THE EVOLUTION OF SPECIES IN THE LAKES OF EAST AFRICA

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THOUGH separated by less than two thousand miles from the Mediterranean, Tropical Africa was less known to European scientists up to the end of the last century than the much more distant tropics of the Americas and the Far East. Though some of the explorers were scientists, notably Emin Pasha and Joseph Thompson, the great expeditions in the mid-19th Century were not primarily scientific and Tropical Africa contributed rather little to Science until the end of the century. The first truly scientific expedition in East Africa was conducted by the geologist J. W. Gregory in 1893. By contrast Tropical America, Asia and Australasia had been the scene of scientific investigations since the 18th Century, and geology and biological sciences owe much to the tropical experiences of such men as Joseph Banks, A. von Humboldt, F. Müller, H. W. Bates, A. R. Wallace and Charles Darwin. The most important consequence of their work was the final acceptance of the concept of Organic Evolution after the middle of the last century, and it is doubtful whether this could have been achieved without inspiration and evidence from the study of tropical life.

It is therefore interesting to consider what, in the light of subsequent geological and biological research, East Africa can show in the way of striking demonstrations of the evolutionary process. Apart from the mesozoic dinosaurs in Tanganyika (Parkinson, 1930), fossil evidence for the history of life in East Africa mainly relates to geologically recent times from the Miocene onwards (the past 20 million years or so). This restriction is due not to the lack of sedimentary rocks of greater age, but to the fact that the attention of palaeontologists in this country has been so far focused upon and around the history of mammals and early man, mostly inspired by the work of E. J. Wayland in Uganda and L. S. B. Leakey in Kenya and Tanganyika.

The process of Evolution can also be studied in the present fauna and flora of East Africa, and there are certain situations in which conditions are, or have recently been, particularly favourable for "speciation", that is, which provide the stimulus for organisms to diverge into new species. A fundamental feature of living organisms is their ability to reproduce, but the copies they make, though tolerably accurate, are by no means exact. There is in fact a special mechanism which ensures a certain degree of inexactitude. In other words organisms vary continuously in structure and physiology and are therefore liable and can, given time and the action of natural selection, become adapted to almost all environments within the limits of tolerance of living matter. In this way through the course of geological ages, life has managed to occupy almost every conceivable "niche" on this earth and, as would be expected, the variety of species in any area is a reflection of the variety of environments or niches to which they are adapted.

We must therefore expect that, in a region in which conditions remain rather uniform, something like equilibrium might be reached, but that if great changes were to occur to alter the range of habitats available to life then appropriate varieties would be selected from the local fauna and flora and new species would ultimately appear. If such changes, due perhaps to climatic or tectonic events (earth movements), not only produced new environments but happened in such a manner that some members of a species became isolated in a restricted area and unable to meet and interbreed with the rest of the population from which they were derived, then we should expect to find some species which are "endemic", that is which are entirely confined to that area. It would also follow that the longer the period of isolation and the more effective the barrier to dispersal, the more the local species would diverge from the original population. In extreme cases endemic genera or even endemic families might evolve and be confined to a relatively small region. Speciation is complete when the divergence of two or more sections of a population involves the reproductive system and thus prevents interbreeding, so that they remain distinct and may continue to diverge if circumstances should bring them together again. The initial conditions for divergence are not however provided only by obvious and impenetrable barriers such as mountain ranges, oceans, deserts, etc.; even an apparently uniform habitat such as a forest or lake can be differentiated into a number of distinct and discontinuous small habitats which may tend to separate sections of a species. If initial divergence involves a change in habits or behaviour the isolation necessary for speciation could occur without geographical barriers. Nevertheless geographical isolation has clearly been of extreme importance and its striking effects on the fauna of certain oceanic islands, especially the Galapagos, impressed Darwin very greatly as clear evidence of the evolutionary process. The phenomenon is however observable on a much larger scale in the divergence of the faunas and floras of continents. Australia in particular has been the scene of a great outburst of local and isolated evolution.

The events which produced the great lakes and present watercourses of East Africa provided a powerful stimulus to the evolution of certain groups of aquatic animals, notably the fish, molluscs and crustacea. That these groups have been affected more than others (e.g. the more drought-resisting aquatic insects) can presumably be attributed to their inability to cross the physical barriers separating the patches of water in which they have been isolated. Geological and palaeontological studies are beginning to make possible a better understanding of the present fauna in the light of events in the recent past, and advances in genetics, ecology and in the study of behaviour have increased our understanding of the process of speciation in such situations.

This subject is now very extensive and it would be impossible in this article to give more than a very superficial review, or to refer to more than some key points in the literature, but enough is now known for an outline to be given of a fascinating story whose details will no doubt be modified in the light of further evidence. Discussions of general problems relating to speciation in the lakes of East Africa are to be found amongst others in the works of Worthington (1937, 1940 and 1954); Trewavas (1948), Brooks (1950), Poll (1950), Greenwood (1951 and 1959) and Fryer (1960).

Evidence suggests that during the Miocene (some 20 million years ago) there was a ridge of high land or range of hills running north and south along a line in the region of the present eastern shore of Lake Victoria. This was a watershed from which rivers flowed westwards into the Atlantic and eastward, by shorter and more precipitous routes, to the Indian Ocean. The Nile Valley existed and perhaps originated during this period (Butzer, 1959, quoted by Monod). There was also a lake or group of lakes associated with these watercourses which included the region of the present Kavirondo gulf of Lake Victoria. The Miocene beds investigated by Dr. Leakey on Rusinga Island showed that this lake contained the Nile Perch (*Lates*) and *Polypterus*, which are not living in the present Lake Victoria, but, along with a number of other characteristic "nilotic" fish, are found widespread over Tropical Africa in the Nile and associated waters, the Congo, the Niger and Lake Chad (Greenwood, 1951). We have in fact good reason to conclude that during the Miocene the major tropical African rivers, at least those draining to the west and north, supported a more or less uniform fauna characterised by certain genera of fish whose relatively unchanged descendants are still to be found in the Nile and the larger rivers west of the Western Rift. This ancient fauna and its modern representatives will be styled "nilotic" in this article. Some characteristic genera of nilotic fish are *Lates* (Nile Perch), *Hydrocyon* (Tiger Fish), *Polypterus* (Bichir), *Distochodus* and *Citharinus*.

Though faulting along the lines of the future Rifts can be traced back to much earlier geological times (Dixey, 1956), it was after the Miocene that this apparently normal type of drainage system was completely disrupted by the gigantic earth movements which, with the associated volcanic activity, ultimately produced the great lake basins within the Rift Valleys and the large shallow depressions between them holding the water of Lake Victoria. The upper reaches of the Miocene rivers were therefore dislocated, but sections of them have survived as inlets or outlets to the lakes. Some, for example the Kafu and Katonga, have had their flow reversed. A hydrological map of East Africa (Fig. 1, inside back cover) shows some very peculiar and indeed fantastic features. Since their geologically recent formation the Great Lakes have suffered many and sometimes drastic changes, and their volume, salinity and interconnections have changed from time to time. Earth movements and volcanic action, together with considerable fluctuations in rainfall, have been responsible for this, though it is difficult in a particular case to decide on the relative importance of tectonic and climatic factors.

These events have provided very favourable conditions for the evolutionary divergence of aquatic animals. Not only have a great variety of new habitats appeared giving opportunities for new adaptations but certain lakes and river systems have been isolated from the rest to varying degrees and for different lengths of time. The degree of divergence of the fauna is often clearly related to these factors.

It is also apparent that certain groups of fish have diverged, at least in recent times, more rapidly than others. The cichlids, and in particular *Haplochromis* (the Nkeje of Lake Victoria) and related genera have evolved at an explosive rate producing a great array of endemic species in certain lakes. The genus *Lates* (Nile Perch) has produced relatively much fewer endemic forms and *Protopterus* (the Lung Fish) is represented in the majority of the waters of East Africa by the single species *aethiopicus*.

It is of great interest to find that the conclusion reached on geological evidence that the lake faunas were derived from those of the pre-existing rivers is supported from ecological studies on the present-day fish. There are signs of a progressive adaptation from a fluviatile to a lacustrine life, an intermediate condition involving for instance feeding in the lake but returning to the rivers to breed. The cichlids have advanced furthest along this course and the fauna of Lake Tanganyika has in general become more fully adapted to lacustrine conditions than that of the much younger Lake Victoria (discussion in Corbet, 1961 p. 86).

It will be necessary now to consider each of the main lakes in turn and we shall start with Lake Nyasa in the extreme south of the Rift Valley system. This is unique among the Great Lakes in draining via the Shiré and Zambezi rivers into the Indian Ocean. On geological and palaeontological evidence the origin of the present lake was estimated by Dixey (1941) as mid-Pleistocene. The evidence is not very good but the lake is unlikely to be more than two million years old (Fryer, 1959 p. 265), and is therefore younger than Lake Tanganyika.

It is perhaps to its recent origin as well as to the eastwardly directed drainage that some of the peculiarities of its fauna may be attributed, though more fossil evidence is needed to confirm this. The main affinities of the fauna are with that of the Zambezi to which the lake is connected by the Shiré River. The Murchison Rapids are now however an effective barrier and the lake fauna has diverged considerably (Worthington, 1933). A striking feature is the absence of all the characteristic genera of nilotic fish listed on p. 46, though there is no doubt that the huge expanse of open and deep water (25,000 square miles, maximum depth 706 metres) is a very suitable environment for them and that they would certainly be there if the lake had been effectively connected in the past, as was Lake Tanganyika, with the Congo basin. The number of families of fish is thus less than in Lake Tanganyika but there has been a remarkable outburst of evolutionary divergence particularly on the part of the cichlids. When the review by Brooks was published (1950) 223 species of fish had been recorded of which 196 are endemic to Lake Nyasa. Even more remarkable is the fact that 174 of these endemic species are cichlids, which include as many as 20 endemic genera. Apart from the great variability of the cichlids, particularly with respect to breeding and feeding habits, this extraordinary production of new species is certainly associated with the fragmentation of the major habitats in the lake. The shore-line for instance is largely cut up into alternate rocky and sandy sections so that the inshore fauna of either of these habitats is separated into effectively disconnected units which do not interbreed (Fryer, 1959). Worthington (1954) suggested that the evolution of the Nyasan cichlids and those of Lake Victoria (*see* below) has been assisted by the absence of the nilotic predator fish *Lates* and *Hydrocyon* which would feed voraciously upon them. This view has been contested by others on the grounds that both these lakes have their own predator fish, e.g. species of *Bagrus, Clarias* and *Barbus*, which, it is contended, would feed upon the cichlids as effectively as the Nile Perch and Tigerfish (Fryer and Iles, 1955).*

The fauna of Lake Tanganyika is now well known to all zoologists as one of the supreme examples of speciation in a geographically isolated environment. It occupies the deepest part of the Western Rift and is itself more than 1,400 metres deep. It seems to have originated during the Pliocene (10 to 15 million years ago) as a double gash across a system of west-flowing rivers whose waters were captured by the lake. The swampy Malagarasy River draining in from the east and the Lukuga flowing out of the lake into the Congo Basin are two sections of one of these rivers. The volume of the outflow through the Lukuga River varies with the level of the lake and, since it was discovered by Burton and Speke in 1858, it has occasionally almost ceased to flow. There is little doubt that Lake Tanganyika was a closed basin for at least two and possibly as much as six million years (Brooks, 1950). During this time it certainly contracted and the water became more saline but, owing to its great depth, it never dried up nor ceased to be a great lake, though it may on occasion have become two lakes occupying the north and south basins.

The fauna has consequently had ample time to diverge in isolation from that of the original Miocene rivers from which it was derived. New conditions and habitats appeared which were not found in the rivers—large expanses of open and deep water and of shallow inshore water, absence of flow in one

* **A recent interesting publication by P.B.N. Jackson, (Proc. Zool. Soc. London, 136, 603–722. 1961), deals with the question of the influence of predators, especially *Lates* and *Hydrocyon*, on speciation of other fish in the African Lakes. More direct evidence than hitherto presented, mainly from the study of feeding habits, appears to support Worthington's contention that these voracious predators could well have had**

particular direction, and water of higher salinity. Another probably important change was that species of fish normally more or less separated in different regions of the rivers were more mixed together in the lake so that interspecific predation and competition became more intense. This variety of conditions in time and space as well as the long continued isolation of the lake would be expected to favour the evolution of new species (Poll, 1950).

The fish of Lake Tanganyika are descended mainly from those of the Miocene west-flowing rivers and thus the ancient nilotic genera are represented, most of which have produced new species and a few have evolved into new genera. Of a total of about 160 species of fish more than 125 are endemic and of these about 90 are cichlids. There are 42 endemic genera of which 34 are cichlids. A curious feature is the presence of two endemic genera and species of the herring family (*Clupeidae*) which is represented also in some rivers of the Congo but not in any of the other Rift Valley Lakes. They are very small fish and one of them, *Stolothrissa tanganyikae* ("Ndakala"), collects in vast numbers at night to feed on the microscopic organisms near the surface. There it is caught in hand nets with the help of lamps and provides an important item in the local diet. Another interesting vertebrate which has evolved in Lake Tanganyika is the Cobra *Boulangeria annulata stormsi*, which is completely aquatic and feeds on fish. It is occasionally attracted by fish already caught on lines and so taken by fishermen. (Poll, 1952.)

The effects of prolonged isolation are also to be seen among the invertebrates. There is even a sub-family of waterbug (*Idiocorinae*) endemic to Lake Tanganyika and a remarkable endemic caddisfly, *Limnoecetis tanganyikae*, which has lost its power of flight and skates over the surface of the open water like a pondskater and is attracted by the lamps of the Ndakala fishermen (Marlier, 1955). The Crustacea include a large number of endemic genera and species of crabs, prawns and of the microscopic groups (Copepods, Cladocera and Ostracods). The molluscs which are the best known, both snails and bivalves, have produced very many species and genera peculiar to the lake. The prosobranch snails are the most remarkable with about 65 endemic species. The peculiar shape of some of these with their spines and other protuberances, which resemble some well known marine snails, together with the presence of the medusa or "jelly-fish" *Limnocnida tanganyikae*, led to the suggestion that the lake had at one time been connected with the sea (Moore, 1903). This has however not been supported by subsequent geological and biological evidence (Cunnington, 1920, Capart, 1952). Another idea that such marine or "thalassoid" forms amongst the molluscs were induced by the high salinity of the water during dry periods in the Pleistocene is interesting but can hardly be taken seriously in the absence of experimental evidence.

The fauna of Lake Tanganyika is in fact one of the world's most striking examples of the evolutionary process working in isolation, comparable with the fauna of Lake Baikal in Siberia or with that of the more famous of the oceanic islands. It is to be hoped that the extraordinary beauty of form and colour of many of these unique animals will one day be enjoyed by more than a few experts.

Until geologically very recent times the highlands of Ruanda drained mainly to the north into the Lake Edward basin and so into the Nile. In the late Pleistocene (perhaps 100,000 years ago) came the great eruptions of the Bufumbiro volcanoes (Muhavura to Nyamlagira) which threw a barrage of lava across the Rift Valley, impounding this drainage to form Lake Kivu, which ultimately overflowed to the south down the cataracts at Bukavu to reach Lake Tanganyika

a greater restraining influence than *Bagrus* and *Clarias* on speciation in the Cichlids.

That the *Lates* of L. Tanganyika have not prevented a wealth of speciation in most of the other fish is understandable because they have learnt to feed mainly on the pelagic clupeids *Stolothrissa tanganyikae*, which is not found in the other lakes. Jackson regards the spawning migrations of certain fish from lakes into rivers as primas the Ruzizi River. It was this which probably put an end to the long and complete isolation of Lake Tanganyika by raising the level sufficiently to start the overflow by the Lukuga River, and was thus responsible for the recent invasion of the lake by a few species of fish from the Congo basin (Poll, 1950).

Lake Kivu is thus very young and, like Lake Bunyoni in Western Uganda, its beautiful fjord-like form is due to its origin as a flooded, branching, steep-sided mountain river valley, which previously drained to the north. The poverty of its indigenous fauna is no doubt partly due to the fact that, though the maximum depth is 478 metres (average about 200 metres) all the water below about 75 metres is stagnant, devoid of oxygen and charged with sulphuretted hydrogen, and is thus an impossible environment except for certain micro-organisms. The lack of vertical circulation of water, which this condition denotes, prevents the plant nutrients which accumulate below from reaching the surface, and only the shallow inshore waters can support a considerable fauna (Damas, 1937). It is probable also that some of the original fauna of the river was destroyed by volcanic action and what remains is poor both in total numbers of individuals and in number of species, only three families of fish being represented by the 32 species present.

Nevertheless, in spite of these disadvantages and of the shortness of time available since the lake was formed, the genus *Haplochromis* has evolved into 7 endemic species and the only *Tilapia* species, *nilotica,* is represented by an endemic subspecies. One fish (*Barilius moori*) has somehow managed to surmount Ruzizi rapids from Lake Tanganyika, but otherwise the fauna is, as would be expected from the past history of the lake, more closely related to that of Lake Edward (Poll, 1939 *a* and *b*).

The Lake Edward basin, now containing Lakes Edward and George connected by the Kazinga Channel, has had a complicated history, but recent discoveries have made possible a reconstruction of the main features of the story. Though the Lake George fishery is one of the most productive in Africa the number of genera and species of fish there and in Lake Edward is relatively small, and several families common in other large lakes are missing, including most of the characteristic nilotic forms. But the early Pleistocene "Kaiso" fossil beds in the Lake Albert and Lake Edward basins show that both lakes at that time had a similar nilotic fish and molluscan fauna. Fish such as *Lates* (Nile Perch) and *Hydrocyon* (Tigerfish) were common to both but now survive only in Lake Albert. The evidence suggests that an early Pleistocene connection between Lakes Edward and Albert was interrupted in the mid-Pleistocene and that at some later date the principal nilotic species in Lake Edward for some reason disappeared. At present the Semliki rapids are an effective barrier to further interchanges.

Another feature of the Lake Edward fauna which needs explanation is the presence of certain species of fish, in particular those of the genus *Haplochromis,* some of which are identical with Lake Victoria species and others which are endemic to Lake Edward but are clearly derived from Lake Victoria. This can best be explained on the available evidence as the result of a connection with Lake Victoria, perhaps via swampy watersheds into the Kagera and Katonga Valleys, during the middle Pleistocene (Greenwood, 1951 and 1959). Such a connection would presumably be possible only during a period of excessive rainfall, but earth movements may have played an important if not predominant part.

It was originally thought that the final disappearance of the main nilotic elements in the Lake Edward fauna was caused by the contraction of the lake during a dry period in the mid-Pleistocene (Worthington, 1932 and 1937). But

arily a means of protecting the young from being devoured by such predators and speculates that even in lakes from which these predators are now absent the habit may have originated before geological events had removed them.

some recent very important Belgian archaeological discoveries at Ishango near the exit of the Semliki from Lake Edward have shown that the Nile Perch, now extinct from Lake Edward, was being caught and eaten by mesolithic man less than 8,000 years ago (de Heinzelin, 1955). It is now considered likely that the very recent destruction of these and certain other species was due to the violent volcanic eruptions which have left the innumerable explosion craters around Katwe (Greenwood, 1959). It is possible that poisonous substances ejected from the volcanoes contaminated the water enough to destroy the more sensitive species, as had presumably happened earlier in Lake Kivu. It is at least certain that the extinction occurred during the volcanic period some 6–8,000 years ago, since the Ishango beds are immediately overlayed by layers of volcanic dust. Lake Edward was left with a not very varied fauna compounded of some nilotic, some Victorian and some endemic species which had evolved in the lake since the mid-Pleistocene. The very productive fishery of Lake George is based mainly on nilotic survivors such as *Tilapia nilotica* and *Bagrus docmac*.

The fauna of Lake Albert, of the Victoria Nile below the Murchison Falls and of the Albert Nile is, by definition, "nilotic" and is derived without very great change from the ancient Miocene freshwater fauna of Tropical Africa. Lake Albert is now in fact in open communication with the Nile and as a result there are relatively few endemic species of fish. A few however have been sufficiently restricted to certain habitats to have diverged to some extent from the parent stock. Thus two endemic subspecies of the Nile Perch have been described, *Lates niloticus albertianus* in inshore waters and *Lates niloticus macrophthalmus* in deep water (Worthington, 1940). The Kaiso fossil beds show that during the early Pleistocene, in addition to the nilotic fish still surviving, the fauna of Lake Albert included a number of species of molluscs, which also lived in Lake Edward at that time, but are now extinct (Wayland, 1934). The extinction of these species therefore remains to be explained and, whatever the cause—tectonic, volcanic or climatic, the most susceptible of the nilotic fish, such as the Nile Perch, are not likely to have survived. The lake must therefore have been recolonised from the Nile and some of the present fauna may be of considerably more recent origin than the lake itself.

Lake Rudolf on the Kenya–Ethiopian border is another of the Great Rift Valley Lakes whose fauna is predominantly nilotic. It is particularly interesting because it is now a completely closed basin, but from geological evidence it is clear that it flowed out to the north to join the Sobat River and the Nile more than once during the Pleistocene and for the last time quite recently, perhaps no more than a few thousand years ago (Fuchs, 1939). Whether earth movements or climatic change played the major part in finally breaking this connection is uncertain from present evidence. But there is no doubt that the rainfall in East Africa has fluctuated greatly during the Pleistocene (Pluvials and interpluvials of Wayland and Leakey) and recent palaeontological and archaeological research in the Sahara has confirmed this and shown that as late as neolithic times the climate, at least over large areas, was considerably more humid than at present (Monod). Since its discovery by Teleki and von Höhnel in 1888 the lake has on the whole been contracting and becoming more saline (Beadle, 1932). If this process continues much longer most of its present very rich fauna is doomed to destruction.

As would be expected from the similarity in history and structure of Lakes Rudolph and Albert their faunas are basically of the same type but the isolation of the former, though of short duration, has resulted in a greater divergence of species. There are about 12 endemic species of fish in Lake Rudolf compared with 4 in Lake Albert. In Lake Rudolf, as in Lake Albert, the Nile Perch has diverged into two subspecies (Worthington, 1932 b).

There remains Lake Victoria, the largest lake of all, which, unlike the others, is not situated in either Rift Valley, but in a shallow basin between them. In the Miocene, before the present lake came into existence there was as already mentioned, another rather large lake named Karunga by Wayland (1931) on at least part of the same site. This contained a nilotic fauna including *Lates* and *Polypterus* which together with the other characteristic nilotic fish listed on p. 46 are now absent from the lake (Greenwood, 1951 a). Towards the end of the Miocene it appears that the old lake dried up and most if not all its fauna was destroyed. The fauna of the present lake, though probably mainly nilotic in origin, has been sufficiently isolated to have produced 59 endemic species of cichlid fish of a total of 65 species including 4 endemic genera, and 28 of the 49 non-cichlid species are also endemic. The well known Lake Victoria ngege, *Tilapia esculenta* and *variabilis*, have evolved in the lake and, apart from Lake Kyoga, are found nowhere else.

The history of Lake Victoria is rather obscure, but from the geological evidence (Wayland, 1931 p. 40–44) and from studies by Greenwood (1951 b) on the *Haplochromis* species-flocks it can be concluded that very great fluctuations in amount and distribution of water in the basin occurred during the Pliocene and Pleistocene, and that both climatic and tectonic factors were involved. It is unlikely that the lake ever completely dried up during this period, but the evolution of the three main groups of *Haplochromis* species was probably associated with different types of habitat appearing at different times. The early stages of flooding of the basin in the late Pliocene produced disconnected swampy lake. Then came heavy rainfall and extensive deep water during the early Pleistocene when swampy connections were thereby established with Lake Edward and certain Victorian species reached that lake (*see* p. 49). A dry period in the middle Pleistocene cut this connection and once more reduced the lake to a smaller scale with perhaps isolated outlying swamps. Since then with less severe climatic fluctuations the present conditions developed. During the whole of this period since the Miocene the basin was sinking, and after the mid-Pleistocene more violent movements resulted in an up-tilting of the western edge of the basin, and the water of the lake was thus tipped over the brim to the north to flood an old branching river valley which became Lake Kioga, which then drained out to the northwest as the Victoria Nile over the Murchison Falls into the Western Rift and Lake Albert. This comparatively recent event did not establish a faunal connection with Lake Albert since the Murchison Falls have remained an effective barrier. The above rather fanciful history is not inconsistent with, and is in fact suggested by the geological and biological facts. The considerable amount of evolutionary progress made by the fauna of the post-Miocene waters in the Victoria basin was thus associated not only with isolation but also with great fluctuations in types of habitat, giving a succession of new opportunities for adaptation.

The recent introductions of the Nile Perch into Lake Kioga, a few of which have unaccountably appeared in Lake Victoria, of *Tilapia zillii* into Lake Victoria, and of both of these species into Lake Nabugabo, will no doubt have some extremely interesting effects on the ecology and on the further course of speciation. It is to be hoped that the economic consequences of these experiments will be beneficial.

Lake Nabugabo, a small shallow lake about three miles in diameter off the western shore of Lake Victoria, demonstrates in a remarkable way the effects of isolation on speciation. It was formed by a sand and gravel longshore bar across the mouth of a river behind which the water has been ponded (Bishop, 1958, Beadle and Lind, 1960, p. 90). A large swamp has formed through which the water seeps to the north into the Katonga Bay of Lake Victoria. The age of Lake Nabugabo has been estimated to be about 4,000 years. This has been done by radiocarbon dating of waved-rolled fragments of charcoal found in deposits of a former shoreline at Hippo Bay, Entebbe at about the same height above the present level of Lake Victoria as the sandbar which blocked the connection with Lake Nabugabo (personal communication from Dr. W. W. Bishop).

There are a number of species of fish in Lake Nabugabo which are identical with their relatives in the main lake, including *Tilapia esculenta* and *variabilis*. The genus *Haplochromis* however is represented by four species one of which is found in Lake Victoria, the remaining three being endemic to Lake Nabugabo. These three are each similar to a Victorian species from which each was presumably derived (Trewavas, 1933). Four species of *Haplochromis* from Lake Victoria have therefore managed to establish themselves in Lake Nabugabo and three of these have evolved into new species during the past four thousand years.

Lake Nabugabo thus demonstrates the process of speciation in a very much more restricted space than in the Great Lakes. I will conclude this survey by mentioning two even more remarkable examples of localised evolution of cichlid fish in East Africa. Some of the lakes in the Eastern Rift have been very much contracted by desiccation and the water has become extremely saline and alkaline, the soda being derived by leaching from the surrounding volcanic rocks and often carried to the surface and discharged as hot springs. Most aquatic animals, as would be expected, are incapable of living in such an extreme environment but two species of *Tilapia* have evolved which have managed to develop the necessary physiological devices needed to live in highly saline and alkaline water.

Lake Manyara in northern Tanganyika is one of the desiccated lakes which in the dry season becomes a salt-flat with a few streams flowing onto it. A total of eight species of fish have been recorded which in the dry season are mainly confined to the freshwater streams. One however, *Tilapia amphimelas*, is endemic to Lake Manyara and is capable of living both in fresh water and in water containing more than 5 per cent of salt which is mostly sodium carbonate and therefore extremely alkaline (Makerere Expedition, 1961).

A still more remarkable species of *Tilapia* has evolved in Lake Magadi, the well known commercially exploited soda lake in the Eastern Rift Valley in southern Kenya. The main bulk of the lake is saturated and is in fact largely solid soda, but at certain points there are hot springs continually discharging saline water into the lake. On the course of the streams which flow for a few yards from these springs into the lake there are shallow lagoons in which live large numbers of the endemic *Tilapia grahami* which are confined to a very small volume of water and are found nowhere else. They feed on the masses of blue-green algae which flourish in this water. There are thus a number of colonies normally isolated from each other. Occasionally however rainfall is sufficient to flood the lake and the colonies can join and interbreed and there is consequently no divergence among them (White, 1953, and M. Coe, personal communication).

The springs at the south end of Lake Magadi issue at 45°C and with a salinity of about 2 per cent, and the fish are found in the streams where the temperature has dropped to 42°C or lower. A higher temperature will in fact kill them. They can live in fresh water and at a much lower temperature but will not apparently breed in captivity at a temperature lower than about 32°C (unpublished observations of M. Coe and L. C. Beadle). This is an extraordinary example of the evolution of a species adapted to extreme conditions close to the limits possible for living organisms and in a very confined space. The origin of *Tilapia grahami* is in doubt, but 40 feet above the present lake level there are recent sediments laid down in obviously fresher water containing remains of a *Tilapia* species similar to but larger than *grahami* (White, 1953). Whether or not these were their ancestors, the *Tilapia grahami* of the saline hot-springs must have been derived from a species previously adapted to life in a large and freshwater Lake Magadi. They are certainly closely related to the *Tilapia amphimelas* of Lake Manyara and it is of great interest to record that a similar species has been found in the springs surrounding Lake Natron which is another soda lake in the Rift Valley between Lakes Magadi and Manyara. A comparative study of these three species and of their habitats would probably solve a number of interesting problems.

The great geological and climatic changes which have transformed the face of East Africa during the past 15–20 million years since the Miocene have thus provided a powerful stimulus for the evolution of aquatic animals, especially the fish. The East African Lakes are particularly suitable for the study of this process because of the great differences in types and variety of habitats, past history, duration and degree of isolation, and in the range of species available at the start. Even in the present inadequate state of our knowledge we can link the present situation with events in the recent geological past to a degree not often possible elsewhere. We have here a challenging field for research through the application of modern techniques in ecology, genetics, physiology and palaeontology which should throw more light on some very fundamental problems and provide the necessary scientific basis for conservation and useful exploitation.

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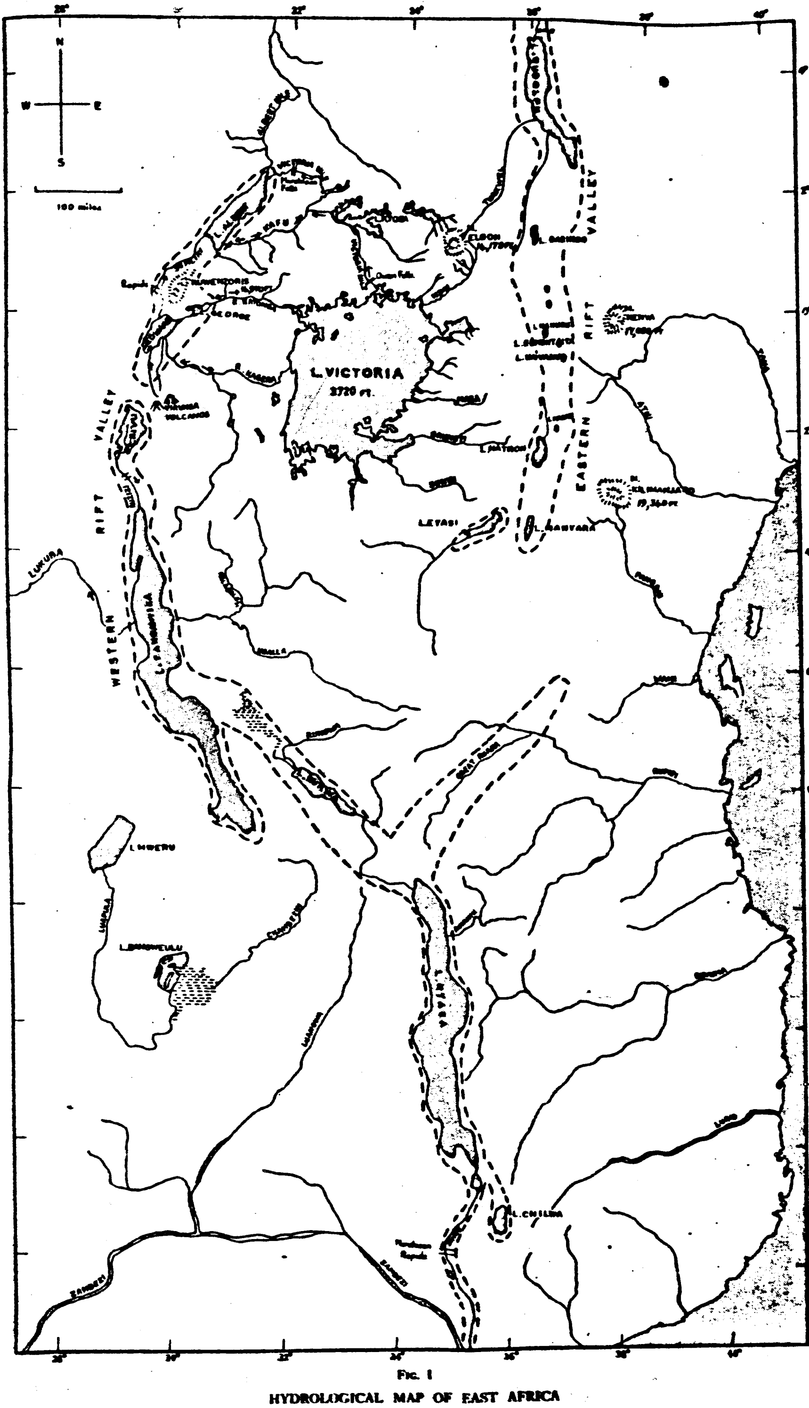

Fig. 1

HYDROLOGICAL MAP OF EAST AFRICA