PALEOLIMNOLOGICAL RESEARCH AT LAKE TURKANA, KENYA

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ABSTRACT

Lake Turkana, a large rift valley lake of Northern Kenya, has a geological and limnological history extending back in time to at least the Late Miocene. Its early history (prior to the Late Pliocene) was largely one of discontinuous, small lakes and intermittent bodies of water, coalescing by 5m yr BP into a single, large lake in the developing (tectonic) Turkana Basin.

From 4.5-3.2m yr BP the lake regularly underwent fluctuations in terms of lake level. These disturbances may have been tectonic rather than climatic however, as paleochemical analyses suggest a relatively fresh body of water throughout this time.

Major transgressive episodes, initiating prior to 3.2m yr BP, and continuing irregularly until 1.8 m yr BP, resulted in important speciation events amongst several groups of lacustrine organisms. A slight increase in alkalinity and salinity is indicated for this time.

At about 1.8 m yr BP, an important climatic shift caused widespread declines in lake levels throughout East Africa. Continual fluctuation in lake level between open and closed basin conditions have characterized the time interval from 1.8 m yr BP to the present, with the most recent open lake condition having occurred about 9500 yr BP. The water chemistry during this time also varied widely through the range of Talling & Talling's Class II (CO_3 + HCO_3, Na) lake types. Faunas of this time period are mostly cosmopolitan, widely dispersed species, with fewer speciation events occurring in the basin.

1. INTRODUCTION

This discussion is an attempt to summarize the rapidly expanding understanding of the paleolimnological history of Lake Turkana. Situated in the northernmost part of Kenya, the lake lies partially within the Eastern or Gregory Rift Valley, and partially in a region of more complex faulting known as the Turkana Depression (Figures 1 and 2). The entire region within the Turkana Basin

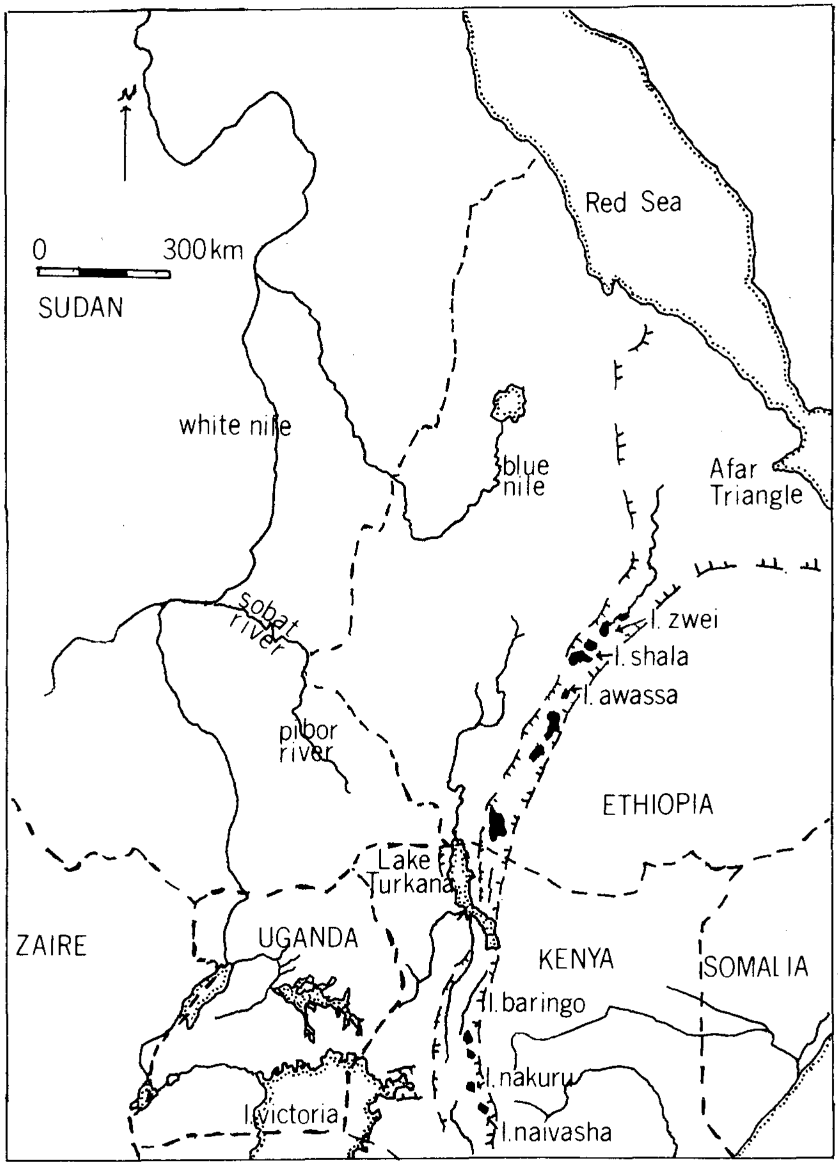

Figure 1. Location map, showing Lake Turkana, the Eastern Rift, and other areas mentioned in the text. Eastern Rift Valley shown in hatchured lines. National boundaries are dashed lines.

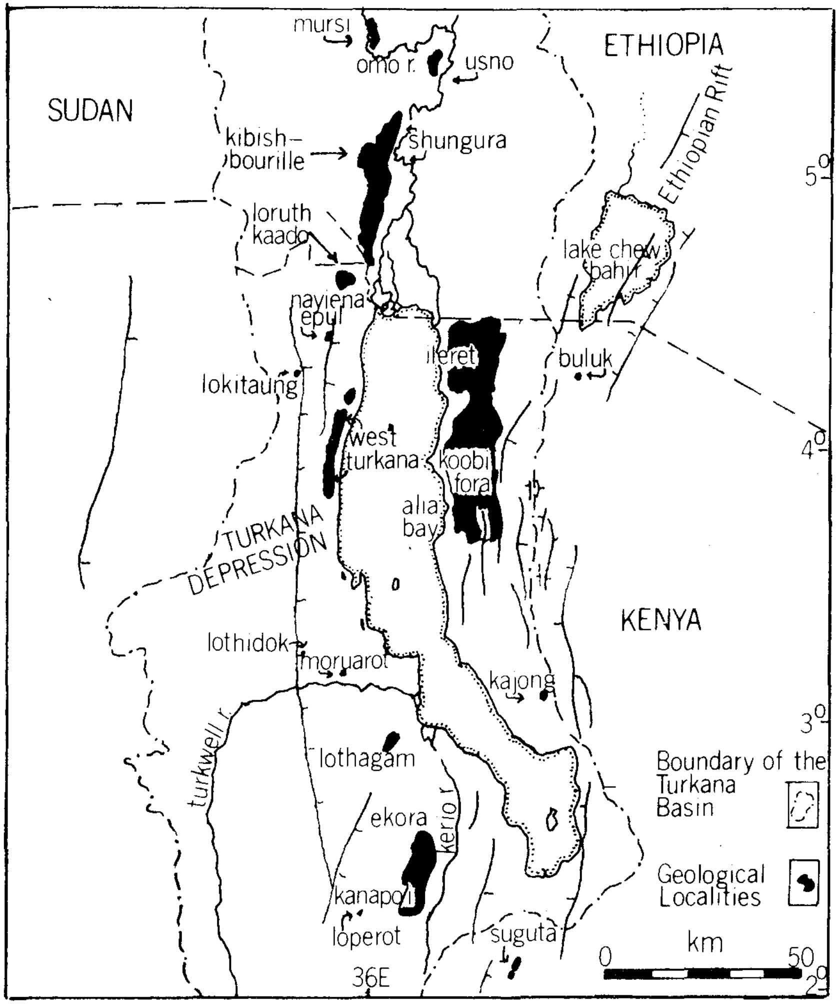

Figure 2. Map of Lake Turkana and its surroundings, showing the geological localities discussed in the text. The principal normal faults (after Fitch & Vondra 1976) are shown, hatchured on the downthrown side. The southern basin of the lake lies within the Rift Valley proper, while the northern basin lies in the structurally more complex Turkana Depression. Figure modified from Behrensmeyer (1976).

has acted as a catchment area, not only for water, but also for enormous quantities of volcanic and sedimentary rocks, and their concomitant fossil record.

The impetus for studying the lake's history first arose due to the wealth

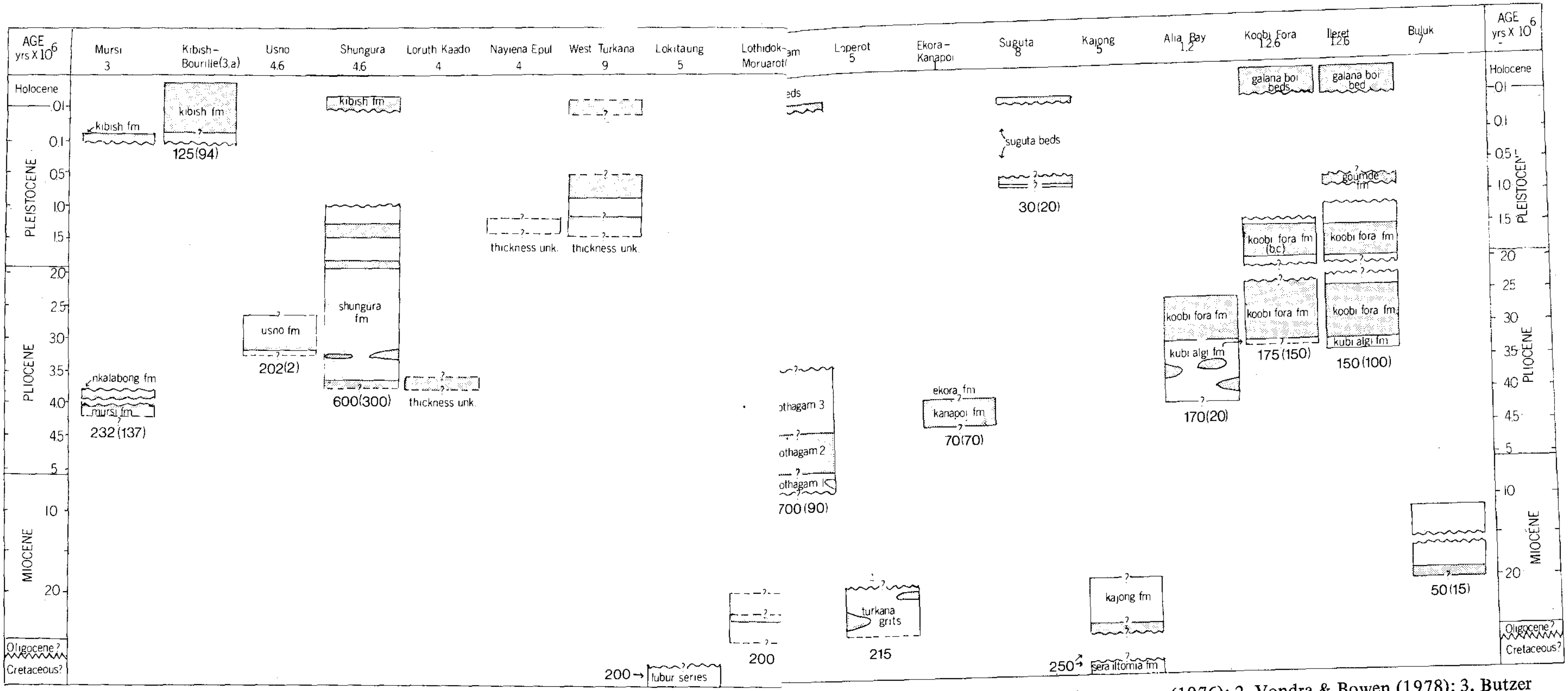

Figure 3. Correlation chart for the Lake Turkana Basin. Volcanic sequences have been eliminated for simplification. Lacustrine portions of each section are shaded. Question marks indicate uncertainty about absolute age or stratigraphic position of upper or lower surfaces. Dashed lines indicate contact is unexposed. Wavy lines indicate unconformities. Unlabelled localities lack formal formational designation. The thickness of each column refers to the time axis. Stratigraphic thickness is given in the number of meters, below the column. The number in parentheses (where given) is the thickness of exclusively lacustrine units (including marginal lacustrine deposits). References are given, numbered, below the locality names: 1. Behrensmeyer (1976); 2. Vondra & Bowen (1978); 3. Butzer (1976); 4. De Heinzelin et al. (1976); 5. Savage & Williamson (1978);6.Brown et al. (1978); 7. Harris & Watkins (1974); 8. Truckle (1976); 9. This report.

Notes: a) the Bourille is probably the tectonically disturbed equivalent of the lower part of the Kibish Formation; b) the unconformity shown in the Koobi Fora Formation is not equivalent to the Upper-Lower Member division of this formation; c) thickness of lacustrine sediments near the Koobi Fora Point. Elsewhere they are of lesser thickness.

of vertebrate, and particularly hominid fossil remains uncovered in the basin's sedimentary record. Originally, questions concerning the lacustrine part of this record were directed at answering specifically terrestrial problems, such as deciphering paleoclimates and shoreline paleoenvironments. More recently, the approach has been one which recognizes the intrinsic interest of the lake itself, as a 'laboratory' for understanding extremely long term biological and nonbiological processes of the lacustrine environment.

With a geological history extending well back into the Miocene, Lake Turkana ranks as one of the oldest existing lakes in the world today. Its sedimentary record, exposed through falling lake levels and tectonic activity, is probably second to none amongst inland waters, in terms of the continuity of its exposed stratigraphic history. Figure 2 illustrates the principal locations of lacustrine exposures discussed in this paper, and Figure 3, their approximate correlations. Some of these dates have been the subjects of controversy, but the salient feature of this diagram is the long term continuity of lacustrine sediments exposed around the basin. These exposures (and in particular those of the North and Northeast parts of the basin) have provided the fossil and geological evidence for the paleolimnological interpretations presented here.

2. PHYSICAL SETTING

While the precise age of the Turkana Basin is still uncertain, there is good evidence at Lokitaung for an initial cycle of basin downwarping and sedimentation beginning as early as the Late Mesozoic (Savage & Williamson 1978). These sediments (which are primarily fluvial in origin) are clearly unrelated to the formation of the modern lake, but nevertheless underscore the great antiquity of the basin. The earliest extensive lacustrine deposits in the basin occur at Kajong, where playa deposits in Member 1 of the Kajong Formation record the presence of large intermittent lakes in the central part of the basin during the Early Miocene (Savage & Williamson 1978). This period of time (i.e. Early-Middle Miocene) saw the establishment of the domal swell-rift structures, which established the drainage patterns that have, in a very general sense, dominated the Turkana Basin up to the present. These patterns consisted of elongated bodies of water (small lakes and playas of various sizes) in the early phase, giving way to a large permanent lake by the Late Miocene, fed by numerous, and usually intermittent streams. That the basin had well developed oceanic connections via some large river system even by the Early-Middle Miocene is dramatically illustrated by the presence at Loperot (Southwest Turkana), of a non-marine ziphiid whale fossil (Mead 1975). Indeed, Loperot is the only area in the basin, of this age, whose molluscan fauna suggests specialized lacustrine adaptations. This can be seen in contrast to the generalized, marshland or riverine faunas present elsewhere (Van Damme, personal communication 1979).

Most of the Middle Miocene (16-10 m yr BP) is absent from the record of lacustrine sedimentation in the basin. Minor, short-lived lacustrine basins, probably unrelated to the Turkana Basin proper, are known to have occurred near Buluk, to the northeast of the modern lake (Harris & Watkins 1974). Late Miocene-Early Pliocene lake beds are exposed at Lothagam Hill. These are primarily in Lothagam 2, but marginal lake shore deposits occur lower in the section, in Lothagam 1, as well. From what little information is available, the Late Miocene lake system seems to have been similar to that which existed during the Early Miocene. However, the extensive nature of deeper water, Early Pliocene lacustrine deposits in both Lothagam 2 and at Kanapoi (some 60 km south of Lothagam) indicate the presence of a large lake, the Proto-Lake Turkana, at least as early as 5 m yr BP. The nature of this lake can only be guessed at, since its deposits are only exposed at these two sites, in the southern part of the basin. By no later than 4.5 m yr BP, deltaic deposits of the ancestral Omo River were entering the lake near Mursi (see map), thus demonstrating that an elongate lake, of approximately the North-South dimensions of the present lake, occupied the basin at this time. This interconnection is strongly supported by the similarity of ostracode faunas from the northern and southern regions. While we have no data from the north-west side of the basin. fluvial sediments at Kubi Algi (near Alia Bay), and terrestrial volcanics at Suguta, show that this lake could not have been considerably *larger* to the east or south than at the present time. The lacustrine faunas of this time period suggest a shallow, open basin during the Early Pliocene (Van Damme, personal communication 1979).

The Middle Pliocene (4.5-3.2 m yr BP or Early Pliocene of Europe and North America) as shown in both the Omo and East Turkana Sequences, was a period of intense tectonic activity in the Turkana Basin. The swell-fault system, which currently dominates the structure of the north end of the lake, developed at this time, allowing for the accumulation (in the depression caused by this feature) of thick piles of deltaic and lacustrine sediments (Vondra & Bowen 1978). It appears that the lake during most of this time was 'relatively' small, as indicated by its shoreline positions. Cerling (1977) suggested that the basin may have been closed at about 4.0 m yr BP, and faunal data from this period (Williamson 1978, Carbonnel & Peypouquet 1976, Cohen, unpublished) corroborates this idea, by giving evidence for a general instability and fluctuation of lake levels at this time.

This phase of lake development seems to have been rather abruptly truncated in the earliest Late Pliocene. A series of open basin transgressions, interspersed with periods of regression and lake level instability was initiated at about this time, and is the general pattern which has continued up to the present. The best documented of these early major transgressive episodes was recorded at Northeast Turkana (Areas 12 and 129 of Findlater 1976) by the Surgaei Diatomite, formerly known as the Surgaei Tuff. The age of this transgression is uncertain but some constraints may be suggested. The bracketing ages of tuffs below and above the Surgaei are 3.9 and 1.8 m yr BP respectively. Brown et al. (1978) suggested a relatively young age for the transgression, perhaps between 2.4-3.0 m yr BP. If, as I suspect on lithologic grounds, this transgression is correlative with the one suggested by the basal Nkalabong Formation deposits, then the age of this northern Surgaei may well be about 3.9 m yr BP. Williamson (personal communication 1980) is firmly convinced that the Surgaei diatomites are highly time transgressive. He states that it is highly likely, on biostratigraphic grounds, that the Surgaei diatomites near Koobi Fora and Alia Bay (Areas 102, 202 and 203 of Findlater 1976) are of Late Pliocene age, in keeping with Brown et al.'s suggestion. Different authors are in some disagreement about the nature of this Mid-Pliocene lake. Cerling (1979) believed it to be a graben bounded lake, similar in morphology to those of the Western Rift, while Van Damme (personal communication 1979) favors a rather shallower, gently sloping basin. In fact it is really only the great areal extent of the lake surface which can be firmly established for this time period.

In the post-Mid-Pliocene Lake Turkana, most of the major changes in lake morphology (with one important exception to be discussed later) appear to have been related to climatic, rather than tectonic, instability. This hypothesis receives strong support from the broad contemporaneity of lake level fluctuations between the Eastern and Western Rift Valley lakes. Since the two systems are effectively decoupled tectonically at the microscale, only climatic events could produce such a pattern of events. Williamson (1978) has reviewed the similarity in sequence of Pliocene events between the Kaiso Lake of the Albertine Basin and that of Lake Turkana. Vondra & Bowen (1978) are however, of the opinion that local tectonic adjustments throughout the basin (as opposed to climatic ones) continue to exert the dominant effect on the supply and distribution of sediments into the lake. Therefore, we must be extremely cautious in interpreting 'local' transgressive and regressive episodes as being due to patterns of instability in lake level; when they can be equally well explained as being due to retro- and progradation of the ancient shorelines. Vondra & Bowen (1978) and Findlater (1978) have demonstrated a westward progradation of the shoreline on the northeastern margin of the lake, probably due to deltaic formation in that area. Evidence from the Omo Sequence, however indicates that this may in part be due to a more general decline in lake level. It seems probable Lake Turkana reached its maximum size either during one of the Middle Pliocene or the Early Holocene transgressions. Tectonically undisturbed lake beds of probable Middle Pliocene age occur at Nkalabong (460 m above MSL) and Liwan (450 m above MSL), while Holocene deposits of approximately the same, or slightly higher elevations are widely scattered throughout the basin (Butzer 1976). Nevertheless, the post Middle Pliocene Lake, by all indications was still, despite some regression, quite deep and probably meromictic (Williamson 1978). Most available evidence would point towards the lake having been an open basin from 3.2-1.8 m yr BP, with possible short intervals (as evidenced by short term lake level instability) as a closed basin (Findlater 1978).

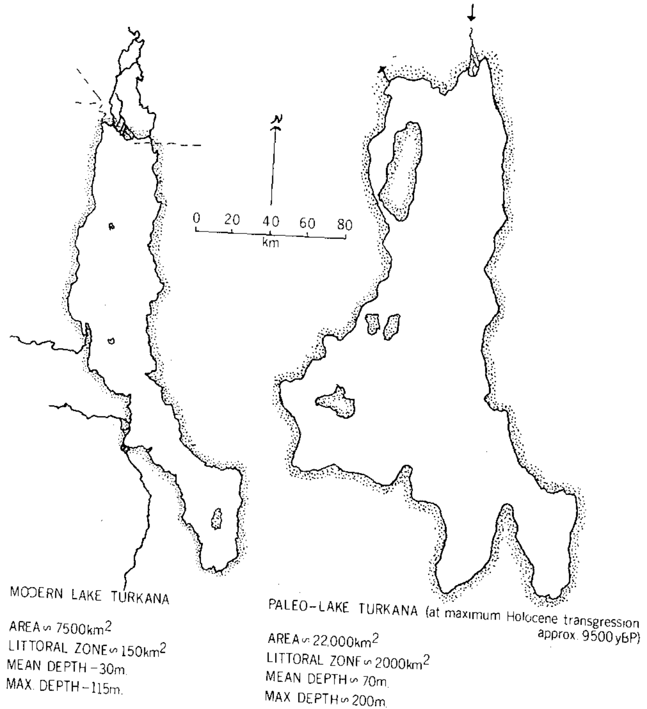

Figure 4. A comparison of modern and paleo-Lake Turkana (at the 9500 yr BP transgression). External drainage of the lake at that time, through the Pibor-Sobat drainage (arrows show inflow and probable outflow directions) connected the lake hydraulically and biogeographically with the Nile and its Central African lake system. Areal extent of the lake was determined through a comparison of ERTS satellite imagery with land based, altimetric data.

It is quite clear that at about 1.8 m yr BP (earliest Pleistocene) an important climatic shift, affecting much of East Africa (Hay 1976, Cerling 1979, Bonnefille 1976, 1979) reduced the level of rainfall (or increased evapotranspiration) throughout the Turkana Basin. After the beginning of this change in climatic regime (recorded at East Turkana by a small unconformity known locally as the post KBS erosion surface), the lake level receded to below its outlet level. The next 0.6 m yr saw a continuous series of fluctuations in lake level, resulting in a geologically rapid alternation between open and closed conditions. Williamson (1978) believes the lake during this time period to have been relatively shallow and either poly- or holomictic, similar in essence to the modern lake. It might be argued that this phase of the lake's history is still in effect, but for the fact that we have very little data for the time period 1.2-0.1 m yr BP. Brief transgressive episodes of Middle Pleistocene age, possibly 0.7 m yr BP, are recorded by the Goumde Formation at Ileret and Upper Member L of the Shungura Formation near the Omo. Brown et al. (1978) have suggested that these are in fact correlative, although more recent K-Ar dating by Drake et al. (1980) may imply a somewhat older age for Upper Member L. A third area of possible Middle Pleistocene lacustrine sedimentation, Member B of the Suguta Beds (Truckle 1976) has not yet been studied in sufficient detail to draw any conclusions as to its significance. Extensive lacustrine deposits exposed on the Northwest shore of Lake Turkana near Lowareng may prove to be of Middle Pleistocene age as well. These fossiliferous beds are perhaps the least studied lake sediments in the basin and will form the basis for much future investigation.

The latest series of transgressive events resulting in open basin conditions began in the Late Pleistocene. The Kibish Formation of the Omo Sequence, the Galana Boi Beds of East Turkana, and the extensive, unnamed Holocene beach deposits of West Turkana (including the '220' beds at Lothagam Hill, Behrensmeyer 1976) were all deposited during these most recent high lake stands. Butzer et al. (1969) have discussed the evidence from the Kibish Formation which is, stratigraphically, the most complete of these sequences. They conclude that, at approximately 9,500 yr BP, the lake was open, via a northwesterly, nilotic drainage, the Pibor-Sobat River. This lake, standing some 70 m above the present lake level, has been calculated by Cohen (1979a) to have been approximately 22 000 km² in area, and is illustrated in Figure 4. I suggest it to have been a meromictic lake, with a maximum depth of approximately 200 m.

Somewhat before this latest series of transgressions, the Suguta Trough at the southern end of the lake was cut off from the main lake by a volcanic pile known as the Barrier. Lake Suguta (or Logipi as it is currently known) henceforth continued its independent development, also showing high lake strand lines at 9660 ± 210 yr BP (Truckle 1976). It is possible but unlikely that this volcanic obstruction was responsible for the widespread transgressive event seen at this time for two reasons. First, lake levels rose over a wide area of East Africa at this time, apparently due to climatic influences (Butzer et al. 1972) rather than local tectonically controlled events. Second, I have found that the maximum volume of water displaced from the equilibrium volume of Lake Turkana by the obstruction of the Suguta Trough is about 200 km^3. However, the actual lake rise entailed a volumetric increase of about 900 km^3, far in excess of what the displaced Suguta water could provide.

In the past 8000 years an erratic decline in the lake's level has occurred, with the current elevation being about 403 m above MSL. This value has fluctuated vigorously, even in historic times (Yuretich 1976), but there is no evidence for an outlet subsequent to the Early Holocene transgression. Butzer (1976) in the Omo River region and Owen & Renaut in East Turkana (1979) have documented lake level variations through the Holocene. Both studies suggest three transgressive maxima. Butzer placed them at 9500 yr BP (as previously mentioned), 6200 yr BP, and just before 3000 yr BP, with regressive minima at 7500 yr BP and about 4000 yr BP. Owen & Renaut reached similar conclusions, except for placing the second transgression somewhat later, about 5500 yr BP.

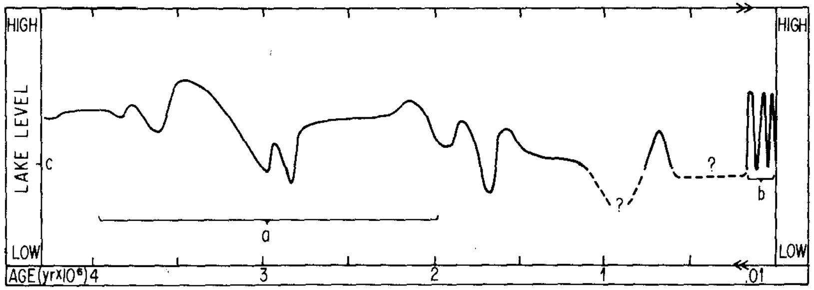

Figure 5. Relative lake level variations in Lake Turkana and its precursors during the past 4.3 m.y. as determined from lithologic sequences throughout the Turkana Basin. As absolute level values are not available for all time intervals they have been omitted from this diagram. However, maximum transgressions are likely to have been approximately 480 m above MSL. Possible tectonic complications make the pre-Pleistocene variations less certain than the Pleistocene and Holocene variations.

Notes: a) the interval 4-2 m.y. BP is characterized by a number of questionably dated hiatuses in sedimentation, whose duration is likewise, unknown. Therefore, the absolute timing of events, although not the relative order, during this period is, of necessity, only approximate; b) the curve for this interval is diagrammatic, implying a period of rapidly fluctuating lake levels in the Late Pleistocene-Recent. Aside from the three transgressions illustrated here, several other Late Pleistocene transgressions (the earliest being probably before 100,000 yr BP) are known; c) for reference, this elevation on the curve would represent the current lake level (approximately 400 m above MSL).

Figure 5 shows a best fit lake level curve, based on lithological and paleochemical data for Lake Turkana for the past 4.3 m yr.

Several attempts have been made in recent years to estimate deep water sediment accumulation rates for Lake Turkana. Barton (1979) suggested a sediment accumulation rate of about 4.5 mm/yr, from preliminary studies of the paleomagnetic declination wandering rates in several 6 m cores. Laminae counts on the same cores gave values of about 10 mm/yr. Yuretich (1976), by estimating rates of calcium removal from the lake, obtained values of 0.5-1 mm/yr. This is in general agreement with estimates by Brown et al. (1978) of 0.57-1.54 mm/yr for the Koobi Fora and Shungura Formations (lacustrine portions only), despite the fact that the comparison is between watered and dewatered sediments. This is in close concordance with accumulation rates obtained from other rift valley lakes (D.Livingstone, personal communication 1980).

3. CHEMICAL SETTING

A number of authors have attempted to make quantitative or semi-quantitative estimates of various aspects of Lake Turkana's paleochemical history. These analyses have been based on one of the following:

1. An index faunal approach (Carbonnel & Peypouquet 1976, Van Damme 1975, Cerling 1979, Cohen this paper, and unpublished manuscript) where given assemblages of fossils are taken as indicative of particular water chemistries.
2. A geochemical approach (Cerling 1979, Yuretich 1976), where specific authigenic mineralogies are interpreted, on the basis of their respective stability field diagrams, for a given aqueous chemistry, to indicate in what part of the field (i.e. under what specific set of paleochemical parameters) the minerals could form.
3. Stable isotope studies (Cerling 1977, P.Abell, personal communication 1980), where isotopic ratios are used to infer evaporative conditions, and thus indirectly, aquatic paleochemistry.

Traditionally, the fossil diatom record has served as the primary tool of paleolimnologists in obtaining chemical histories of African lakes. Due to preservation problems, probably associated with the dissolution of silica in alkaline groundwaters, the diatom record of Lake Turkana has proven frus-

RANGE #	NAME	Na^+	Cl^-	Alkalinity	K_{20}	COMPARISON WITH TALLING & TALLING CLASSIFICATION
I	STENOCYPRIS ASSEMBLAGE	< 75	< 20	< 5	< 500	Class 1 (< 600)
II	PARACYPRIA ASSEMBLAGE	75-150	20-50	5-15	500-1500	Class 2 (600-6000)
III	GOMPHOCYTHERE ASSEMBLAGE	150-900	50-500	15-30	1500-4000	
IV	LIMNOCYTHERE ASSEMBLAGE	> 900	> 500	> 30	> 4000	Class 3 (> 6000)

Figure 6. Ostracode, water chemistry related assemblages. The Range # is followed by the most distinctive or commonplace genus of that range. Only for Range 11 is the genus absolutely restricted to that range, however. This system has been found to have widespread application amongst the East African lakes. Na and Cl values are in mg/l, Alkalinity ($CO_3 + HCO_3$) in milliequivalents per liter, and K_{20} (conductivity) in μmho/cm. Talling & Talling's (1965) classification scheme (values are in K_{20}) is included for comparison. After Cohen (1980, unpublished manuscript).

tratingly inadequate. While Holocene deposits are rich in diatom floras, the Pleistocene and Tertiary sediments around the lake only occasionally yield identifiable diatoms. Often, partially dissolved frustules are found which cannot be accurately identified.

An alternative to using fossil diatoms for paleochemical analysis may be found in the fossil ostracode fauna of the lake. These minute, calcite secreting, benthic crustaceans are, like diatoms, extremely sensitive to water chemistry variations. They are moderately abundant in most African shallow water lake sediments examined to date. A full discussion of the techniques involved in fossil ostracode typology as it relates to African lakes, will appear shortly (Cohen, in preparation).

Distinct ostracode species assemblages can be correlated with increasing ionic concentrations in African waters. I have termed these assemblage groupings *Ostracode Paleochemical Ranges*, each range being named after a characteristic ostracode taxon, typical of, though not necessarily restricted to, that range. Figure 6 shows the Ostracode Range water chemistry characteristics. The ranges are compared with Talling & Talling's (1965) African water chemistry classification, for those readers familiar with that scheme.

The physiological-ecological reasons for these differing ranges are not entirely clear, but one important explanation can be suggested. In waters of increasing alkalinity, Ca^{++} becomes progressively less soluble, and therefore, less available to $CaCO_3$ secreting organisms. Almost certainly, major physiological costs are incurred by calcite secreting organisms in continually more Ca poor waters to retain the ability to extract Ca^{++} from the water column, as it is a highly energy intensive process. Therefore, ostracode species may enter more alkaline waters only at the expense of some other, unspecified, energy intensive capabilities, a classic example of ecological optimization.

In a core extracted from Lake Nakuru by J.Richardson, both ostracodes and diatoms were present, allowing for independent paleochemical analyses to be performed. For 80 % of the core's analyzed length (approximately 12 m, representing a 25,000 yr record) the agreement in paleochemical interpretations between ostracode and diatom typologies was either good or excellent.

I have analyzed 136 samples from East Turkana, Northwest Turkana, and Lothagam, for ostracode faunas and 77 have yielded interpretable faunas. An additional 45 ostracode species lists for Northern and Western Turkana have been published by Carbonel & Peypoquet (1979), and have been incorporated into this study. Their interpretations however (Peypoquet, Carbonel & De Heinzelin 1979, Peypoquet & Carbonel 1980) have not been used here, due to difficulties in comparing their methodologies with my own. The total fauna thus far recovered gives us a good picture of the paleochemical history of the lake (Figure 7). For intervals during which no ostracode data is yet available, I have supplemented the analysis with additional data from Cerling (1977, 1979) and Van Damme (1979). Following both of these authors it is convenient to subdivide the paleochemical history of the lake into three episodes since the Early Pliocene:

Phase 1: 5.0-3.2 m yr BP. A relatively freshwater lake, undersaturated in

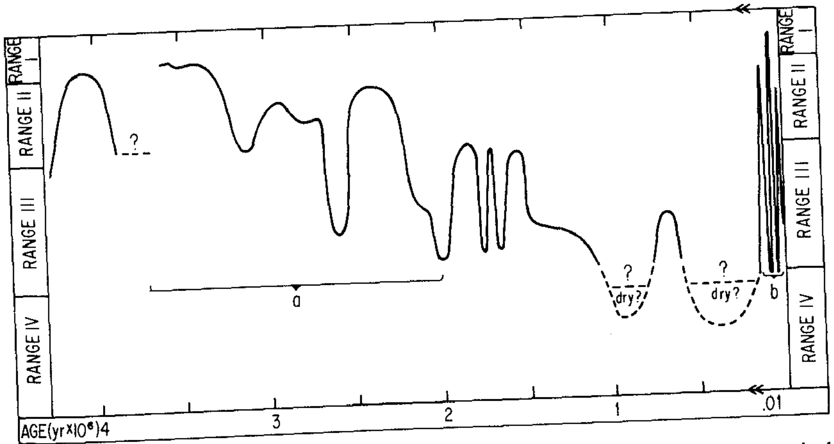

Figure 7. Water chemistry variation of Lake Turkana for the past 4.3 m.y. The chemical variations are expressed in terms of the Ostracode Paleochemical Ranges as indicated by fossil faunas current to each time interval. The y-axis is approximately linear for Na, Cl, and Alkalinity and Conductivity. See Figure 6 and the text for further explanation.

Notes: a), b) see comments a) and b) respectively for Figure 5.

$CaCO_3$, with alkalinities less than 4 meq/1, and total salinities in the range of 0.05-0.1 g/l. In comparison with modern East African rift valley lakes, this would have been remarkably like the Ethiopian Lake Zwei (or to a lesser degree like Kenya's Lake Baringo). Ostracode data are still very scanty for this period. However, where present, they suggest that some episodes of high alkalinity (High Ostracode Range 3) may have occurred during this period.

Phase 2: 3.2-1.8 m yr BP. A freshwater lake with occasional brackish water episodes. Cerling (1977) suggests an alkalinity range of 7-14 meq/l and Van Damme (1975) thinks that total salinity may have ranged from 0.09-0.2 g/l. This lake has no very close modern analogue, perhaps however being closest to Lake Awassa of the Ethiopian Rift.

Phase 3: 1.8 m yr BP-Present. A highly fluctuating water chemistry characterized this time of rapidly varying lake levels. It was usually, and remains, a typical Class II lake (after Talling & Talling 1965) with the appropriate ionic ratios along various parts of its evaporation-concentration chord. During the fresher phases (such as during the Early Holocene) it would have been quite similar to the Phase 2 lake, while at its extreme low levels, it may have been similar to the more alkaline Lake Shala (perhaps drying completely at times).

4. BIOLOGICAL HISTORY

Not surprisingly, the fortunes of Lake Turkana's lacustrine biota have been intimately associated with the variation in the lake's physical and chemical evolution, and as alluded to earlier, have formed the data bases for many of our conclusions about the lake's history. The Lake Turkana fossil record is truly exceptional among non-marine sedimentary sequences, both in terms of its completeness of preservation of the various taxa, and its longevity. All major groups of organisms present in modern Lake Turkana, with the exception of the zooplankton, aquatic insects, benthic protists, and the planktonic blue-green algae, have left us a generous fossil data base for evolutionary and paleoecological studies. Furthermore, all of these groups have been, or are currently, the subjects of investigation: Stromatolites-benthic blue green algae (Johnson 1974, Aramwik unpublished, Schwartz unpublished); Diatoms (Owen & Renaut 1979); Higher aquatic plants (Cohen 1979b); Molluscs (Van Damme 1975, 1979, Williamson 1978, 1980); Ostracodes (Carbonel & Peypoquet 1979, Cohen 1980); Fish (Schwartz unpublished); Reptiles — particularly crocodylians (Tchernov 1976); Hippopotamidae (Coryndon 1976); Whales – ziphiidae (Mead 1975).

Pliocene crocodylians and hippopotamids both occur in unusually high diversity, the hippos having apparently radiated intrabasinally, while the crocodylians were exotically derived. Tchernov & Coryndon both argue for increased habitat heterogeneity to explain this phenomenon.

The study of many of the groups listed above, and in particular the stro-

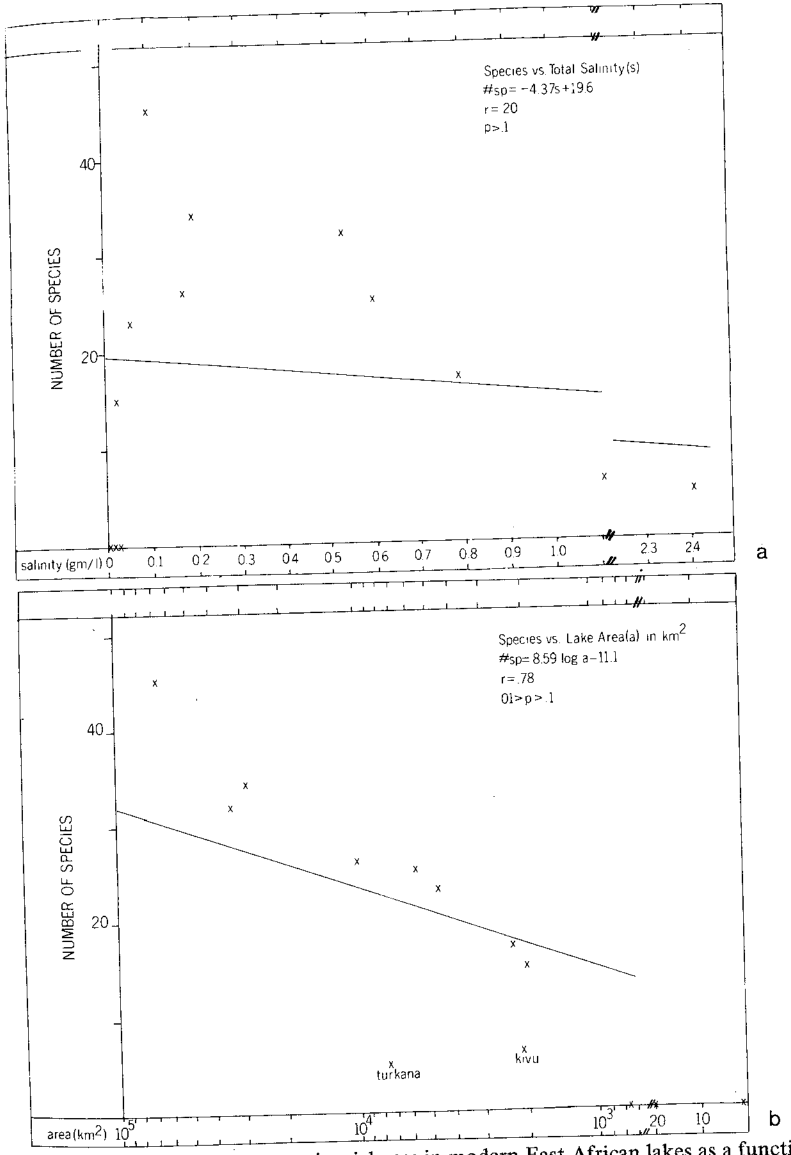

Figure 8. Total molluscan species richness in modern East African lakes as a function of total ionic salinity (a), and total area (b). Species richness and water chemistry data after Van Damme (1975, 1979). Only those species inhabiting the lakes themselves (as opposed to marginal swamps and deltas) were counted. Pearson product moment correlation of species richness with salinity is poor in comparison with the species area correlation. The large, saline lakes, Turkana and Kivu do however have anomalously low species numbers, although several causative factors aside from high salinity have been put forward to explain this phenomenon.

matolites, diatoms, ostracodes and molluscs have yielded extremely valuable information on local environmental and paleochemical settings. This type of information has been particularly useful in the geological interpretation of many sedimentary sequences, where the sedimentary evidence alone would have been ambiguous.

Van Damme (1979) has discussed the geographical ecology and paleoecology of molluscan faunas at Turkana. He concluded that almost all Miocene molluscan faunas were dominated by cosmopolitan, pulmonate species. During the Late Miocene or Early Pliocene, European Paleoarctic faunas appeared in the basin (most importantly *Pseudobovaria*). These may have entered Africa during the Late Miocene, when the Mediterranean Sea dried up. Early Pliocene faunas at Lothagam and Kanapoi show the earliest evidence for widespread lacustrine adaptation, suggesting the presence of a large, stable lake by this time. Van Damme states that the Late Pliocene was a period of intense adaptive radiation amongst molluscan lineages, an opinion also presented by Williamson (1978). Finally, a dwarfing and gradual extinction of these Pliocene faunas occurred during the Early Pleistocene, to be replaced by species of the cosmopolitan, East African molluscan fauna.

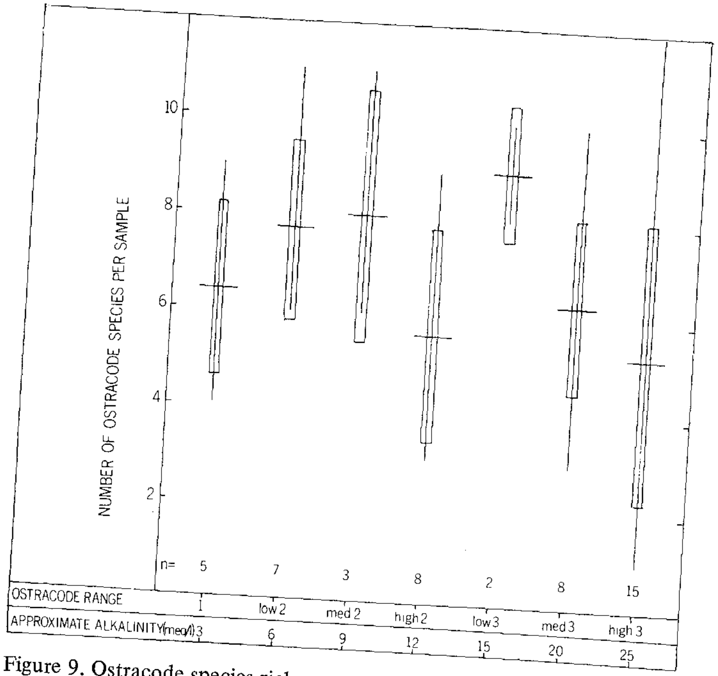

Figure 9. Ostracode species richness per sample at various water palaeochemistries for paleo-Lake Turkana. The samples (100 individuals per sample) are from all stratigraphic horizons in the Turkana Basin thus far collected for ostracodes, from which unambiguous water paleochemistries have been determined. Horizontal bars are the mean number of species per sample. Thin vertical bars are the absolute range of values. Thick bars are the standard deviations with N-1 degrees of freedom. 'n' is the total number of samples available for study for each Paleochemical Range. See text and Figure 7 for a discussion of paleochemical determinations using ostracodes. The figure illustrates the lack of any significant correlation between species richness (and in this case also, species diversity) and either increasing or decreasing ionic concentration of the surrounding water mass, amongst ostracodes, within the range 3-25 meq/l alkalinity.

Van Damme (1979) also noted the close correlation between total molluscan diversity and total salinity in the modern East African lakes, and proposed that ionic concentration was, in fact, the causative agent in episodes of species diversification and extinction. Reinspection of the diversity data by Cohen (1979a) however, showed that correlation coefficients were actually higher (Figure 8) between total lake area and diversity, than between low salinity and diversity. At high alkalinities (greater than 20 meq/l), Van Damme is almost certainly correct, in that molluscan growth eventually becomes extremely stunted and thin shelled. Bivalves, as he noted, disappear before gastropods in increasingly alkaline waters, perhaps due to the greater strains imposed in a bivalve's shell by adductor musculature than occurs amongst gastropods.

In fact, within the Turkana Basin, there is little correlation between paleochemical determinations and species diversity for most of the lake's history. Figure 9 illustrates the mean species richness (and standard deviation) at various calculated chemistries through the Turkana fossil record, for ostracodes per sample (sample size was 100 individuals).

Cohen (1979a, 1980), after a study of molluscan and ostracode trophic structures through time, suggested that habitat homogeneity may play at least as important a role as changing lake paleochemistries in initiating extinction events. This suggestion was based on the observation of superior survival rates of those trophic groups or 'guilds' of benthic invertebrates (specifically the epibenthic detritivores), least affected by the loss of benthic patchiness and spatial heterogeneity (in particular, the major reduction which occurred in the Lake Turkana littoral zone, due to the basin's morphologic configuration).

For example, detritivore diversity varies little through time, because habitat and food supply (littoral and sublittoral muds) are less affected by basinwide lake level events than for any other trophic group. A greater percentage of the fossil ostracodes of Lake Turkana were detritivorous than was the case amongst molluscs. Thus, ostracode diversity does not show the profound fluctuations through time at Turkana that can be observed amongst the Mollusca.

At the other extreme, herbivory was much more important for Turkana molluscs than for ostracodes. Herbivorous gastropods undergo rapid diversification (primarily through immigration) during periods of time when the littoral zone is at its greatest expanse. This is not strictly a function of lake area, since either a steeply sloping littoral zone or high turbidity can produce a small total littoral area in an otherwise large lake. This is the case in Lake Turkana today (total area = 7517 km^2), where the total littoral zone area (approximately 150 km^2) is only about three times that of the much smaller, but shallow, Lake Naivasha (total area = approximately 150 km^2, total littoral zone = approximately 50 km^2).

Probably the most exciting and theoretically intriguing of the paleobiological studies on the lacustrine biota has been the work by Williamson (1978, 1980) on the evolution of molluscan faunas. Williamson (1978) has demonstrated the influence of various environmental-trophic resource stimuli on speciation, immigration and extinction events through the lake's history. Through a detailed semi-quantitative-theoretical approach, he has been able to show that both trophic resource and environmental stability have been of paramount importance in the initiation of intrabasinal speciation and diversification events. This is a point which has gained wide acceptance in current, theoretical, ecological literature, but which has rarely been demonstrable in a historical context. Williamson (1980) has more recently demonstrated the evolution of isolate molluscan taxa at East Turkana, involving extremely large populations over geologically instantaneous intervals. This work is of considerable interest to evolutionary biologists studying rates and modes of speciation.

5. SUMMARY

The Lake Turkana Basin has been a region of sedimentation and active tectonism since the Late Mesozoic. The current cycle of tectonic activity and lake formation however, began in the Early Miocene, with major downwarping of Paleogene erosion surfaces. Through the Early and Middle Miocene, temporary, unstable lakes and swamps occupied many parts of the basin. These were inhabited by cosmopolitan, eurytopic, riverine derived faunas, in all known areas except Loperot. The presence of a non-marine whale fossil argues for important hydrologic connections with the Indian Ocean, though only vague evidence exists to place this connection geographically.

The Turkana Depression, the structural feature which encloses the northern Turkana Basin, developed in the Late Miocene, through a combination of domal upwarping and an echelon normal faulting. Sometimes after 7 m yr BP, the first large lake developed in the Basin. The first widespread appearance of endemic lacustrine faunas can be observed in the Lothagam 2 section, shortly after the appearance of Paleoarctic exotics, probably spreading into Africa from Europe during the Mediterranean drying episode.

The Middle Pliocene saw an intensification of tectonism in the Basin, with major subsidence centers and delta formation developing on the North and Northeast sides of the lake. Water chemistry and lake level fluctuations were relatively slow during this time, with low alkalinities predominating. Important speciation events have been documented amongst molluscs and hippos for this time.

In the Early Pleistocene a dramatic climatic shift occurred throughout East Africa, as conditions became much drier in the region. The Pleistocene and Holocene in the Turkana Basin have been marked by rapid lake level reversals. Concommitant with this event was the disappearance of many presumably stenotopic, specialist molluscan species, and their repeated replacement by the eurytopic, cosmopolitan, African lake fauna. The south basin of the lake probably developed during the Early Pleistocene, being subsequently (Middle-Late Pleistocene?) bisected through the closure of the Barrier, and thus isolating the Suguta Trough from the remainder of the lake.

After a particularly high transgression in the earliest Holocene (when the lake was probably open) Turkana has fluctuated rapidly in level and water chemistry, in close response to climatic variation within the local basin and drainage area.

In this paper, I have tried to briefly summarize the historical development of Lake Turkana, Kenya, emphasizing the past five million years. Physical, chemical, and biological aspects of this history have been considered, though I have not tried to cover all the data in equivalent detail. Rather, I have tried to cover more completely those points with the greatest general interest, in the belief that they may stimulate the investigation of similar phenomena in other ancient lakes.

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