PERCOMORPHI

Fam. CENTROPOMIDAE.

Lates sp.

Only three bones, a caudal vertebra from a fish *ca.* 72 cm standard length and a fragment of dentary, together with a pectoral spine (also from a small fish), can be referred to this genus. Although the identity of the fin-spine might be called to doubt, there can be no confusion regarding the vertebra and dentary.

The vertebra and fin-spine are heavily mineralized and differ markedly from other specimens in this deposit; they were, thus, probably derived from earlier strata. The dentary, on the other hand, is poorly mineralized and its state of preservation is strictly comparable with the other specimens from this site.

Fam. CICHLIDAE.

Tilapia sp.

Vertebrae. — Seven anterior precaudal vertebrae. Six of these are derived from a fish, or fishes about 45 cm standard length, and the seventh from a slightly larger individual.

Fin-spines.

Dorsal fin. — Fifteen spines, all from fishes of a size comparable with those from which the vertebrae were derived. Two of the spines are lighter in colour and less mineralized than the others.

Anal spine. — One.

Pectoral spine. — One specimen, complete except for its most distal extremity.

GENERICALLY INDETERMINABLE MATERIAL.

(i) Parasphenoid (middle section).
(ii) Fragment of basioccipital.
(iii) Two articulars (from different genera).
(iv) Two halves of soft fin-rays.
(v) Twelve vertebrae.
(vi) One hypural element.
(vii) Sixteen unidentifiable fragments.

DISCUSSION AND SUMMARY.

Before considering the evidence furnished by the fossils described in this paper, some attention must be given to the faunal affinities of the fishes inhabiting present-day Lake Edward.

When attempting to discover this relationship, the cichlid and non-cichlid elements should be examined separately. Of the twenty-four non-cichlid species recorded, only three are endemic to Lake Edward. Seven species have a relatively restricted geographical distribution within the area surrounding the lake, although three of these species also occur in Lake Kivu, and the range of one of these extends to Lake Tanganyika. One species otherwise only occurs in Lakes Kivu and Victoria, another is known only from Lake Victoria, a third occurs in Lakes Victoria and Nyasa; and finally, there is one species which, apart from its being recorded in Lake Edward, is known only from the streams of Mount Kilimanjaro.

The remaining ten species may be considered as Nilotic, with some species widely distributed in East Africa. It is interesting to note that five of the ten Nilotic species do not occur in Lake Victoria. A point of probable significance is that the three endemic species and the six species with restricted distribution are all small cyprinids and cyprinodonts, whereas the Nilotic species are mostly large fishes.

The *Cichlidae* show dual affinity. The *Tilapia* species are Nilotic but the *Haplochromis* are clearly related to species endemic to Lake Victoria; three *Haplochromis* species and one monotypic genus are common to both lakes. (Data derived from POLL, 1939; POLL and DAMAS, 1939; TREWAVAS, 1933).

Perhaps the most outstanding feature of the Lake Edward ichthyofauna is the absence of several families which are widespread in eastern and tropical Africa; the *Polypteridae*, *Characidae*, *Citharinidae*, *Schilbeidae*, *Mochocidae*, *Malapteruridae*, *Centropomidae* and *Mastacembelidae* are all without representatives. Furthermore, as compared with Lakes Albert and Victoria, there are fewer genera per family in Lake Edward. In certain respects this absence of otherwise widely distributed families is paralleled in Lake Victoria, although here only the *Polypteridae*, *Citharinidae*, *Malapteruridae* and *Centropomidae* are absent.

DE HEINZELIN (1955) has aptly described the contemporary fauna of Lake Edward as « ... une faune pauvre, tronquée, dépourvue de bon nombre d'éléments qu'on s'attendrait à y trouver... ».

Data summarised in Table I show that during the Pleistocene, gradual changes took place in at least the generic constitution of the fish-fauna of the Edward basin. It is also obvious that until Makalian times (Epi-

Pleistocene) the fauna was more markedly Nilotic than at present and that representatives of many of the absentee families and genera were then living in the Edward basin. Two of these genera, *Lates* and *Synodontis*, occurred in Lake Edward as recently as the early Holocene. In fact, when considered at the species level, the known late Pleistocene fishes of Lake Edward are comparable with those of the present fauna of Lake Albert.

Although some typically Nilotic fishes such as *Hydrocyon* (*Characidae*), *Auchenoglanis* and *Clarotes* (*Bagridae*) were apparently lost before the end of the Pleistocene, the fauna retained its more complete Nilotic facies until the close of the Gamblian period. A possible explanation for the loss of several Nilotic genera and species which occurred at that time, will be discussed later.

Genera recovered from Kaiso deposits in the Edward basin (Sites I to V and Site VIII a) are similar to those from the Kaiso beds of Lake Albert (WAYLAND *et. al.*, 1926). This similarity is not surprising since the two lakes were then probably continuous or at least in broad contact (DE HEINZELIN, *op. cit.*; MORTELMANS, 1950). In all probability the fishes preserved in these deposits should be looked upon as members of an archaic, pan-African ichthyofauna which populated African rivers before the formation of the Rift lakes. They would correspond to « the general ancient fauna of Tropical Africa » which WORTHINGTON postulated as having « been widespread over the continent in the early part of the Tertiary epoch... » (WORTHINGTON and RICARDO, 1936). That the affinities of this fauna are with the present Nilotic group of fishes should not be misconstrued to imply that the Nilotic fauna *per se* is more ancient than those of the other major river systems. When comparing the fishes of the Nile, Congo and Niger, one is impressed by the large number of genera common to the three systems. This evidence, derived from present distributions, can only be interpreted as indicating earlier contact between the various systems. WORTHINGTON (1954) postulated temporary connections between the Nile, Congo and western rivers across a largely inundated Sudan plain during an early, but unspecified, Pluvial. However, WAYLAND's evidence (1931) indicates an even earlier contact between the rivers of eastern Africa and the Congo. In pre-Rift times (? Miocene) Uganda was drained by a number of westward flowing rivers which ultimately emptied into the Congo. It would not be unreasonable to suppose that these rivers were populated by fishes belonging to a group which may be considered archaic and, from its modern distribution, of an essentially Nilotic-Congoan type (see above). There is palaeontological evidence that, during the Miocene, at least two typically Nilotic genera, *Lates* and *Polypterus* were present in the area now occupied by Lake Victoria (GREENWOOD, 1951 *a*). Lack of other fish-bearing Miocene deposits in East Africa makes it impossible to determine whether these fishes gained access to the lake as a result of its having direct contact with the Nile, or, whether they were representatives of the archaic fauna.

The earliest fish-fossils in the Edward basin are from deposits of Kaiso-age. DE HEINZELIN subdivides these deposits into four series on the basis of the Mollusca present. Following his classification, the fishes found at Kanyatsi (Sites I and II) are from Series I, which was laid down in a period of relative aridity, tentatively correlated with WAYLAND'S « Kageran Interpluvial ».

The only other fish-bearing Kaiso deposits which can be refered to one of DE HEINZELIN'S sub-divisions are those from Sites IV, V and V *a*. These are placed in series III which post-date the Kageran interpluvial; at the time of their deposition the climate was relatively humid (DE HEINZELIN, *op. cit.*). This assemblage contains typically Nilotic genera and does not differ from the generic complex preserved at Kanyatsi (Kaiso Series I).

Thus, the fish-fossils provide little evidence on the effect and intensity of the first (Kageran-Kamasian) interpluvial arid period. It is clear from the fossil Mollusca, however, that there was a gradual increase in the concentration of dissolved salts during the period prior to their preservation. The increased salinity had the effect of producing a gastropod fauna with a pseudomarine facies (DE HEINZELIN, *op. cit.*; FUCHS, 1936; BEAUCHAMP, 1946).

WORTHINGTON (1932; 1937) and WAYLAND (1934) (whose opinions were based on those of WORTHINGTON), considered the first interpluvial to be of such aridity as to almost completely dry out the lake. It is to this period that WORTHINGTON (1932; 1937), using the palaeontological data then available, ascribed the major change in the affinities of the Lake Edward fishes. But, as mentioned above (p. 67), such an early date for this event can no longer be entertained. Evidence from Series III Kaiso fossil shows clearly that after the Kageran-Kamasian interpluvial Lake Edward was still populated by fishes of a Nilotic type, including many of the present-day absentee genera.

There are two possible explanation for this phenomenon. One explanation would assume that the Kageran fish-fauna was destroyed during the interpluvial, but, with the increased rainfall of the second (Kamasian) Pluvial, Lakes Edward and Albert were once again connected; this hypothesis also assumes that Lake Albert was little affected by the interpluvial arid period and that fishes from the lake would be able to recolonize Lake Edward. The second explanation assumes that aridity in the Edward basin was insufficient to destroy the Kageran fish-fauna, which persisted; this theory has, of course, the necessary correlate that the majority of fishes was not adversely affected by the increased salinity of the water (see above).

From the data available it is difficult to decide which hypothesis can be considered the more reasonable, but, recent research seems to provide less support for the concept of an intensely arid interpluvial. As mentioned earlier, fish-fossils from certain Lake Edward Kaiso-beds were interpreted to show almost complete desiccation of the lake because they apparently represented the last record of certain Nilotic species in the Edward basin.

This view is no longer tenable in its original form; furthermore, on DE HEINZELIN's dating these fishes were from post-interpluvial deposits. In Lake Albert, WAYLAND (1926) considered that the Kaiso bone-beds were indicative of a period of intense aridity during which the lake almost dried up. From their associated molluscan fauna, however, both these sites should be equated with DE HEINZELIN's Series III and IV (post-Kageran interpluvial) when, in the Edward basin, the climate was humid.

SOLOMON (1939) does not agree with WAYLAND's climatic deductions from the Lake Albert Kaiso-beds. On the contrary, he considers their ferruginous, sandy, fossiliferous horizons to be indicative of either « ... slightly more open water conditions... » (than the preceeding clays which were laid down under swamp conditions), or « of more complete desiccation than postulated by WAYLAND ». SOLOMON favours the interpretation of more open-water conditions. His reasons for this are that the fossils comprise mainly fishes, crocodiles and hippopotami, and that other mammalian remains are never found as complete skeletons, which would be the case if the animals had died around gradually diminishing water-pools, as suggested by WAYLAND. Instead, the mammalian remains are found as individual bones apparently washed into position. SOLOMON's conclusion is of interest since it parallels DE HEINZELIN's opinion that the climate during the later Kaiso period was relatively humid.

There remain, then, only the Kanyatsi deposits (Kaiso Series I) as evidence for a period of aridity. Again, the fishes provide little satisfactory information regarding the intensity and effects of this dry phase. Only one genus, *Hydrocyon*, does not reappear in deposits younger than the third Kaiso level. The associated gastropod Mollusca, on the other hand, seem to indicate an increase or change in the salinity of the water, in response to which there evolved a number of spinous and carinate species (DE HEINZELIN, *op. cit.*; FUCHS, 1936). Most of these species do not occur in later Kaiso beds. Their virtual disappearance has been taken to indicate that they were destroyed by the lake drying up (FUCHS, *op. cit.*; BROOKS, 1950). Yet, an alternative and opposite explanation seems feasible. If it is accepted that the spinous and carinate facies was a response to increased salinity, is it not possible that the morphological type might be changed when the water was freshened during subsequent periods of increased rainfall ? Or, alternatively, the species may have been unable to adapt themselves to the new « freshwater » conditions and were destroyed, not by aridity, but by increased humidity.

On the evidence available, it only seems possible to say that during the Kageran-Kamasian interpluvial the lake underwent an increase, or change, in salinity caused by a period of relative aridity. At present the intensity of this arid period cannot be accurately determined.

Fishes from the Middle Pleistocene (Kamasian period, *sensu lato*) are very poorly represented by specimens from one deposit at Katanda amont (Sites VI and VII) in the upper Semliki Valley. DE HEINZELIN places these deposits in the Semliki-Series of the Middle Pleistocene. The fish-fossils require little comment, except to note that the genus *Barbus* makes its first appearance. There are too few fossils from these beds to give any indication of faunal relationship, but two typically Nilotic genera, *Synodontis* and *Clarotes*, were probably present.

The Middle Pleistocene was an important period in the evolution of the fish-fauna of Lake Edward. All evidence points towards this period as the time when the lake probably received its major influx of fishes from Lake Victoria. The result of this invasion is most clearly seen in the Lake Edward species flock of the cichlid genus *Haplochromis*. The *Haplochromis* species of Lake Edward and Victoria are more closely related to oneanother than to any other *Haplochromis* flock in Africa. There can be no doubt that the two flocks were derived from the same ancestral species group, which had probably reached an advanced stage of adaptative divergence when the flocks were separated. Not only are the majority of species very similar, but three species of *Haplochromis* and one related monotypic genus occur in both Lake Edward and Lake Victoria.

Another important evolutionary factor associated with the Middle Pleistocene was the loss of direct contact between Lakes Edward and Albert (DE HEINZELIN, *op. cit.*, and *in litt.*). From this time onwards Lake Edward must be considered as a discrete faunal unit.

Arguing from evidence supplied by fishes preserved in the Epi-Pleistocene, Ishango beds, it is apparent that the postulated climatic oscillations of the Upper Pleistocene had few long-term effects on the nature, or, affinities of the fish-fauna. This evidence derives from the still typically Nilotic facies of the Epi-Pleistocene and even early Holocene fishes, which could well be described as a segment of the modern Lake Albert fauna. This relationship between the Epi-Pleistocene fauna of Lake Edward and that of modern Lake Albert includes not only the genera *Lates* and *Synodontis*, but also extends to the species level in these and other genera (see Table I and pages 29-54).

The conclusion that there was continuity of faunal type in Lake Edward is, however, dependant upon the assumption that contact between this lake and Lake Albert was lost and not re-established after the Middle Pleistocene. If this can be accepted, and there is little evidence to the contrary, then the typically Nilotic mid-Pleistocene fishes must have persisted in the Edward basin despite postulated extremes of climate (see WAYLAND, 1934, and WORTHINGTON, 1937). It seems most improbable that *Lates*, a species with low tolerance to deoxygenated waters (FISH, 1956) could have survived if the lake was reduced to swamp conditions.

Furthermore, if it can be accepted that the major invasion of fishes from Lake Victoria took place during the Middle Pleistocene, then the extant *Haplochromis* would indicate that the lake did not suffer severe desiccation during the Upper Pleistocene.

DE HEINZELIN (*op. cit.*), summarizing data relating to climatic changes detectable in Pleistocene deposits of the Lake Edward basin, finds no traces of the postulated three intra-pluvial maxima during the Gamblian, but only for an important wet phase corresponding to the Gamblian *sensu lato*. He does, however, find indications of a probable arid phase prior to the Makalian pluvial. The fishes apparently survived this dry phase. If, at this time, the lake basin had achieved its present form, the deeper parts may well have provided a refuge for many species.

Because there are so few Middle Pleistocene fish-fossils, it is impossible to assess the significance of species which, although present in Kaiso and Epi-Pleistocene deposits, are not recorded from the intervening Middle Pleistocene beds. Two genera, *Protopterus* and *Bagrus*, which occured in Kaiso deposits are not represented amongst the mid-Pleistocene material. *Protopterus* is recorded from Epi-Pleistocene beds, but *Bagrus* does nor reappear until it becomes the predominant fish-fossil of the latest deposits of Z.POST-EM., which are typically Mesolithic and of Holocene age.

The Epi-Pleistocene fishes are especially well-preserved and in most genera it is possible to identify the species present.

Both species of large *Clarias* (*C. lazera* and *C. mossambicus*) at present inhabiting Lake Edward are represented as fossils. Also, a few skull fragments have been tentatively identified as *Heterobranchus*, a clariid genus, once thought to be absent from the Edward basin, but recently discovered in the lake (HULOT, 1956).

Two *Barbus* species, *Barbus* cf. *B. bynni* and *Barbus* cf. *B. altianalis* are recorded. Although only *Barbus altianalis* survived until the present-day, the greater number of specifically identifiable fossils is nearer the Nilotic *B. bynni* (see p. 42).

In a preliminary list of the Ishango fishes (published in DE HEINZELIN, 1955) two species of *Synodontis*, *S. nigrita* and *S. schall*, were given. Further study of the fossils showed, however, that the specimens previously identified as *S. nigrita* should be referred to *S. frontosus*.

Specimens of *Lates* from the N.F.PR. Ishango deposits are provisionally refered to *L. niloticus* since no clear-cut differences are manifest in the skeletons of the various species or sub-species in the extant *L. niloticus* complex.

No specific identity can be given to the *Tilapia* remains, which are peculiar in that the majority of specimens is of the first anal pterygiophore; other skeletal parts are less well represented, especially in comparison with other species. No immediate explanation can be provided for this biased sample of *Tilapia*.

The Ishango fishes do not yield any information on the ecological conditions obtaining at the time of their preservation. Furthermore, since the N.F.PR. (Epi-Pleistocene) deposit is probably a sub-aquatic kitchen-midden and the Z.POST-EM. (Holocene) deposit a subaerial kitchen-midden, the assemblage of species may be artificial; that is, either representative of species which were caught by man, or, of species which were attracted to the area by domestic refuse thrown into the water.

Before considering the critical phase during which the Edward fish-fauna underwent alterations leading to its present truncated and impoverished form, it is necessary to examine the fishes preserved in the most recent deposit (Site X), which is Mesolithic and of Holocene age. Unfortunately, most of these specimens can only be identified as far as the genus. But, amongst the genera preserved are *Lates* and *Synodontis*, two Nilotic genera which have since become extinct in the area. The other genera occur in present-day Lake Edward. The *Lates* specimens are more heavily mineralized than are the other specimens from this deposit and may therefore be derived from an earlier (Epi-Pleistocene ?) deposit. The *Synodontis* remains, on the other hand, are only lightly mineralized and compare closely with the other fish remains from the Holocene beds. It is therefore difficult to interpret the significance of the specimens. Two explanations seem possible : first, a few populations of *Synodontis* survived the critical phase but were unable to maintain themselves, possibly through changed ecological conditions affecting breeding habits, or, secondly, the fossil bones were derived from fishes caught below the Semliki falls and brought back to the settlement at Ishango. Neither explanation is entirely satisfactory and the question of their provenance should remain open.

Thus, from the fossil fishes alone it is impossible to date the changes which took place in the fundamental relationships of the fish-fauna of Lake Edward. Other evidence of environmental changes occurring in Epi-Pleistocene and early Holocene times (DE HEINZELIN, 1955) suggests, however, that the ichthyofaunal hiatus could have been contemporaneous.

Since the present affinities of Lake Edward fishes are both Nilotic and Victorian, there are two important questions relating to this hiatus : first, what environmental factors can be implicated; and secondly, why did certain Nilotic species survive whilst others were killed off ?

A probable answer to the first question is provided by DE HEINZELIN's opinion that volcanicity, coupled with changes in the chemical composition of the water, was the major factor influencing faunal changes. Indeed, it seems that during this period of intense and local volcanic activity (DE HEINZELIN, 1955), Lake Edward could have undergone hydrological changes leading to conditions comparable with those of present-day Lake Kivu. That is, the lower water-strata would become heavily charged with dissolved toxic substances (hydrogen-sulphide, carbonic acid and ammoniacal salts) and would be azooic at all times. Because Lake Edward is relatively shallow and occupies a basin of different shape to that of Kivu, even the surface waters could be polluted during intervals of water-mixing and overturn. Present-day Lake Edward differs from Kivu where no overturn and mixing of surface and bottom waters occurs.

That Lake Edward did not remain in a Kivu-like condition was probably due to three major factors : a different sub-aquatic topography; the existence of large affluent streams flowing into the lake through country distant from the centres of volcanic activity, and thirdly, hydrographical conditions allowing for periodic mixing of the epi- and hypolimnia, thereby preventing the formation of a permanent, dense lower layer.

If such postulated conditions of foul water did obtain, even for a relatively short period, it is not surprising that many species suffered local extinction. It is, in fact, rather more difficult to understand how so many species survived. Presumably for these species survival was the result either of their temporarily colonizing affluent rivers and the areas adjoining river mouths (where some freshening of the water might be expected), or, of the inherent ability of the species to tolerate the hydrological conditions then existing. A possible factor influencing the decline and ultimate extinction of these species might be the loss of suitable breeding grounds through changes in the ecology of the lake. Consideration of this and other ecological conditions affecting late Pleistocene and early Holocene fishes leads directly to the second question posed above.

Speculation is hampered by the lack of fundamental information on the physiological requirements and breeding habits of many of the species concerned. Some data are available on the respiratory characteristics of *Lates* (FISH, 1956). These suggest that the species is intolerant of reduced oxygen and increased carbon dioxide tensions. It is therefore reasonable to infer that breeding would be unsuccessful (if it occurred at all) under such conditions. Regrettably, nothing is known about the physiology of members of the *Characidae* and *Schilbediae*, or of the majority of *Cichlidae* and *Cyprinidae*. In Lake Edward the latter family provides an intriguing puzzle. Two species of *Barbus* coexisted in Lake Edward during the upper Pleistocene. One species closely resembled the Nilotic *B. bynni*, the other resembled *B. altianalis*, a species occurring in Lakes Edward, Victoria and Kivu. Only *B. altianalis* survived the critical Epi-Pleistocene and early Holocene periods.

Indirect evidence on the physiological adaptability and tolerance of these various families can be derived from Lake Kivu. The fish-fauna of this lake is even poorer than that of Lake Edward, from which source it was derived (POLL, 1939), probably at some time after the invasion of Edward by certain Victoria species. The point of particular significance is that all the absentee families of Lake Edward are also absent from Lake Kivu. Since volcanicity played an important part in the evolution of both lakes (Lake Kivu was formed during the middle, or, late Pleistocene by the Mfumbiro volcanic chain damming the valley of a river flowing into Lake Edward) the conclusion seems inescapable that representatives of these families were unable to surmount the ecological and hydrological conditions associated with volcanicity. The more extreme hydrological conditions of

Lake Kivu may also account for the absence of *Bagridae* and *Mormyridae* from the lake. It is difficult to explain the absence of *Lepidosirenidae*, *Cyprinodontidae* and *Anabantidae* on the grounds of adverse ecological conditions since in other lakes all three families tolerate deoxygenated and stagnant water. But here again, factors connected with breeding may have been ultimately responsible for the local extinction of these families.

In conclusion, the faunal affinities of Lake Edward must be reconsidered, particularly in view of the recent classification proposed by WORTHINGTON (1954). Data from the extensive fossil collections reviewed above show clearly that for a considerable period the fish-fauna of Lake Albert was broadly comparable with that of Lake Albert. The correspondence is not exact, because certain Albertine genera apparently never populated the Edward basin. The evolution of the present Edward fauna has been brought about by two principal factors : first, the effects of extreme environmental conditions which further reduced the number of Albertine species, and secondly, the invasion of Lake Edward by certain species of fishes from Lake Victoria. Although the results of this invasion are impressive, they are virtually restricted to one genus, *Haplochromis*, and must not be allowed to obscure the historical background. Lake Edward had a Nilotic fish fauna throughout the Pleistocene period, and the fauna is still essentially Nilotic despite its truncated and impoverished species list.

This conclusion is not in accordance with WORTHINGTON's classification, in which he allies the Victoria and Edward faunal types as distinct from the Nilotic. However, the palaeontological evidence, as well as the relationships of the present-day fishes (excepting *Haplochromis*), both emphasise the Nilotic affinities of Lake Edward.

There remains one other much debated point on which the fossils throw some light. This concerns the thesis that certain predatory fishes, particularly *Lates* and *Hydrocyon*, have had an inhibiting effect on speciation and adaptive radiation amongst the smaller cichlids in lakes where these species occur together (*vide* WORTHINGTON, 1940; also MAYR, 1952, for criticism).

WORTHINGTON's ideas were apparently supported by the adaptively multiradiate *Haplochromis* species flocks of Lakes Edward and Victoria, lakes in which *Lates* had not been present for some considerable time (WORTHINGTON, 1940, and 1954). However, it is now known that *Lates* inhabited the Lake Edward basin until as recently as the early Holocene. This is turn implies that the ancestral *Haplochromis* species, or, small species flock, coexisted with *Lates* (see above, p. 71). Yet, this species flock, although smaller than that of Lake Victoria, is one cited by WORTHINGTON as an example of speciation unretarded by the influence of large predatory species.

At first sight this observation seems to tell against WORTHINGTON's general views on the overall retarding influence of *Lates* on adaptive

Period		Site	*Lepidosirenidae*	*Characidae*	*Cyprinidae*
HOLOCENE		Ishango; Z.POST-EM. Mesolithic (Site X *a*+X *b*+X *c*)	*Protopterus* sp.	—	*Barbus* sp.
EPI-PLEISTOCENE		Ishango; N.F.PR. Main fossiliferous level (Site IX)	*Protopterus* cf. *aethiopicus*	—	*Barbus* cf. *bynni* *Barbus* cf. *altianalis*
		Ishango; G.INF. Lower gravels (Site VIII *b*+VIII *c*)	*Protopterus* cf. *aethiopicus*	—	—
MIDDLE-PLEISTOCENE		27-30 m	—	—	—
		Katanda amont 23 m (Site VI+VII)	—	—	*Barbus* sp.
LOWER PLEISTOCENE	THIRD KAISO LEVEL	Kasaka-Senga (Site IV+V)	—	—	—
		Between Ishango and Kanyatsi (Site V *a*)	—	*Hydrocyon* sp.	—
		Katanda aval (Site III)	—	—	—
	FIRST KAISO LEVEL	Kanyatsi (Site I+II)	*Protopterus* sp.	*Hydrocyon* sp.	—

Clariidae	*Mochocidae*	*Bagridae*	*Centropomidae*	*Cichlidae*
Clarias sp.	*Synodontis* cf. *frontosus*	*Bagrus* sp.	*Lates* sp.	*Tilapia* sp.
? *Heterobranchus* *Clarias lazera* *Clarias mossambicus*	*Synodontis* cf. *schall* *Synodontis* cf. *frontosus*	—	*Lates* cf. *niloticus*	*Tilapia* sp.
Clarias cf. *lazera* *Clarias* cf. *mossambicus*	*Synodontis* cf. *frontosus*	*Clarotes* sp.	*Lates* sp.	*Tilapia* sp.
—	*Synodontis* sp.	—	*Lates* sp.	—
Clarias sp.	*Synodontis* sp.	? *Clarotes* sp.	—	—
—	*Synodontis* sp.	? *Auchenoglanis* sp. (*Bagrus*, very dubious)	*Lates* sp.	—
—	—	—	*Lates* sp.	—
—	—	*Clarotes* sp. (*Bagrus*, very dubious)	—	—
Clarias sp.	*Synodontis* sp.	*Clarotes* sp. *Bagrus* sp. *Auchenoglanis* sp.	*Lates* cf. *niloticus*	(*Tilapia* sp., very dubious)

speciation. However, WORTHINGTON's conclusions were based on the assumption that *Lates* would eliminate those forms which passed through stages of imperfect adaptation in the course of evolution, and particularly those species attempting to colonize new adaptive niches. As the Lake Edward *Haplochromis* flock was apparently derived from an already multiradiate group in Lake Victoria, many invading species would be prospectively adapted to particular niches and might therefore be less affected by the presence of *Lates*.

Recent field studies on some of the African species flocks (FRYER and ILES, 1955; GREENWOOD, unpublished) show that WORTHINGTON underestimated the effect that other predatory species (for example, *Clarias*, *Bagrus* and *Barilius*) could have had on the development of cichlid species flocks. Since these other predators are associated with the flocks whose multiplicity of species was attributed to the absence of *Lates*, it is unlikely that predation did have such far-reaching inhibitory effects as WORTHINGTON postulated. Likewise, the demonstrated occurrence of *Lates* in the late Pleistocene Lake Edward, and its presumed coexistence with a developing *Haplochromis* species flock, helps to place the evolutionary significance of *Lates* in a truer perspective. *Lates* can only be considered as one of the many environmental factors which moulded the remarkable species flock of Lake Edward.

EAST AFRICAN FISHERIES RESEARCH ORGANIZATION.
DEPARTMENT OF ZOOLOGY,
BRITISH MUSEUM (NATURAL HISTORY),
LONDON.

BIBLIOGRAPHY.

ARAMBOURG, C., 1947, Mission Scientifique de l'Omo 1932-1933, t. I, fasc. 3 (Paris, éd. du Muséum, 57, rue Cuvier).

BEAUCHAMP, R. S. A., 1946, Lake Tanganyika (*Nature*, vol. CLVII, p. 193).

BROOKS, J. L., 1950, Speciation in ancient lakes (*Quart. Rev. Biol.*, XXV, pp. 31-176).

DE HEINZELIN, J., 1955, Le fossé tectonique sous le parallèle d'Ishango [*Inst. des Parcs Nationaux du Congo Belge*, Explor. du Parc Nat. Albert, Mission J. DE HEINZELIN DE BRAUCOURT (1950), fasc. 1].

FISH, G. R., 1956, Some aspects of the respiration of six species of fish from Uganda (*Journ. Exp. Biol.*, vol. XXXIII, pp. 186-195).

FRYER, G. and ILES, T. D., 1955, Predation pressure and evolution in Lake Nyasa (*Nature*, vol. CLXXVI, p. 407).

FUCHS, V. E., 1934, The geological work of the Cambridge Expedition to the East African lakes, 1930-1931 (*Geol. Mag.*, vol. LXXI, pp. 97-112, 145-166, pl. V, VI).

— 1936, Extinct Pleistocene molluscs from Lake Edward, Uganda, and their bearing on the Tanganyika problem (*J. Linn. Soc. London*, vol. XL, pp. 93-106, pl. I-III).

GREENWOOD, P. H., 1951 A, Evolution of the African cichlid fishes: the *Haplochromis* species-flock in Lake Victoria (*Nature*, vol. CLXVII, pp. 19-20).

— 1951 B, Fish remains from Miocene deposits of Rusinga island and Kavirondo Province, Kenya [*Ann. Mag. Nat. Hist.*, (12), vol. IV, pp. 1192-1201, pl. XXI].

HULOT, A., 1956, Aperçu sur la question de la pêche industrielle aux lacs Kivu, Edouard et Albert (*Bull. Agric. Congo Belge*, vol. XLVII).

MAYR, E., 1942, Systematics and the origin of Species (Columbia).

MORTELMANS, G., 1950, Le Quaternaire de l'Afrique sud-équatoriale. Essai de corrélation (*III^{e} Congrès Nat. des Sciences*, Bruxelles, 1950).

O'BRIEN, T. P., 1939, Prehistory of Uganda Protectorate (Cambridge).

POLL, M., 1939, Poissons [*Inst. des Parcs Nationaux du Congo Belge*, Explor. du Parc Nat. Albert, Mission G. F. DE WITTE (1933-1935), fasc. 24].

POLL, M. and DAMAS, H., 1939, Poissons [*Ibid.*, Explor. du Parc Nat. Albert, Mission H. DAMAS (1935-1936), fasc. 6].

SOLOMON, J. D., 1939, in: *Prehistory of Uganda Protectorate* (see O'BRIEN).

TREWAVAS, E., 1933, Scientific results of the Cambridge Expedition to the East African lakes, 1930-1931. II: The cichlid fishes [*J. Linn. Soc. (Zool.)*, vol. XXXVIII, pp. 309-341].

— 1937, Fossil cichlid fishes of Dr. L. S. B. LEAKEY's Expedition to Kenya in 1934-1935 [*Ann. Mag. Nat. Hist.*, (10), vol. XIX, p. 381].

WAYLAND, E. J., 1931, Summary Progress Geol. Survey Uganda (Entebbe).

— 1934, Rifts, rivers, rains and early man in Uganda (*Journ. Roy. Anthrop. Inst.*, vol. LXIV, pp. 333-352, pls).

WAYLAND, E. J. and OTHERS, 1926, The Geology and palaeontology of the Kaiso Bone Beds (*Geol. Survey of Uganda*, pp. 1-71).

WHITE, E. I. and OTHERS, 1926, The Geology and palaeontology of the Kaiso Bone Beds (*Ibid.*, pp. 49-51).

WORTHINTGON, E. B., 1932, The lakes of Kenya and Uganda (*Geogr. Journ.*, vol. LXXIX, pp. 278-297, pl.).

— 1937, On the evolution of fish in the great lakes of Africa (*Inst. Rev. Hydrobiol. Leipzig*, vol. XXXV, pp. 304-317, map.).

— 1940, Geographical differentiation in fresh waters with special reference to fish, in : *The New Systematics*, pp. 287-302, Oxford.

— 1954, Fresh water organisms (*Proc. Linn. Soc. London*, vol. 165, Pt. I, pp. 68-74).