find their closest analogues, for the most part, in water bodies shallower and chemically more concentrated than Naivasha is today. *Cyclotella meneghiniana* and *Coscinodiscus rudolfi,* for example, have been found abundantly together with *Nitzschia palea* in a shallow (1–1.5 m deep) bay of Lake Rudolf (Bachmann 1938). *Nitzschia palea* is not by itself an indicator of alkaline conditions, but the species with which it is associated in the Naivasha core leave little doubt that the communities in which it and *Nitzschia* "sp. A" were prominent indeed represent alkaline water. Another indicator of alkaline conditions is *Navicula el Kab.* Originally described from alkaline springs in Egypt (Müller 1899), it was the dominant diatom in samples we took from Lake Nakuru in 1969, and it is a common species in the alkaline Momella lakes in Tanzania (Hecky 1971).

These analogies suggest that during the past 9,000 years Lake Naivasha has progressed from ecological conditions similar to those in modern Lake Victoria through a phase bearing resemblances to Lake George to a condition that has for the most part resembled modern Lake Naivasha, but has intermittently been more shallow and chemically concentrated. Lake Victoria and Lake George are both warmer lakes than modern Naivasha, and both are more dilute: the

TABLE 5. History of Lake Naivasha inferred from core stratigraphy

Carbon-14 age[a]	Core level	Dominant diatom assemblages	Lake level	Alkalinity and total ion content	Dissolved silica	Water temperature	Productivity
0	Surface of mud	*Melosira/Synedra*, alternating with several other distinct types: *Coscinodiscus/Cyclotella*, *Nitzschia* spp., *Navicula el Kab*	Fluctuating near and below modern levels	Often higher than today	Similar to today (sometimes above)	Near today	Often high, but overall less than earlier
	to						
3,000 ± 60 (Y−1436)	7.67	None	Dry	—	—	—	—
3,040 ± 140 (I−1769)	8.32	*Melosira/Synedra*	Low	Lower than today	Similar to today	Probably above today	Intermediate
	to	(*Synedra berolinensis*)	Falling		Rising		High
5,650 ± 120 (Y−1339)	14.20						
	to	Single, variable community type: *Stephanodiscus/Nitzschia fonticola/Melosira/Fragilaria/Cyclotella ocellata*	High, overflowing	Similar to today or slightly lower	Lower than today (at least near surface)	Probably above today	High
9,200 ± 160 (Y−1340)	27.57						

[a]Years before 1950 (Y = Yale Radiocarbon Laboratory; I = Isotopes, Inc.).

conductivities of the three lakes are ca. 100, 200, and 325 μmho, according to the analyses of Talling and Talling (1965). Victoria is a relatively clear lake with a varied plankton, George a turbid, greenish lake in which blue-green algae are dominant. Lake George ranks very high among the world's lakes in primary productivity; Lake Victoria is less productive, ranging between one-third and two-thirds of the levels recorded from Lake George (Talling 1965). The algal productivity of modern Lake Naivasha seems to vary within the range recorded from Lake Victoria (*authors' measurements*), although sometimes it may fall below this.

The modern analogues of Naivasha's fossil diatom communities are not perfect analogues, however suggestive. The imperfections invite further inference, based on the autecology of individual species and on general aspects of each community type. Other microfossils and the nonfossil analyses contribute to the interpretation.

Lake depth and area

The predominant diatoms of the lower half of the core are euplanktonic forms. Those of the upper part, also largely planktonic, are species most frequently found in small or shallow lakes in Africa today, or in bays of larger lakes. Benthic diatoms appear in greater numbers and variety in the upper part of the core than in the lower part. Together with evidence of a dry phase in meter 9 and of intermittent chemical concentration in the upper 8 m, these changes indicate that the size of the lake has varied markedly during the past 9,200 years. The lower 14 m of the core represent a lake considerably larger than the one which has existed since that time; the upper 12 m represent a lake seldom if ever exceeding the modern one in size, and often considerably smaller. A three-stage history is indicated: a fairly stable, large lake existing from prior to 9,200 B.P. to approximately 5,700 B.P.; a lake shrinking to dryness between 5,700 B.P. and 3040 B.P.; and a rejuvenated lake since 3,000 B.P., of small size and fluctuating conditions.

How large was the early lake? The similarity of the diatom communities from level to level in the lower part of the core agrees with evidence from the chemical and mineralogical studies that conditions in this lake were rather stable. The most reasonable explanation for this stability is that during this period Naivasha was overflowing through its surface outlet. This outlet, the lip of Njorowa Gorge, stood about 58 m (190 ft) above the lake's shoreline at the time the core was taken. When overflowing, Naivasha would have been about four times as extensive as in 1960, and many times as deep. The small but appreciable numbers of nonplanktonic diatoms in the assemblages from this overflow phase are not surprising. The coring site would have been relatively near shore even when water levels were high. Furthermore, benthic and epiphytic diatoms find their way into deep-water sediments in many large, modern lakes in Africa (Richardson 1968).

All the diatoms fluctuated in relative abundance in the lower part of the core, probably more frequently than is indicated on the stratigraphic diagrams, so ecological conditions were not completely static (or restricted to seasonal variations) during this period. Whenever *Nitzschia fonticola* was one of the two most common species, its consort almost invariably was either *Stephanodiscus astraea* or *Melosira granulata* v. *angustissima*. At the few levels where *Melosira agassizii* or *M. ambigua* dominated, their consort was almost always *Cyclotella ocellata;* in one case, *M. ambigua* was paired with *Fragilaria construens*. The ecology of these species in African lakes today suggests that dominance by representatives of the first group could indicate a more fully planktonic situation (i.e., a higher lake level) than dominance by representatives of the second. This is a rather difficult interpretation to accept if one also accepts that the lake was overflowing during this period, since overflow would have maintained a relatively stable water level. Fluctuations in water temperature or chemistry are perhaps more likely explanations for these diatom changes.

The shrinking lake phase, which we believe is represented by meters 14 through 9 of the core, saw Naivasha decline from levels well above those of today to complete dryness, at least in its crater portion. During this period the crater and the main basin undoubtedly lost their confluence, and the history of water levels in the main basin becomes somewhat speculative. Undoubtedly the main lake also fell below modern levels, and since the main basin is shallower today than the crater, it may also have dried completely, perhaps for a longer period than the crater. But the main basin receives inflow from rivers which probably were more or less permanent even during this time of drought, and it may have always contained some water.

This period was not one of steady, progressive decline in lake level. There seems to have been a steep decline at first, then slower change. The great fluctuations of *Nitzschia fonticola* in meters 13 and 12 perhaps reflect alternate rupture and reestablishment of connections between the crater and the main lake basin, i.e., a period of oscillation, with water levels already below modern levels. The disappearance of *N. fonticola* at the top of meter 12, coincident with a peak of the essentially littoral species *Synedra ulna,* probably represents a slight further decline and a semipermanent break in surface connections between the crater and main basin. Between this time and the time it dried completely, an interval of perhaps 1,000–2,000 years, the crater contained a small, weedy lake or pond, quite probably an outcropping of the water table. The final decline to dryness certainly represents a minor climatic event compared to the initial fall in level from the large lake phase. Apparently during the short period when the crater was dry, the water table never fell more than one-half meter below the exposed mud surface; if it had, the organic matter in the underlying sediments would have been oxidized to greater depths.

Following the dry phase, the crater again contained a small lake, the third stage of the history we have recorded. Represented by the upper 8 m of the core, this lake seems to have led a much more hazardous and varied existence than the pond that existed prior to drying. Planktonic species occur in the assemblages of this part of the core, but all are species often abundant today in small lakes or in shallow parts of large lakes. The strongest indications of the small and fluctuating nature of this lake are indirect, being derived from diatoms that are indicative of chemical changes in the water and from the variability of nearly all of the sedimentary parameters. Why this lake was so much more variable, especially chemically, than the pond of the previous phase is a puzzling question. Possibly the sediment that was deposited and cemented during the dry interval created a seal, separating the rejuvenated lake from the underlying water table. The periods of lower chemical concentration undoubtedly represent periods of higher water level; the *Melosira/Synedra* diatom community is indicative of such periods, and the *Coscinodiscus/Cyclotella, Navicula el Kab,* and sparse, *Nitzschia*-dominated communities indicate times of lower water. We suspect that the highest water levels during this period are represented by the times when *Melosira ambigua* predominated over *M. granulata* v. *jonensis* in the *Melosira/Synedra* community. By this interpretation the 20th century has seen some of the highest water levels in the Naivasha basin in the past 3,000 years.

Water temperature and chemistry

Inferences about past thermal and chemical conditions in Lake Naivasha are partly interdependent and are best discussed together. Our suggestion that the lake was warmer during its large and shrinking phases than it is today is based principally on the abundance of one species—*Nitzschia fonticola*—during those phases. Elsewhere (Richardson 1968, 1969) we have pointed out that members of the genus *Nitzschia* occur prominently in the phytoplankton only of lakes that are relatively warm and relatively rich ionically. Naivasha does not now support a *Nitzschia* phytoplankton, although the chemical conditions seem suitable; we concluded (Richardson 1968) that the modern lake is too cool to support such a plankton.

Nitzschia fonticola was probably either a free-living phytoplankter or an epiphyte on other phytoplankton in the early Naivasha lake. In either case, its abundance at that time may signify water rather rich in nutrients, probably including organic nutrients (cf. Richardson 1968). Either higher temperatures or somewhat greater ionic concentrations than today might have brought about such conditions. Although volcanic activity during the large lake phase could have supplied considerable amounts of nutrients, it is difficult to imagine the overflowing lake as being more concentrated than the present lake, which has no surface outlet. The alternative explanation, that the lake was warmer than today, is more reasonable.

The ionic history of Naivasha, as suggested by the diatoms, is complex and rather surprising. Much of our interpretation is in terms of total ion content or conductivity, but in these soda-dominated African lakes ion content can be considered a measure of alkalinity as well.

If the large Naivasha lake was warmer than today, it need not have been very concentrated to support the diatom community we have recorded. *Nitzschia fonticola* is the most common planktonic diatom in Lake Edward (Hustedt 1949), which is about three times as concentrated as modern Lake Naivasha, but it also occurs (less commonly) in Lake Victoria, which is considerably less concentrated than Naivasha. *Melosira granulata* v. *angustissima* is a constituent of the present flora of Naivasha, though it was much more common in the large-lake phase. Richardson (1968) suggests that this diatom favors waters of moderate to fairly high alkalinity, but as in the case of planktonic species of *Nitzschia*, its primary requirement may be a rich organic environment. *Stephanodiscus astraea* is common in both Lake Victoria (Richardson 1968) and Lake Albert (Talling 1963), i.e., in waters both less and more concentrated than Naivasha today.

The secondary species provide indications that the large lake phase was ionically less rich than today's lake. *Melosira agassizii,* which occurred in significant numbers throughout the lower meters, is not known to be abundant in any ionically rich lake, but is common in two lakes more dilute than Naivasha today—Victoria and Shiwa Ngandu (Richardson 1968). The latter lake is extremely dilute, with a total solids content about one-twentieth that of Naivasha (Livingstone 1963). *Cyclotella ocellata* has not been recorded in appreciable numbers from any modern lake in Africa; the sparse tropical evidence indicates that this species is not excluded from fairly alkaline waters, but much more extensive evidence from temperate regions indicates its frequent occurrence in waters relatively low in nutrients (Ruth Patrick, *personal communication*). The species of *Fragilaria* most common in the large Naivasha lake, *F. construens* and *F. pinnata,* are chiefly found in lakes less concentrated than Naivasha today.

The evidence cited thus far is consistent with the inference that ionic concentrations in the large Naivasha lake were not unlike those of Lake Victoria today, but were perhaps somewhat higher. Other indications of a higher ionic content are the apparently high productivity of this lake, soon to be discussed, and the presence of a number of benthic diatoms indicative of rather rich ionic conditions: species of *Epithemia, Rhopalodia* (notably *R. gibberula*), *Mastogloia,* and *Diploneis ovalis*. *Epithemia* and *Rhopalodia* were recorded sparingly from surface sediments in Lake Victoria (Richardson 1968), but more frequently in sediment at the top of the Naivasha core. We conclude that the total ion content of Naivasha during this period lay between its present ion content and that of Lake Victoria today, perhaps closer to that of modern Naivasha.

TABLE 6. Silica concentrations in African lakes from which *Stephanodiscus* spp. are recorded

Lake	Dissolved SiO_2 (mg/liter)[a]	Species	Abundance
Albert	0.04−3.4	*S. astraea*	Codominant diatom (1)[b]
Tanganyika	0.3−13.5	*S. astraea*	0.9% of all diatoms (2)
Edward	2−8	*S. damasi*	Common (3)
Victoria, bay	3−9	*S. astraea*	6% of all diatoms (2)
Victoria, open lake	3−9	*S. astraea*	31% of all diatoms (2)
Rukwa	76.7	*S. astraea*	3.4% of all diatoms (2)

[a]For each lake, lower values are generally surface concentrations.
[b]References:
Dissolved silica values taken from Talling and Talling 1965;
(1) Talling 1963; (2) Richardson 1968; (3) Hustedt 1949.

Although total ion content during the large-lake phase may not have differed greatly from today's, dissolved silica was apparently much lower, at least in the upper, euphotic layer. Kilham (1971) has convincingly shown that certain planktonic diatoms are characteristic of low-silica waters, and others of waters much richer in silica. *Stephanodiscus astraea* is a low-silica indicator both in temperate lakes (Kilham 1971) and in the lakes of East Africa (Table 6). Although it has been recorded from at least one African lake high in silica, it seems to be dominant or near-dominant only in lakes with less than 5 mg/liter SiO_2 in their surface waters. Many of these lakes are stratified with regard to silica, with higher concentrations at depth than in the euphotic zone where *Stephanodiscus* occurs. This could certainly have been the case in Naivasha during its large-lake phase; silica could have been relatively rich in deeper waters, but poor near the surface.

During the shrinking phase of the lake (meters 14–9 of the core), concentration by evaporation might be expected once the water level fell below the outlet. Surprisingly, the diatoms indicate no appreciable increase in ionic content during this period; in fact, they indicate the opposite during at least the latter part, when the crater was presumably isolated from the main lake. At the same time, however, the disappearance of *Stephanodiscus* and the rise to prominence of *Synedra* indicate a rise in dissolved silica (Kilham 1971 and *personal communication*). As already stated, the diatom communities early in this phase resemble the present diatoms of Lake George. This lake lies roughly halfway between Victoria and modern Naivasha in its ionic content, i.e., it is close to the ionic content we have suggested for the large-lake phase of Naivasha. Hence, there are no grounds for suggesting that Naivasha became more or less concentrated during its initial decline. Later, however, the isolated water body in the crater basin seems to have been more dilute, as evidenced by the prominence of *Melosira agassizii* in the diatom communities (meters 10 and 11), and, even more, by the increased abundance of *Eunotia, Pinnularia,* and *Neidium*. These three genera are all more typical of relatively dilute than of concentrated waters. All are littoral, and it could be argued that their abundance at the core site might increase as the lake shrank, irrespective of any chemical change. However, other littoral genera of alkalophilous tendencies declined in this part of the core. The trend to more dilute conditions was perhaps not great, but it seems unmistakable from the evidence of the diatoms. Rising cation levels in this part of the core might be considered contradictory evidence, but a single interpretation of the cation curves is difficult, as we have pointed out. The presence of *Nymphaea* and *Typha* at this time (Fig. 15) supports the conclusion that this was a small, fresh lake.

There remains the paradox of a silica concentration that seemingly rose while the total ionic concentration remained stable or fell somewhat. The paradox is resolved if the suggestion is accepted that only the surface waters of the large lake were depleted of silica. As water levels fell, silica stratification ended through more thorough mixing of the shorter water column, or the silica-enriched lower layers simply became part of the euphotic zone. Thus the average silica content of the water column may not have risen, but a richer silica environment was provided for the algal plankton. During this period the silica content of surface waters perhaps approached the modern Naivasha level of 30 mg/liter, but may have been lower. African lakes in which *Synedra* is today prominent have a range in dissolved silica of perhaps 15–30 mg/liter SiO_2 (Talling and Talling 1965, Richardson 1968).

The diatoms of the upper 8 m of the core indicate a history of sharp chemical fluctuations during the past 3,000 years. The lower part of the fifth meter, which is marked by reappearance of *Melosira agassizii* and an increase in *Pinnularia,* represents the one brief period for which strong indications exist of lower ionic levels. Otherwise, concentrations ranged from near present levels to much higher levels. Lake Rukwa's south basin, whose salt content is more than twice that of Naivasha today, contains *Coscinodiscus, Navicula el Kab,* and *Nitzschia* "sp. A" in important numbers (Richardson 1968), but the Rukwa flora is considerably more varied than Naivasha assemblages in which these taxa were abundant. This may mean that Naivasha reached ionic levels appreciably higher than the south basin of Rukwa today. In 1969 Lake Nakuru was relatively dilute by modern standards (conductivity about 12,000 meq/liter), but still some 40 times as concentrated as modern Naivasha. The diatoms of Lake Nakuru at this time were heavily dominated by *Navicula el Kab,* suggesting that at least the crater portion of Naivasha could have approached similar ionic levels during the fluctuating phase of its history. During this period dissolved silica probably varied more or less in phase with ionic content, from levels near today's when *Synedra* was abundant to considerably higher levels when species indicating alkaline water predominated. Highly alkaline lakes of present-day Africa are unusually rich in SiO_2, presumably because silicon compounds readily dissolve in such waters (Talling and Talling 1965, Jones, Rettig, and Eugster 1967). We suspect that several species of the lower core may be absent from the upper meters because, like *Stephanodiscus,* they are not favored by high silica concentrations. The striking segregation within the core of *Cyclotella ocellata, Navicula zanoni,* and most species of *Fragilaria* may signify a preference for rather low silica levels. This is possibly true also of *Nitzschia fonticola;* if so, our inference regarding temperature during the large and shrinking phases of the lake loses much of its support and must rest heavily on the evidence for high productivity to be presented in the next section.

The striking species segregation of *Pediastrum* may also be mentioned at this point. *Pediastrum simplex* characterizes the lower part of the core, *P. boryanum* levels above meter 12. Morphologically the porous, attenuate colonies of *P. simplex* seem better suited to planktonic life than do the denser colonies of *P. boryanum,* but different chemical preferences may also be important in their core distribution. *Pediastrum* is unusual among the green algae in having the cell wall strengthened by silica. Salmi (1963) has suggested that *P. boryanum* is a very adaptable species in terms of water chemistry, but that *P. simplex* may avoid calcareous waters.

Two series of close-interval samples (Fig. 14) point up the rapidity of fluctuations in dominance by different diatom species during the latest period of the lake's history. Diatom differences in the three adjacent laminae in meter 8 suggest cyclic change and reinforce our belief that these bands represent wet and dry seasons. Through much of the past 3,000 years the benthic and epiphytic floras of the lake seem to have been rather impoverished; perhaps the changing chemistry discouraged the establishment of a variety of aquatic plants (Fig. 15), or perhaps the water was frequently turbid. The restoration of genera such as *Surirella, Cymbella,* and *Epithemia* to greater prominence near the top of the core may indicate somewhat more stable conditions in the very recent past.

Productivity

Two approaches to the past productivity of Lake Naivasha are possible. The first is to examine the productivities of the modern lakes which contain analogues of the fossil Naivasha diatom communities; the second is to explore the implications of Naivasha's rates of organic sedimentation in the past. Data on phytoplankton productivity exist for Lakes Victoria and George, whose diatoms resemble those of Naivasha during its large-lake phase and the first stage of its shrinking phase; for three lakes with a *Melosira*/*Synedra* or *Synedra*-dominated diatom plankton; and for two fairly alkaline lakes (Talling 1965, Richardson 1964*a,* 1968).

The most complete data are for Lake Victoria; Talling (1965) has 14 measurements spread over 9 months from the open lake and several other records from bays. In the open lake, phytoplankton productivity averaged 7.4 g O_2/m^2 per day. This is not especially high for Africa, but, as far as we know, exceeds the recorded productivity of any temperate lake. A higher average productivity, 9.6 g O_2/m^2 per day, characterized the four bays of Lake Victoria that Talling studied. The phytoplankton productivity of Lake George, averaging 14 g O_2/m^2 per day in two measurements by Talling, is close to the maximum recorded for any lake in the world. Lakes Mulehe and Bunyoni in western Uganda and Naivasha itself are the three lakes presently rich in *Synedra* (or *Melosira*/*Synedra*) for which productivity data exist. A value near 7 g O_2/m^2 per day was obtained for Naivasha in a single experiment in 1961 (Richardson 1964*a*), but recent measurements by us indicate that this is unusually high for the modern lake. The high figure coincided with a bloom of *Botryococcus*. In Lake Bunyoni and Lake Mulehe Talling (1965) obtained values of 4.8 g O_2/m^2 per day and 2.3 g O_2/m^2 per day in single experiments.

The alkaline stages of Naivasha are those for which comparative modern productivity data are most scarce. In Lake Rukwa, which is dominated by species of *Nitzschia* and *Coscinodiscus,* we recorded a productivity of only about 1 g O_2/m^2 per day, in a less than ideal experiment (Richardson 1968). Production was very high near the surface of this shallow lake, but the euphotic zone was reduced greatly by wind-induced turbidity (probably a normal condition in this lake). In Lake Baringo, another lake rendered turbid by suspended mineral matter, we have recorded a productivity of 1.6 g O_2/m^2 per day. Baringo has about twice the ion content of modern Naivasha, Rukwa slightly more than twice. It is likely that small, alkaline lakes more sheltered than these two are considerably more productive. In Nakuru, Elmenteita, and other lakes with permanent algal blooms, production near the surface should be extremely high, but the euphotic zone is certainly very thin. (In a recent report Melack and Kilham (1971) have confirmed these suggestions, recording very high productivities per square meter in such lakes despite the shallow photosynthetic zone.)

From these data we can estimate the average primary productivity of Lake Naivasha at various stages in its history:

1) For the period of the large lake, gross productivity perhaps lay somewhere between the modern averages for Lake Victoria and Lake George; i.e., it may have been of the order of 9–12 g O_2/m^2 per day. As we have pointed out, the water seems to have been richer in nutrients during this time than is Lake Victoria, at least in its open-water portions today; hence a higher productivity than Victoria's seems likely.

2) The first part of Naivasha's shrinking phase may have witnessed productivities near the upper end of the estimate given above for the large-lake phase. The early shrinking phase was that in which the diatoms most resembled those of modern Lake George. The differences we have noted between the Naivasha and George diatom assemblages lead us to infer, however, that Naivasha's productivity was somewhat less than that of modern Lake George. The prominence in Naivasha of *Melosira agassizii* (an unusually heavy planktonic species which is probably at a disadvantage in turbid waters), as well as the greater numbers of benthic diatoms, suggests strongly that the lake at that time was more transparent than is modern Lake George. If so, algal density was less and productivity was probably lower.

3) Productivity may have averaged 3–6 g O_2/m^2 per day during subsequent periods when a *Melosira*/*Synedra* plankton dominated Naivasha. The more alkaline phases of this small, fluctuating lake may have had considerably higher productivities, however, unless suspended sediment reduced the available light.

It is interesting to compare these estimates, based on modern productivity data from various African lakes, with the changing rates of organic sedimentation in the Naivasha core (Table 2). Organic deposition was most rapid during the period of the large, stable lake. The organic sedimentation rate fell by

15% during the shrinking phase (the carbon-dated interval includes both the "Lake George phase" and several meters of *Melosira/Synedra* diatom assemblages), and by 40% during the period of the fluctuating lake.

Quantitative estimation of Naivasha's past productivity can be attempted directly from organic deposition rates, since modern deposition rates in Lake Victoria can be calculated crudely from data in Kendall (1969). The result of such an attempt is hardly believable, however, since the organic deposition rate during Naivasha's large phase appears to have been about six times the present rate in the offshore parts of Victoria. Why the rate in Naivasha was so high is difficult to explain, but the deeper crater where the core was taken may have served as a sink for suspended materials.

In any case, both approaches suggest that Naivasha was highly productive during its large, stable phase. This evidence for high productivity reinforces our earlier suggestion that the lake may have been warmer at that time than today. Levels of primary productivity probably were quite variable during the shrinking and fluctuating phases of the lake, and perhaps less variable during the large phase. Except for the period when aquatic macrophytes assumed importance (meters 12 through 9), the primary productivity was probably based largely on phytoplankton.

Lake Naivasha as a Developing Ecosystem

We turn now to the comparative limnological problem posed in the introduction: to what extent does the history of this tropical lake conform to suggested developmental patterns of temperate lakes? The incomplete Naivasha record gives no answers regarding early development, but the lake's later history casts light on the question.

Hydrarch succession

This tenet of historical ecology, one of the "facts" of most basic ecology courses, refers to the process whereby a lake basin fills with sediment, becoming progressively shallower until replaced first by marsh, then by some terrestrial community type. As usually described, hydrarch succession is inexorable, unidirectional, and final. The history of Lake Naivasha does not fit this mold, and a moment's reflection reveals that strict application of the concept must be an oversimplification, if not a distortion, of the true histories of many lakes. Certainly this is true of "closed" lakes, i.e., those without outlets. In response to climatic change such lakes may become deeper rather than shallower over long periods of time; or they may fluctuate so markedly as to completely overshadow the unidirectional effects of basin sedimentation.

The recorded history of Naivasha is mainly of this sort. To a great extent, changes in depth, area, and amount of aquatic vegetation have been independent of the accumulation of sediment in the basin. Changes due to climate always may have been more rapid than changes due to sediment deposition, rapid as the latter has been; and for at least the later portion of its history, Naivasha has fluctuated in the manner of a closed lake, whether or not it really is one.

During its large-lake stage Naivasha apparently had an outlet to the south which kept its level from changing markedly. However, there followed a period of rapid pseudosenescence, so called because sediment accumulation contributed only minimally to the decrease in depth and invasion of aquatic plants that occurred. Water eventually disappeared from the crater, and probably from the entire basin, but the subsequent rejuvenation of the lake illustrates the climatic rather than successional control of this particular history. Biologically speaking, Naivasha is now no closer to senescent lake conditions than it was several thousand years ago.

The later history of Naivasha exemplifies a simple generalization: no ecosystem should be expected to follow a stereotyped, dialectical pattern of development if it is subject to major perturbation by unpredictable external agencies.

Productivity

The widely accepted generalization that lakes pass from oligotrophy to eutrophy involves assumptions about changing biological productivity through time. Hutchinson and Wollack (1940) and Deevey (1942) were among the first to suggest from paleolimnological evidence that productivity during lake development follows an early sigmoid pattern, similar to the growth patterns of organisms and populations. Livingstone (1957) later argued for other interpretations of the evidence, but the sigmoid model has continued to attract historical ecologists.

Tropical lakes such as Naivasha originated under climatic and nutrient circumstances undoubtedly more benign than those attending young glacial lakes. Since the sigmoid productivity model was adduced from the latter, it is unfortunate that our truncated Naivasha record provides no information about the lake's early stages and youthful trends of productivity. Our record begins with the lake in an apparently mature state.

Lindeman (1942), in a largely hypothetical description of productivity changes during hydrarch succession, suggested that the sigmoid growth phase was followed by a rather long period of high and relatively stable productivity which he termed eutrophic stage-equilibrium. The large-lake phase, with which our history of Naivasha begins, resembles Lindeman's eutrophic equilibrium in several ways:

it was a period of high productivity and relative biological stability lasting several thousand years. Not all the diatoms common in the lake at this time were indicators of eutrophic conditions, and nutrient levels may well have been higher at some later stages in the lake's history. We believe, however, that our evidence supports the concept of a eutrophic stage-equilibrium, and that the large-lake phase of Naivasha represented such a phase.

Following stage-equilibrium, Lindeman's scheme posits a period of senescence during which productivity falls off markedly, with the lake finally giving way to more productive marsh and terrestrial communities. In Naivasha the pseudosenescence of the shrinking lake stage began with a period that may have been even more productive than the large-lake stage. At this time the waters fell below the lake's outlet and perhaps accumulated more nutrients. After this rather brief episode (which would not be expected during true successional senescence), the productivity of Naivasha does seem to have dropped in accordance with Lindeman's hypothesis. The rate of organic deposition during this period, represented by core interval 8.32 to 14.20, was only slightly less than during the large-lake phase (Table 2), but the decrease in productivity may have been more than this suggests. The pseudosenescence of Naivasha culminated in a shallow, weedy pond where organic preservation may have been higher relative to productivity than it had been in the deep lake. Both the shorter water column and the preponderance of macrophytic producers in the pond should have resulted in less decomposition of organic matter prior to burial than occurred in the large lake.

The productivity trend we have outlined for the period of Naivasha's pseudosenescence seems to accord largely with Lindeman's ideas, but we should reiterate that during the latter part of the shrinking phase the crater became cut off from the main lake. It may not be legimate to suggest agreement with Lindeman's scheme when the frame of reference changed so markedly during the course of pseudosenescence.

The most recent phase of Naivasha's history, that of the fluctuating lake, runs counter to the concept of hydrarch succession. Thus we cannot discuss its productivity in terms of Lindeman's hypothesis, which deals only with the successional model.

Diversity of diatom assemblages

In recent years a variety of explanations has been advanced for differences in species diversity among natural ecosystems. At least one explanation, the stability-time hypothesis, invokes differing histories as a cause. This hypothesis suggests that as time progresses in an undisturbed ecosystem, niche specialization leads to increased species diversity. The stability-time hypothesis would maintain, for example, that diversity of trees and birds is higher in tropical forests than in temperate forests because of the former's greater age and environmental stability.

Goulden's paleolimnological study of a lake in Guatemala (1966) provides some of the strongest evidence favoring the stability-time hypothesis. He found that the diversity of chydorid Cladocera increased through time, except when the lake was disturbed by human activities. Goulden concluded that superabundance of one or two chydorid species and unusual rarity of others is characteristic of an immature community that has not achieved equilibrium, or of a situation displaced from equilibrium by externally imposed disturbances. Recently (1969) he has extended these findings to other lakes.

The early part of our Naivasha record provides a test of the stability-time hypothesis: the large-lake stage represents approximately 3,550 years of comparative stability, during which time the diatom community remained rather similar and the lake apparently overflowed continuously. The stability-time hy-

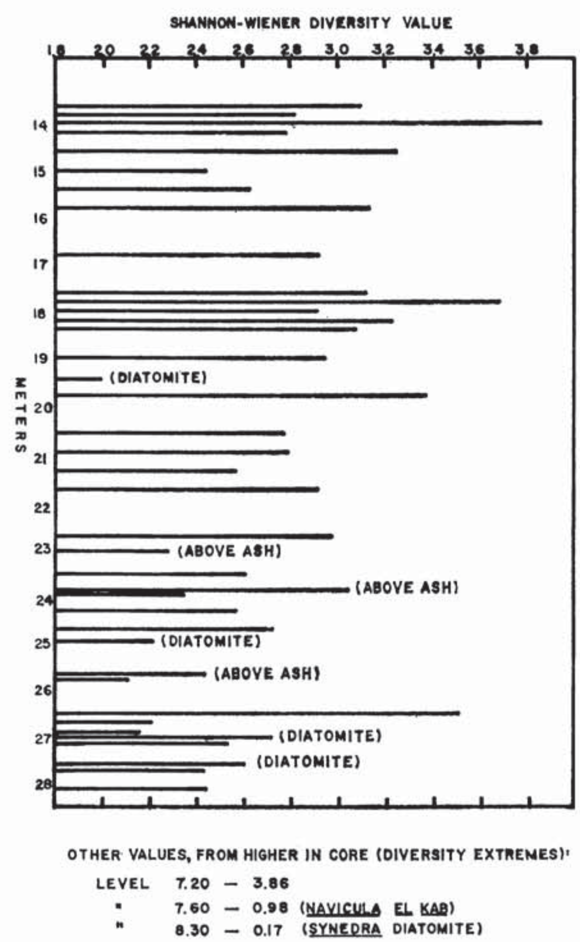


FIG. 16. Species-diversity values for the lower half of the Naivasha core and for three higher levels.

pothesis would predict a gradual increase in diatom diversity during this period. Our graphical representation of relative dominance, which is related to diversity, seems to show such a trend (Fig. 11). Species other than the two dominants gradually assume a greater role in the assemblages as one moves up the lower 12 m of the core. A plot of Shannon-Wiener diversity values for this part of the core (Fig. 16) also shows this trend, although the progression certainly is not smooth or particularly striking. Two instances of surprisingly high diversity near the bottom of the core, in meters 27 and 24, run counter to the expectations of the stability-time hypothesis, but can perhaps be explained in terms of some environmental disruption. (In assemblages of mostly planktonic diatoms, disruptions which might increase rather than decrease diversity are not hard to conceive. Examples are an influx of littoral diatoms, rafted to the coring site by papyrus islands such as those now floating on the lake, or perhaps simply a nutrient-rich ashfall.) Some of the low-diversity assemblages in this part of the core are from layers of unusual diatom abundance (labeled "diatomite" in Fig. 16). Probably responsible for these were subtle environmental changes that temporarily produced optimal conditions for an already important member of the community.

The instability of the lake during its shrinking and fluctuating phases makes the stability-time hypothesis inappropriate to a discussion of diversity changes in the upper half of the core. At times during this later period a rich variety of diatom habitats, suitable for planktonic, epiphytic, and epipelic species, probably existed close to the coring site; these situations are reflected by occasional assemblages of great diversity. There also occur numerous later assemblages of very low diversity; some of these represent diatom bloom layers such as those in the lower part of the core, whereas others reflect conditions of extreme chemical concentration or turbidity, or both, tolerable only to one or a few species.

Paleochemistry and the lake's present freshness

A fundamental geochemical generalization states that the chemical concentration of closed-water bodies increases through time until equilibria between solution and precipitation become established. This seems a sound statement, since evaporation—the only mechanism of discharge from such water bodies—invariably results in a discharge more dilute than the inflow. Most closed-water bodies do seem to behave in accordance with this generalization, but exceptions have long been known.

Gilbert (1890), in one of the earliest paleolimnological investigations, cites one such exception in Rush Lake, a fresh-water relict of Lake Bonneville. In addition, it is now well established (see e.g., Livingstone 1963*b*) that the earth's largest closed-water body, the ocean, is far less concentrated than would be predicted if the difference between ionic inflow and ionic discharge by evaporation is the only factor considered. Lake Naivasha, too, during the latest 5,000 years of its existence seems to have been defying this geochemical "rule." During all of this period we believe it has had no surface outlet.

Why is Naivasha presently so fresh? At least three explanations have been advanced by geologists:

1) Capture by the Melawa River of additional drainage from the Aberdares has caused relatively recent freshening of the lake (Cole 1950).

2) Rapid sedimentation has buried chemically concentrated deposits beneath the lake, preventing progressive ionic accumulations within the water itself (Nilsson 1940).

3) Naivasha is not truly a closed lake, but has subterranean discharge (Gregory 1921, Baker 1958, Thompson and Dodson 1963). Baker thinks that Naivasha is a hydrographic window in a generally southward-sloping water table, and that the lake is continually freshened by leaching through the sediments. This ion-rich subterranean discharge, in Baker's view, eventually surfaces far to the south as Lake Magadi, a much lower and very concentrated lake.

Our stratigraphic record provides evidence unavailable to these earlier workers. Pertinent to any explanation of the lake's present freshness are at least four findings from the core study: the rapid sedimentation rate; the lack of appreciable concentration of the water during the lake's shrinking stage; periods of considerable concentration during the last 3,000 years; and the fluctuating condition of the lake during this later time, with the present level probably representing a relatively high stand. Our findings appear to invalidate Cole's suggestion, to support that of Nilsson, and to raise questions about that of Baker. No single explanation is likely to explain Naivasha's freshness; indeed, to the suggestions already raised, we will add others.

Rapid sedimentation in Naivasha, burying sediments more concentrated than those now being formed, has undoubtedly helped prevent the progressive salinization of the lake. However, we found no layers of the more soluble evaporites, such as trona (nor have we found them in cores taken recently from Lakes Nakuru and Elmenteita). Perhaps more important, salts have been removed from exposed lake beds by deflation. Langbein (1961) suggests that this is a major mechanism of salt removal from closed lakes, and its importance in our study area is attested by the soda clouds raised in recent years from the dry flats of Lake Nakuru (Cole 1963). In Naivasha's case the core site has been dry only once during the past 3,000 years, but during this period most presently submerged parts of the basin have probably been exposed repeatedly to deflation.

Appreciable freshening by underground drainage during the past 3,000 years seems unlikely in light of our evidence that the water was frequently much more concentrated than today. If seepage were occurring, it presumably would be doing so toward the south, but the borehole data of Thompson and Dodson (1963) indicate that water tables near the south shore of the lake stand slightly higher than the lake surface. These authors also report springs in the northern end of Njorowa Gorge, but these could as easily represent drainage from hills in this vicinity as drainage from the lake. Njorowa Gorge is now dry through much of its extent, even at levels well below the present lake surface, so these springs should not in any case represent large losses from the lake. Thompson and Dodson's borehole data suggest, however, that some seepage to the water table may occur today on the lake's eastern side.

An important study by the hydrological section of the Ministry of Works of Kenya[3] attempts to relate modern lake-level changes to measured inflow, evaporation, and rainfall on the lake. On a yearly basis, rainfall and inflow have repeatedly failed to balance evaporation and water-level change, and the authors suggest underground seepage from the lake as a cause of the discrepancy. We accept their calculations as strong evidence that the lake does presently lose water and salts by seepage. However, the evaporation values used in the study seem of questionable accuracy, partly because of traditional questions regarding the translation of pan values to actual evaporation values, and partly because evaporation from the swamps fringing the lake was not calculated separately. Another report from the hydrological section[4] indicates that evapotranspiration from papyrus swamps may be as much as four times the evaporation from open water. Possibly most of the discrepancy between water-level changes and the measured hydrological parameters is explicable in these terms, rather than in terms of underground drainage. Perhaps the best current synthesis of evidence would be that the lake is probably presently losing some water and salts by seepage, but that when levels stood lower in the past the crater basin, at least, was truly a closed lake.

What of seepage during the shrinking phase of Lake Naivasha, after the lake had lost its surface outlet through Njorowa Gorge? The lack of appreciable concentration of the water during this phase seems most easily explained by the freshening mechanism of underground discharge suggested by Baker. But another mechanism of ion removal, the activity of aquatic macrophytes, was possibly important during the shrinking phase and may also be operating today. Ruttner (1953) indicates that the process of bog formation from shallow temperate lakes is characteristically accompanied by a decrease in ionic content and an increase in acidity of the water. *Sphagnum,* which has well-known ion-hoarding capabilities, is probably the chief agent of these changes in temperate waters, but it is not impossible that certain aquatic plants or swamp sediments play a similar role in the tropics. Talling (1957) found that, although the White Nile loses approximately half its water by evapotranspiration in the papyrus swamps of the Sudd, it is approximately as dilute when it leaves the swamps as when it entered. This suggests ion removal within the swamps by some means. Naivasha today supports considerable tracts of papyrus, particularly in the delta regions of its two major influents. During the period when the crater was occupied by a small, weedy pond, ion removal by plants or sediments could perhaps explain why the fossil diatoms indicate relatively dilute water, despite higher levels of extractable cations in the sediment at this time.

To sum up, Naivasha is presently fresh because burial and deflation of salts, their possible removal by fringing swamps, and their intermittent removal by seepage have prevented their progressive accumulation in the lake water. Also significant is the relatively recent expansion of Naivasha from a previous low state (Sikes 1936, Dale 1952, and our own inference from the core record). The importance of this is illustrated by the considerable freshening of Lakes Nakuru and Elmenteita, and the more modest freshening of Naivasha, during the wet years of the early 1960's. Our conductivity measurements in 1969, several years after the lakes had begun to shrink once again, showed them to be only 8%, 32%, and 80% as concentrated as they were in 1960–61 (Talling and Talling 1965), before the onset of the rainy years. Finally, any explanation of the present contrast between Naivasha and its two alkaline neighbors must take into account the more dilute river inflow to Naivasha, and the fact that both Elmenteita and Nakuru are fed partly by alkaline springs (Richardson and Richardson, *unpublished data*).

Paleoclimatic Reconstruction

Chronology

Recent studies and carbon dates from the Nakuru, Rudolf, and Victoria basins permit expansion of our

[3] Ministry of Works, Kenya, Section of Hydrology (ca. 1956). The hydrology of Lake Naivasha. Unpubl. report, 9 p. + 9 diagrams (mimeo.).

[4] Ministry of Works, Kenya, Section of Hydrology (no date). Notes on experiments to determine evapo-transpiration in papyrus swamps. Unpubl. report, 5 p. + 1 diagram (mimeo.).

TABLE 7. Proposed climatic sequences in East African lake basins in the Late Quaternary

Nakuru-Elmenteita and Naivasha basins		Victoria basin
Earlier sequence[a] proposed by Leakey et al. (adapted from Cole 1963)	Sequence[b] proposed in this paper	Sequence[b] proposed by Kendall (1969)
Nakuran wet phase, becoming progressively drier (ca. 2,750 B.P. to present)	Climate quite similar to present, often somewhat drier (3,000 B.P. to present)	Climatic interpretation uncertain (3,000 B.P. to present)
Dry interval (ca. 4,450 B.P.)	Drier than today (about 4,000 B.P. to 3,000 B.P.)	
Makalian wet phase II (ca. 7,450 to 4,450 B.P.)	Climate becoming drier (5650 to ca. 4,000 B.P.)	Somewhat drier (or rainfall more seasonal) (after 6,500 B.P.)
Drier	Gamblian pluvial[c] (from before 9,200 B.P. to 5,650 B.P.)	Second pluvial peak (wetter) (9,500 to 6,500 B.P.)
Makalian wet phase I?		Moderately dry (10,500 to 9,500 B.P.)
Drier		
Gamblian pluvial III (ca. 12,500 to 10,000 B.P.)		First pluvial peak (moderately wet) (12,500 to 10,500 B.P.)
Drier (ca. 18,000 B.P.)		Dry (from before 14,500 B.P. to 12,500 B.P.)
Gamblian pluvial II		
Drier (ca. 25,000 B.P.)		
Gamblian pluvial I (ca. 30,000 B.P.)		

[a]Dates were estimated.
[b]Chronology based on radiocarbon dates.
[c]From thickness of sediments Gamblian pluvial is estimated to have begun between 13,770 and 17,650 B.P.

earlier discussions of climatic history (Richardson 1964*b*, 1966). We can now correlate more definitely the stages of Naivasha with previously recognized paleoclimatic episodes, establish a climatic chronology, and describe (roughly) the climates that characterized the Naivasha basin. The episodes with which we are concerned are the Gamblian pluvial period and the post-Gamblian "interpluvial," with its two supposed wet phases, the Makalian and Nakuran.[5] Earlier and current climatic chronologies are presented in Table 7.

New dates from Gamble's Caves, Leakey's type location for the Gamblian pluvial, and from a high beach above Lake Elmenteita, establish that a large pluvial lake joined the Nakuru and Elmenteita basins 8,600–9,600 years ago (Washbourn-Kamau 1970, Isaac, *personal communication*). These dates erase any doubt that the large lake we have recorded in the Naivasha basin was the lake of Leakey's Gamblian pluvial. Our own record indicates that in this region the Gamblian pluvial ended about 5,650 years ago.

Whether this pluvial ended simultaneously in other parts of East Africa is uncertain. An earlier end to the pluvial (6,500 B.P.) has been suggested by Kendall (1969) for the northern borders of Lake Victoria, 370 km west of Naivasha (Table 7). This seems compatible with our own date, which actually fixes the time when Naivasha began to shrink significantly, i.e., when it fell below its outlet. The first consequence of drier conditions at Naivasha would simply have been decreased overflow through Njorowa Gorge. Therefore the Gamblian may have ended earlier at Naivasha than our date indicates.

At Lake Rudolf, however, some 450 km to the north (Fig. 2), a discrete end to the pluvial cannot be established until about 3,000 B.P. Butzer, Brown, and Thurber (1969) have recorded high levels in Rudolf between 9,500 and 7,500 B.P., but between the latter date and 3,000 B.P. there were apparently two regressions and two substantial expansions of the lake, before final subsidence to levels near today's. This complicated sequence suggests a somewhat different climatic history in the Ethiopian highlands, from which Rudolf gets most of its water, than in equatorial East Africa.

Our record does not chronicle the initial expansion

[5] It is difficult to correlate confidently the geographically scattered paleoclimatic evidence that has formerly been designated Gamblian, Makalian, and Nakuran. Therefore many workers currently advocate abandoning these terms. While in agreement with this proposal, we think it less confusing here, as we reexamine Leakey's climatic scheme in the locality where he developed it, to retain his original terminology.

of Gamblian Lake Naivasha, but we can nevertheless estimate the length of this pluvial phase. Thompson and Dodson (1963) report that nowhere in the Naivasha basin are exposed Gamblian sediments appreciably thicker than 100 ft (30.5 m). If these beds were deposited at the same rate as the Gamblian sediments in the core, the duration of this pluvial phase was about 8,120 years and it began about 13,770 years ago. Possibly, however, deposition rates were not the same; the deepest parts of lake basins usually accumulate sediment more rapidly than do shallower regions. If we postulate that in the center of the Naivasha basin the Gamblian sediments are half again as thick as any now exposed, the Gamblian pluvial began about 17,650 B.P. and lasted about 12,000 years.

Kendall's results (1969) suggest that our first estimate is closer to the truth. His Lake Victoria pluvial, which we confidently equate with the Naivasha Gamblian, began about 12,500 B.P. and consisted of two peaks separated by a drier interval. Only the latter peak falls within the period of the Naivasha record.

Leakey and Nilsson (Table 7) believed that the Gamblian started considerably earlier and contained three wet peaks. Their scheme seemingly needs revision in light of Kendall's persuasive evidence for only two pluvial peaks, preceded by a dry period lasting at least 2,200 years (Kendall's cores did not reach sediments older than 14,500 years). The early dry period was a drought by present standards and seems much closer to a true interpluvial than to a "dry interval" within a pluvial period. In the Nakuru and Naivasha basins, moreover, there is not only the relative thinness of the Gamblian sediments, but also the fact that the lake which cut Gamble's Caves was considered by Leakey to be the lake of the *second* Gamblian maximum. Since this maximum is now dated at 8,600 B.P., both it and Leakey's third Gamblian maximum should be recorded in our Naivasha core. The core contains no clear evidence for any division of Naivasha's large-lake phase, unless the unusual level in meter 19, which we have ascribed to a flood, actually represents a brief but severe recession. Whether or not two pluvial peaks are represented in our record, Kendall's first pluvial maximum at Lake Victoria is left as the probable equivalent of "Gamblian I." The beginning of this pluvial period is thus updated many thousand years (Table 7).

The drier post-Gamblian period (which may be termed, with predictive license, an interpluvial) has lasted for more than 5,600 years at Naivasha. Our record clearly shows that climates have been variable during this period, but we are unable to identify with any assurance the wetter interludes, the Makalian and Nakuran, which Leakey and Nilsson originally recognized within this time span. The Makalian wet phase, with its single or double peak, should be recognizable—if it occurred—in the core record of Naivasha's shrinking phase. We have noted apparent reversals of the shrinking trend, but all seem too minor and short lived to be considered equivalent to the Makalian. The Naivasha record supports Washbourn's suggestion (1967) that there was no such discrete climatic episode (or episodes, see Table 7). The latest and weakest wet phase recognized in the older chronology, the Nakuran, was thought to have begun about 2,750 B.P., very close to the time when we have recorded the rejuvenation of Lake Naivasha. This synchrony is suggestive, but if the period of the small, fluctuating lake is to be synonymized with the Nakuran wet phase, certain former ideas about this climatic phase must be abandoned. First, we do not believe that during this period Lake Naivasha ever stood as high (23 m above the 1960 water line) as the strandline formerly attributed to the Nakuran wet phase in this basin. (Washbourn (1967) now questions whether the "Nakuran strandline" in the Nakuru basin represents a discrete climatic phase.) Second, the core evidence clearly denies earlier ideas that the Nakuran period was wettest near its inception and has been trending toward greater dryness ever since. There has been no such progressive trend, and the climate has probably been as wet in the past 100 years as at any time in the past 3,000.

The Gamblian climate

How closely can we characterize the Gamblian climate of the Naivasha and Nakuru-Elmenteita basins? The following calculations are rough and require hydrologic assumptions that are reasonable but perhaps not completely valid.

For both basins we will assume that the Gamblian lakes were fed chiefly by surface runoff and direct precipitation. This seems to be true today for Lake Naivasha,[6] but may be questionable for Lakes Elmenteita and Nakuru, which at times of low water may be maintained chiefly by springs. Our assumption is undoubtedly correct, however, for the much larger Gamblian lakes. We will also assume that the lakes during the Gamblian period did not have subsurface drainage. This is quite questionable, particularly in the case of Lake Naivasha. However, our Gamblian rainfall estimates are based primarily on evidence from the Nakuru-Elmenteita basin, which is considerably less likely to have lost water by seepage. (If we are wrong in this assumption, our Gamblian rainfall estimates will be too low.)

Lake and watershed areas and evaporation values used in our calculations are given in Table 8. Let us first assume, for simplicity, that average basin rainfall was the only climatic parameter during Gam-

[6] See footnote 3.

TABLE 8. Data used in estimating past rainfall in the Naivasha and Nakuru basins

Item	Source of data
Naivasha basin[a]	
Area of watershed: 1,220 square miles	1:250,000 Survey of Kenya map, Ser. Y503, Sheet SA–37–1, Edition 2–GSGS
Area of lake in 1959: 44.1 square miles	1:250,000 Survey of Kenya map
Area of lake in 1927: 77.4 square miles (Average modern area: 61 square miles)	Map in Thompson and Dodson (1963), ca. 1:157,000
Area of basin at 6,370–ft contour (lip of Njorowa Gorge): 157.5 square miles	Interpolated from areas at 200–ft contour intervals on Survey of Kenya map
Area of basin at 6,550–ft contour (highest Gamblian level?): 236.3 square miles	Interpolated from areas at 200–ft contour intervals on Survey of Kenya map
Average modern evaporation at Naivasha: 53.5 inches/year	East African Meteorological Department (1950)
Increase in runoff per 10–inch increase in rainfall, under present conditions: 6.5–8.0 inches	Figure 1 in Schumm (1965)
Nakuru basin[a]	
Area of present Nakuru watershed: 548 square miles	1:1,000,000 "Safari Map of Kenya," SK 41 Kenya 1/1M, Special 1st Edition
Area of present Elmenteita watershed: 246 square miles (Combined watershed area when basins confluent: 794 square miles)	Safari Map of Kenya
Area of Lake Nakuru in 1959: 12.6 square miles	1:250,000 Survey of Kenya map
Area of Lake Elmenteita in 1959: 12.6 square miles	1:250,000 Survey of Kenya map
Area of combined lakes at 6,344–ft contour (Gamble's Caves): ca. 270 square miles	Interpolated from areas at 200–ft contour intervals on Survey of Kenya map
Average modern evaporation at Nakuru: 55 inches/year (estimated)	
Increase in runoff per 10–inch increase in rainfall, under present conditions: 8 inches	Figure 1 in Schumm (1965)

[a]Areas were measured either by planimetry or by weighing traced outlines.

blian times that differed from today. An average yearly rainfall 5.4–6.6 inches above today's would have served to maintain Naivasha near the lip of Njorowa Gorge without overflowing. (Increased evaporation from the larger area of lake surface would, of course, necessitate the higher rainfall.)

However, Gamblian conditions in the Naivasha basin were much wetter than this, judging from the state of Naivasha's neighbors. Eighty-six hundred years ago waves lapped at the entrance to Gamble's Caves, 176 m (577 ft) above the 1959 level of Lake Nakuru. To maintain a closed lake of this size annual precipitation in the Nakuru-Elmenteita watershed would have had to be 19–20 inches (482–507 mm) above today's average. This is 65% higher than the modern rainfall of 35 inches per year at the town of Nakuru (East African Meteorological Department 1956).

This estimate is slightly exaggerated, since we have not considered possible reduction of evaporation under conditions of increased moisture. On the other hand, the outlet for the Nakuru-Elmenteita basin is at nearly the same elevation as Gamble's Caves, and if the lake was overflowing at that time, our rainfall estimate is probably conservative. In either case, precipitation in the adjacent Naivasha watershed must have greatly exceeded the amounts sufficient to maintain Lake Naivasha at the lip of Njorowa Gorge. Indeed, a 65% increase in rainfall over the Naivasha watershed could have raised the lake (in the absence of an outlet) to levels well above the highest Gamblian beds reported in the basin by Thompson and Dodson (1963). These sediments, reaching 6,550 ft, are higher than the entrance to Njorowa Gorge, and were probably deposited in a lake impounded behind the massive lava flow that was eventually breached by overflow. Evernden and Curtis (1965) have dated this lava flow at 29,000 B.P.; the high Gamblian beds are presumably much later. When the Gamblian lake deposited these high beds, it must have very nearly spilled over into the Nakuru-Elmenteita basin. However, no relict channel connecting the two basins appears to exist.

Downcutting at the lip of Njorowa Gorge may have been nearly complete by 9,000 B.P., since the core microfossils suggest no great decline in lake level between then and 5,650 B.P. If so, rainfall 65% above today's levels would have caused very substantial overflow. Discharge through the gorge would have been approximately 1.25×10^9 m^3/year, or 13,000 ft^3/sec. The yearly figure is two-thirds the average modern discharge into the Victoria Nile from Lake Victoria, as listed in Langbein (1961), and five times the total volume of Lake Naivasha in 1956 (Thompson and Dodson 1963). Even in its enlarged state, Naivasha would have had a very short response time as a result of this overflow; that is, variations of inflow and of direct precipitation would have been quickly balanced by changes in discharge, and the lake's fluctuations in level would have been relatively small.

In reconstructing these hydrologic balances, we have attended to certain complicating factors, such as differences in runoff-to-rainfall ratios at different levels of yearly mean rainfall. But we have treated two factors as constants although we know they were not. The first is temperature, the second rainfall seasonality. Our calculations assumed both to be similar to today. What of their actual differences, and the hydrologic effects?

The Naivasha core contains indications that temperatures during the large-lake phase were higher than today's. Judging from the plankton composition and high productivity of Gamblian Lake Naivasha, the temperature difference was probably at least 2°–3°C. It may have been greater, as Kendall (1969) suspects from his Lake Victoria study. High Gamblian temperatures would necessitate higher rainfall than we have postulated to maintain the hydrologic balance of the lakes. Modern meteorological data from Kenya suggest that temperatures 3°C above present levels would increase evapotranspiration from the Naivasha watershed by some 6 inches annually. To maintain pluvial Naivasha at its calculated level under these temperatures would require annual rainfall approximately 80% above today's.

However, rainfall was more seasonal during the Gamblian than today, if the core laminae are correctly interpreted. This would partially negate the rainfall increase demanded by higher temperatures, since under a sharply seasonal regime the runoff-to-rainfall ratio tends to be elevated (Schumm 1965). We are not sure how our rainfall estimates should be modified to account for the combined influence of these two factors. Since they would have opposed each other, we have not attempted any correction for their effects.

To summarize our conception of Gamblian conditions in these basins: average precipitation during the wettest (?) part of the pluvial (at the time of formation of Gamble's Caves) equaled or exceeded rainfall in the wettest modern years, such as 1961, when precipitation at Naivasha was 65% above average (Fig. 17). At least in the Naivasha basin, rainfall was also more seasonal: only a single wet and a single dry season occurred annually. This is the prevailing pattern today both north and south of the equator, but not generally at the equator itself. In the Eastern Rift region, however, the single-season pattern even now approaches the equator closely (Fig. 17). Narok, for example, is only 75 km from Naivasha and only 40 km farther south. Temperatures during the Gamblian were probably at least 2°–3°C above today's. The climate may well have

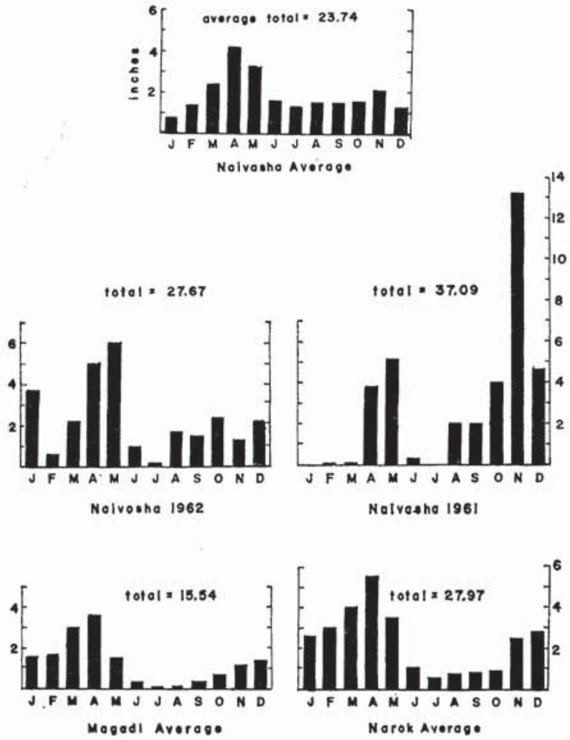


FIG. 17. Rainfall patterns at Naivasha and two localities slightly further from the equator. Top: 48-year average for Naivasha (0° 45′ S) showing muted bimodality. Center: two unusual years at Naivasha. Bottom: 13- and 48-year averages at Magadi (1° 52′ S), within the Rift Valley, and at Narok (1° 8′ S), slightly west of the Rift Valley. Both these stations experience unimodal annual rainfall patterns.

been as variable as today's, but the short-term fluctuations affected lake levels less profoundly than they do now.

Climate of the post-Gamblian "interpluvial"

We have little indication (other than the present low lake level) of conditions in the Nakuru basin following the Gamblian pluvial. Our climatic inferences for this long period (the past 5,650 years) derive only from the Naivasha core study.

Our evidence indicates that this drier phase began rather abruptly. Lake Naivasha fell to levels similar to today's within about 1,500 years. This decline was not primarily due to downcutting at the outlet, since the lake fell far below the lip of Njorowa Gorge.

It is tempting to believe that rising temperatures were instrumental in this drying trend—this was about the time of the worldwide Climatic Optimum. But local temperatures exceeded today's, apparently, even during the late Gamblian, and no reasonable further elevation should alone have caused Naivasha to decline so markedly. We believe that a significant decrease in rainfall must have contributed to the drying trend.

During this period of rapid lake decline, the climate of the Naivasha basin may have been somewhat drier than at present; however, there is no way to be sure of this. The crater from which we took our core perhaps became isolated from the main lake basin at the end of this period, about 4,000 years ago. However, the surprising stability of the weedy pond that occupied the crater between about 4,000 B.P. and 3,000 B.P. suggests that tenuous connections with the main lake may have remained. The latter, with its more reliable influents, is more likely than the crater to have retained some water at all times and may have "fed" the crater through channels deeper then than at present. At any rate, a rather stable climate appears to have existed between about 4,000 B.P. and 3,000 B.P.

Water levels were considerably below those at present when the crater dried about 3,000 B.P. It was without water less than 100 years, however, and the mud dried and oxidized to a depth of only one-half meter. When the crater filled again, the rejuvenated lake apparently led a tenuous existence because of its lack of reliable inflow. The many fluctuations recorded in the core during the last 3,000 years reflect climatic influences doubtless amplified by the vulnerability of the crater whenever isolated from the main lake.

It would take little change in today's hydrologic balance to return Lake Naivasha to the lower levels experienced in the past 3,000 years, or perhaps even to dry the crater completely once again. Although the basin seems to have been driest about 3,000 years ago, we doubt if yearly rainfall at that time was markedly different from today's. However, the more seasonal precipitation pattern seems to have persisted beyond the period of maximum dryness, until about 2,000 years ago. Temperatures 3,000 years ago were perhaps still somewhat higher than today's, and these may have been chiefly responsible for the lower water levels and brief dry phase. The climate has probably been as moist during historic times as at any period during the past 3,000 or 4,000 years, but it has remained variable. Our study supports the contention of Dale (1952) that the last significantly drier time occurred less than 200 years ago, and that periods somewhat drier than the present occurred frequently before that.

Comparisons and conclusion

Our results agree substantially with several recent studies which have helped to clarify the sequence and timing of sub-Saharan climatic changes. Fairbridge (1962) first seems to have challenged the assumption that pluvials in central Africa coincided in time with temperate glacial periods. His studies of downcutting and aggradation in the Nile Valley during the past 15,000 years led him to conclude that the climate of equatorial Africa was drier than today's between 15,000 B.P. (or earlier) and 10,000 B.P.; much wetter between 10,000 B.P. and 5,000 B.P.; and fairly similar thereafter to today's, though with "extended periods of relatively high and low Nile floods."

We have already commented on the points of agreement and contrast between the hydrologic sequence elucidated by Butzer et al. (1969) for Lake Rudolf and our own record for Lake Naivasha. Particularly interesting from a comparative standpoint are the detailed core stratigraphies that have been published for other East African localities (Bakker 1962, 1964, Coetzee 1964, 1967, Livingstone 1967, Morrison 1968, Kendall 1969). Kendall's climatic record from Lake Victoria (1969) is based on both pollen and paleolimnological evidence and is highly comparable to the Naivasha record because of the proximity of the two lakes (Fig. 2) and the similarity of study methods. During their common time period the two stratigraphies agree closely in their climatic indications (Table 7), though the Victoria core provides no clear evidence of the slightly wetter conditions after 3,000 B.P. that occurred at Naivasha. In the Victoria basin climatic events of the past 3,000 years seem to have been obscured by the impact of man on the vegetation and by continued overflow from the lake (Kendall 1969).

The other stratigraphies from East Africa are pollen profiles with no supporting paleohydrologic information. Those most rewarding from a comparative standpoint are the profiles from Mt. Kenya, 140 km northeast of Naivasha; from the Cherangani Hills on the west side of the Rift Valley some 240 km northwest of Naivasha; and from the Ruwenzori range on the Uganda-Congo border, about 750 km due west of Naivasha (Fig. 2). All extend farther back in time than our Naivasha record.

Coetzee's impressive thesis (1967) reinterprets and amplifies the studies in East Africa by Bakker and herself. Two long pollen diagrams from lakes on Mt. Kenya provide rich information about the history of the vegetation on that mountain during the last 33,350 years. The lakes were fortunately located, one in the present montane rain forest and one in the ericaceous belt above the present tree line, so that comparison of the diagrams is especially fruitful in interpreting each. In this report, also, Bakker's history of the Cherangani vegetation is extended back to 27,750 B.P. Although the early record from these sites is highly interesting, it is the later vegetation shifts and their interpretation that are useful in our own comparisons. Coetzee believes the vegetation changes on these mountains were primarily due to changing temperatures, which brought about migration of the vegetation belts both directly and indirectly by influencing the altitudinal distribution of moisture on the mountains. It is unclear whether she thinks that any of the moisture changes she documents represent general moisture changes in East Africa, or whether she regards all as simply vertical migrations of the moisture belts now characterizing the mountains.

Coetzee records cool, dry conditions on these mountains prior to 14,000 B.P. Her data nicely complement the dry conditions Kendall recorded at the bottom of his Lake Victoria core and indicate that this climatic phase began as long ago as 26,000 B.P. She recognizes a warming trend commencing about 14,000 B.P. in the mountains, increasing with brief setbacks to a maximum (the Climatic Optimum) between 5,000 and 2,500 years ago, and then cooling somewhat. Moisture trends embracing all the montane sites are harder to recognize, but conditions seem to have been wet between about 10,400 and 6,200 years ago, and again during the Climatic Optimum. An interesting temporary setback in temperature, and perhaps also in moisture, is suggested between about 6,500 and 5,500 years ago, at about the time Lake Naivasha began to decline.

Coetzee's temperature inferences agree with our own in postulating warm conditions during the period of the Gamblian pluvial and cooler temperatures during the most recent two to three millenia. If Coetzee is correct regarding the period of maximum temperature, however, it occurred during the period of Lake Naivasha's decline and was *not* a period of generally high rainfall, even though rainfall was apparently high at this time at the altitudes of Coetzee's and Bakker's montane sites. Although there appears, in general, to have been coincidence of cool-dry and warm-wet periods in East Africa, as Kendall (1969) concludes, the period of *maximum* warming seems to represent a departure from this pattern; or perhaps moisture increases simply did not keep pace (in a hydrological sense) with temperature increases, the evaporative deficit resulting in the lowered levels at this time of Lakes Naivasha and Victoria.

Although the Gamblian pluvial of the Naivasha basin is recognizable in her studies, Coetzee is probably wise in her apparent unwillingness to extrapolate general climatic moisture trends from her montane evidence. The difficulty is exemplified by Bakker's diagram from Cherangani (1962, 1964), in which vegetation shifts seem to have been much more dramatic during the pluvial than after it ended. There is little hint in his diagram that the climate of the last five millenia has been significantly drier than that of the preceding seven, as the Nakuru-Naivasha evidence indicates.

Mt. Kenya represents the easternmost locality in an equatorial transect of core stratigraphies in East Africa; the Ruwenzori mountains, site of studies by Osmaston (1965) and Livingstone (1967), is the westernmost. Livingstone interprets his pollen record cautiously in climatic terms, but suggests a sequence rather close to those of the Naivasha and Victoria basins. Retreat of montane glaciers from the level of Lake Mahoma began about 15,000 B.P.; Livingstone leans to dryness rather than high temperature as a principal cause. Forest became more abundant near the lake after 12,700 B.P. and remained so to the present. However, important changes in forest composition during that time may indicate that the climate was warmer than today and wet between 12,700 and perhaps 4,000 B.P.; then drier, while remaining warm; and finally, within the past 2,000 years, approaching the cooler conditions of the present.

For regions of Africa south of the equator there is much evidence of past climatic change (see Cooke 1958, Flint 1959, Bakker and Clark 1962, Clark and Bakker 1964), but no continuous stratigraphic studies suitable for detailed comparison with our own record. The southwestern Sahara and sub-Saharan West Africa have been subject to intensive paleoclimatic study in recent years (see Faure 1966, 1969), and some interesting climatic parallels exist between this region and East Africa. Faure, Manguin, and Nydal (1963) demonstrated the existence of conditions much moister than today's some 6,000 to 12,000 years ago in the Chad basin and in other parts of now-arid West Africa. This study uncovered evidence of earlier wet conditions (ca. 21,000 B.P.) as well, and more recent dates suggest high lake levels in a caldera of the Tibesti massif 15,000 years ago (Faure 1969). This has led Kendall (1969) to suspect that the dry period prior to 12,500 B.P. in the Victoria basin had no parallel in West Africa. Whether or not this is true, the much more complete West African record of the last 12,000 years is quite similar to those from East Africa. In the Chad and adjoining Pays Bas basins, recent studies of diatoms and sedimentary features by S. Servant (in press) and M. Servant (in press) indicate that there have been two distinct wet and dry cycles in the past 12,000 years. The wet peaks were from 12,000 to about 10,000 B.P. and again around 7,000 B.P. The more recent dry period, beginning about 5,400 B.P. was still not fully developed by 3,160 B.P., when a lake (perhaps the result of a weaker recurrence of moist conditions) stood in the now-dry Pays Bas.

The emerging picture of late Quaternary climates in tropical Africa is quite different from that advanced before the advent of radiocarbon dating, by workers such as Brooks (1949), Wayland, and Leakey (cf. Cole 1963). In broad terms, it now appears that equatorial East Africa has experienced two interpluvials and one complete pluvial period since the beginning of the last glacial maximum. In the southern Sahara of West Africa the first interpluvial may have been weak or absent, but subsequent climatic sequences there have been quite similar to those of East Africa. By contrast, the moisture regimes of North Africa and Southern Europe have been quite different from those of tropical Africa. Temperature trends, however, may well have been similar in tropical and temperate zones, as Bakker and others have claimed.

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APPENDIX I

Diatom Assemblages: Selected Levels of Naivasha Core and other Lakes

Core / Frequency	> 15%	5 – 15%	3 – 5%	1 – 3%	< 1% but prominent	Rare
Naivasha, 0.00 m	*Melosira ambigua* (Grun.) O. Mull. (61%) *Synedra* sp. cf. *acus* Ktz. (24%)		*Melosira granulata* v. *jonensis* Grun.	*Gomphonema lanceolatum* Ehr. *G. parvulum* (Ktz.) Grun. *Melosira granulata* v. *angustissima* O. Mull. *Nitzschia* sp. cf. *spiculoides* Hust. *Synedra ulna* (Nitzsch.) Ehr.	*Amphora ovalis* v. *lybica* (Ehr.) Cl., *Cymbella turgida* v. *pseudogracilis* Cholnoky, *C. mulleri* Hust., *Epithemia sorex* (Ehr.) Ktz., *E. turgida* (Ehr.) Ktz., *E. zebra* (Ehr.) Ktz., *Eunotia* sp. cf. *tenella* (Grun.) A. Cl., *Surirella* sp. cf. *linearis* W. Sm.	*Amphora gouwsii* Cholnoky, *A. veneta* Ktz., *Anomoeoneis sphaerophora* (Ktz.) Pfitz., *Cocconeis* sp., *Coscinodiscus rudolfi* Bachmann, *Cyclotella meneghiniana* Ktz., *Fragilaria brevistriata* Grun., *F. pinnata* v. *lancettula* (Schumann) Hust., *Navicula cryptocephala* Ktz., *N. nyassensis* O. Mull., *N. radiosa* Ktz., *Nitzschia* sp. cf. *subacicularis* Hust., *N.* sp. cf. *tropica* Hust., *Rhopalodia gibba* (Ehr.) O. Mull., *R. gibberula* (Ehr.) O. Mull., *Stephanodiscus astraea* (Ehr.) Grun.
Naivasha, 4.27 m	*Coscinodiscus rudolfi* Bachmann (31%), *Melosira granulata* v. *jonensis* Grun. (22%) *Nitzschia* "sp. A" (19%)	*Nitzschia palea* (Ktz.) W. Sm.	*Cyclotella ocellata* Pant. *Gomphonema parvulum* (Ktz.) Grun.	*Nitzschia amphibia* Grun. *Synedra rumpens* Ktz.	*Anomoeoneis sphaerophora* (Ktz.) Pfitz., *Cyclotella meneghiniana* Ktz., *Gomphonema* sp. cf. *intricatum* Ktz., *Melosira ambigua* (Grun.) O. Mull., *Nitzschia frustulum* (Ktz.) Grun., *Synedra ulna* (Nitzsch) Ehr.	*Amphora veneta* Ktz., *Epithemia* sp., *Melosira agassizii* Ostf.
Naivasha, 6.20 m	*Cyclotella meneghiniana* Ktz. (25%) *Navicula el Kab* O. Mull. (56%)		*Nitzschia amphibia* Grun.	*Coscinodiscus rudolfi* Bachmann *Melosira ambigua* (Grun.) O. Mull. *Nitzschia* sp. cf. "sp. A" *Stephanodiscus astraea* vars. (Ehr.) Grun. *Synedra ulna* (Nitzsch) Ehr.	*Melosira granulata* v. *jonenis* Grun. *Gomphonema gracile* Ehr., *G. lanceolatum* Ehr., *Navicula nyassensis* O. Mull., *Nitzschia* sp. cf. *adapta* Hust., *Nitzschia* sp. cf. *subcommunis* Hust.	*Amphora veneta* Ktz., *Anomoeoneis sphaerophora* (Ktz.,) Pfitz., *Melosira agassizii* Ostf.
Naivasha, 10.20 m	*Gomphonema parvulum* (Ktz.) Grun. (17%), *Melosira granulata* v. *jonensis* Grun. (18%) *Synedra ulna* (Nitzsch) Ehr. (15%)	*Melosira ambigua* (Grun.) O. Mull. *Nitzschia palea* (Ktz.) W. Sm. *Synedra acus* Ktz.	*Nitzschia amphibia* Grun. *Nitzschia bacata* Hust.	*Amphora ovalis* Ktz., *A. ovalis* v. *lybica* (Ehr.) Cl., *Cymbella mulleri* Hust., *Fragilaria* spp., *Gomphonema gracile* Ehr., *Melosira granulata* v. *angustissima* O. Mull., *Nitzschia frustulum* (Ktz.) Grun., *N.* "sp. A", *N.* sp. cf. *mediocris* Hust.	*Achnanthes exigua* Grun., *Gomphonema longiceps* Ehr., *Navicula nyassensis* O. Mull.	*Anomoeoneis sphaerophora* (Ktz.) Pfitz., *Cyclotella ocellata* Pant., *Cocconeis* sp., *Eunotia* sp., *Gomphonema intricatum* v. *pumila* Grun., *Melosira distans* (Ehr.) Ktz., *Navicula minima* Grun., *Nitzschia* sp. cf. *spiculoides* Hust., *Nitzschia* sp. cf. *tarda* Hust.
Naivasha, 14.02 m	*Melosira agassizii* Ostf. (19%) *Synedra berolinensis* Lemm. (19%)	*Melosira granulata* v. *angustissima* O. Mull. *Nitzschia fonticola* Grun.	*Fragilaria* sp. cf. *brevistriata* Grun.	*Fragilaria construens* (Ehr.) Grun. *F. pinnata* Ehr. *Melosira ambigua* (Grun.) O. Mull. *Nitzschia* sp. cf. *subrostrata* Hust.	*Cyclotella ocellata* Pant. *Fragilaria* sp. cf. *cerealis* Cholnoky *Navicula zanoni* Hust. *Nitzschia goetzeana* O. Mull.	*Achnanthes minutissima* Ktz., *Cocconeis placentula* v. *euglypta* (Ehr.) Cl., *C. thumensis* A. Mayer, *Cyclotella kutzingiana* Thw., *Cymatopleura solea* (Breb.) W. Sm., *Epithemia* sp., *Fragilaria fonticola* Hust., *Gomphonema* sp., *Navicula* sp., *Nitzschia frustulum* v. *perpusilla* (Rabh.) Grun., *N. lancettula* O. Mull., *N. amphibia* Grun., *N.* "sp. A", *N.* sp. cf. *sublinearis* Hust., *N. sp.* cf. *tarda* Hust., *Stephanodiscus astraea* (Ehr.) Grun., *Synedra rumpens* Ktz.
Lake George, surface sediment from open water area	*Nitzschia* sp. cf. *fonticola* Grun. (58%) *(See note below) *Synedra berolinensis* Lemm. (22%) *Note: This species may be either *N. fonticola* or *N. microcephala* (Haworth, personal communication); larger specimens are difficult to distinguish from *N. palea*.	*Fragilaria construens* v. *venter* (Ehr). Grun. (close to *F. brevistriata*)	*Nitzschia* sp. cf. *palea* (Ktz.) W. Sm.	*Fragilaria construens* (Ehr.) Grun. *F. construens* v. *exigua* (W. Sm.) Schulz *Melosira ambigua* (Grun.) O. Mull.	*Melosira granulata* v. *jonensis* Grun. *Nitzschia* sp. cf. *spiculoides* Hust.	*Cyclotella meneghiniana* Ktz., *Cymatopleura* sp., *Melosira granulata* v. *angustissima* O. Mull., *Synedra acus* Ktz.
Naivasha, 17.20 m	*Nitzschia fonticola* Grun. (38%)	*Melosira agassizii* Ostf. *M. granulata* v. *angustissima* O. Mull., *Nitzschia confinis* Hust. *Stephanodiscus astraea* (Ehr.) Grun.	*Cyclotella ocellata* Pant. *Fragilaria construens* (Ehr.) Grun.	*Fragilaria pinnata* Ehr.	*Fragilaria* sp. cf. *brevistriata* Grun., *Epithemia zebra* (Ehr.) Ktz., *Navicula minima* Grun., *N. zanoni* Hust., *Nitzschia frustulum* (Ktz.) Grun., *N. perminuta* Hust., *N.* sp. cf. *van oyei* Cholnoky	*Achnanthes lanceolata* v. *rostrata* Hust., *Amphora ovalis* v. *lybica* (Ehr.) Cl., *Cocconeis placentula* v. *euglypta* (Ehr.) Cl., *Cyclotella* sp. cf. *Kutzingiana* Thw., *Cymbella* sp. cf. *cistula* (Hemp.) Grun., *C. mulleri* Hust., *Diploneis ovalis* (Hilse) Cl., *Epithemia sorex* Ktz., *E. turgida* (Ehr.) Ktz., *Fragilaria* sp. cf. *lapponica* Grun., *Gomphonema* spp., *Mastogloia*

						astraea (Ehr.) Grun., Synedra rumpens Ktz.
Lake George, surface sediment from open water area	Nitzschia sp. cf. fonticola Grun. (58 %) *(See note below) Synedra berolinensis Lemm. (22 %) *Note: This species may be either N. fonticola or N. microcephala (Haworth, personal communication); larger specimens are difficult to distinguish from N. palea.	Fragilaria construens v. venter (Ehr). Grun. (close to F. brevistriata)	Nitzschia sp. cf. palea (Ktz.) W. Sm.	Fragilaria construens (Ehr.) Grun. F. construens v. exigua (W. Sm.) Schulz Melosira ambigua (Grun.) O. Mull.	Melosira granulata v. jonensis Grun. Nitzschia sp. cf. spiculoides Hust.	Cyclotella meneghiniana Ktz., Cymatopleura sp., Melosira granulata v. angustissima O. Mull., Synedra acus Ktz.
Naivasha, 17.20 m	Nitzschia fonticola Grun. (38 %)	Melosira agassizii Ostf. M. granulata v. angustissima O. Mull., Nitzschia confinis Hust. Stephanodiscus astraea (Ehr.) Grun.	Cyclotella ocellata Pant. Fragilaria construens (Ehr.) Grun.	Fragilaria pinnata Ehr.	Fragilaria sp. cf. brevistriata Grun., Epithemia zebra (Ehr.) Ktz., Navicula minima Grun., N. zanoni Hust., Nitzschia frustulum (Ktz.) Grun., N. perminuta Hust., N. sp. cf. van oyei Cholnoky	Achnauthes lanceolata v. rostrata Hust., Amphora ovalis v. lybica (Ehr.) Cl., Cocconeis placentula v. euglypta (Ehr.) Cl., Cyclotella sp. cf. Kutzingiana Thw., Cymbella sp. cf. cistula (Hemp.) Grun., C. mulleri Hust., Diploneis ovalis (Hilse) Cl., Epithemia sorex Ktz., E. turgida (Ehr.) Ktz., Fragilaria sp. cf. lapponica Grun., Gomphonema spp., Mastogloia elliptica (Agardh) Cl., Melosira ambigua (Grun.) O. Mull., Navicula perventralis Hust., N. sp. cf. pseudolagerstedtii Cholnoky, N. seminuloides v. sumatrana Hust., Rhopalodia gibba (Ehr.) O. Mull., Synedra berolinensis Lemm.
Naivasha, 23.20 m	Nitzschia fonticola Grun. (29 %) Stephanodiscus astraea (Ehr.) Grun. (23 %)	Cyclotella ocellata Pant. Melosira granulata v. angustissima O. Mull., Nitzschia confinis Hust.	Melosira agassizii Ostf.	Fragilaria pinnata Ehr. Melosira ambigua (Grun.) O. Mull. M. granulata (Ehr.) Ralfs Navicula zanoni Hust.	Fragilaria construens (Ehr.) Grun. Cocconeis placentula Ehr. Epithemia zebra (Ehr.) Ktz.	Achnanthes sp. cf. minutissima Ktz., Cyclotella sp. cf. kutzingiana Thw., Cymbella sp. cf. cistula (Hemp.) Grun., C. mulleri Hust., Diploneis ovalis (Hilse) Cl., Epithemia intermedia Fr., E. sorex Ktz., E. turgida (Ehr.) Ktz., Fragilaria sp. cf. brevistriata Grun., F. lapponica Grun., Gomphonema sp. cf. gracile Ehr., Mastogloia elliptica (Agardh) Cl., Navicula perventralis Hust., Nitzschia sp. cf. frustulum (Ktz.) Grun., N. lancettula O. Mull., N. sp. cf. perminuta Hust., N. sp. cf. subrostrata Hust., N. tropica Hust., ?Rhoicosphenia curvata (Ktz.) Grun. Rhopalodia gibba (Ehr.) O. Mull., R. vermicularis O. Mull., Stephanodiscus sp. cf. hantzschii Grun., Synedra rumpens Ktz., S. ulna (Nitzsch) Ehr.
Naivasha, 28.60 m	Nitzschia fonticola Grun. (32 %) Stephanodiscus astraea (Ehr.) Grun. (27 %)	Melosira agassizii Ostf. M. granulata v. angustissima O. Mull., Nitzschia confinis Hust.	Cyclotella ocellata Pant. Melosira ambigua (Grun.) O. Mull.		Rhopalodia vermicularis O. Mull.	Amphora ovalis v. lybica (Ehr.) Cl., Cocconeis disculus Schum., C. placentula Ehr., Cymbella sp. cf. cistula (Hemp.) Grun., Diploneis ovalis (Hilse) Cl., Epithemia turgida (Ehr.) Ktz., E. zebra (Ehr.) Ktz., Gomphonema sp. cf. gracile Ehr., G. lanceolatum Ehr., Hantzschia amphioxys (Ehr.) Grun., Mastogloia elliptica (Agardh) Cl., Nitzschia amphibia Grun., N. sp. cf. adapta Hust., N. sp. cf. perminuta Hust., Rhopalodia gibba (Ehr.) O. Mull., Stephanodiscus damasi Hust., Synedra rumpens Ktz., S. ulna (Nitzsch) Ehr., S. ulna v. spathulifera Grun.
Lake Victoria, surface sediment 10 km from shore	Stephanodiscus astraea (Ehr.) Grun. (41 %)	Melosira agassizii Ostf. M. nyassensis v. victoriae O. Mull. Navicula zanoni Hust.	Fragilaria construens (Ehr.) Grun. Nitzschia fonticola Grun.	Fragilaria pinnata Ehr., Melosira ambigua (Grun.) O. Mull., M. granulata v. angustissima O. Mull., Nitzschia lancettula O. Mull., N. sp., Synedra berolinensis Lemm., S. cunningtonii G. S. West	Amphora ovalis v. lybica (Ehr.) Cl., Cymatopleura sp. cf. elliptica (Breb.) W. Sm., Navicula scutelloides W. Sm.	Amphora ovalis v. pediculus Ktz., Cyclotella stelligera Cl. & Grun., Cymbella mulleri Hust., Fragilaria construens v. binodis (Ehr.) Grun., F. construens v. exigua (W. Sm.) Schulz, Navicula barbarica Hust., N. perventralis Hust., N. seminuloides v. sumatrana Hust., N. viridula Ktz., Nitzschia lacustris Hust., Pinnularia sp. cf. eburnea Zanon, Surirella fullebornii O. Mull., S. nyassae O. Mull., Synedra acus Ktz.