THE FISHES OF UGANDA—I

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CHAPTER I

INTRODUCTION

THE fishes of Uganda have been subject to considerable study. Apart from many purely descriptive studies of the fishes themselves, three reports have been published which deal with the ecology of the lakes in relation to fish and fisheries (Worthington (1929a, 1932b); Graham (1929)). Much of the literature is scattered in various scientific journals, dating back to the early part of the century and is difficult to obtain in Uganda. The more recent reports also are out of print and virtually unobtainable. The purpose of this present survey is to bring together the results of these many researches and to present, in the light of recent unpublished information, an account of the taxonomy and biology of the many fish species which are to be found in the lakes and rivers of Uganda. Particular attention has been paid to the provision of keys, so that most of the fishes may be easily identified.

It is hardly necessary to emphasize that our knowledge of the East African freshwater fishes is still in an early and exploratory stage of development. Much that has been written is known to be over-generalized, as conclusions were inevitably drawn from few and scattered observations or specimens.

From the outset it must be stressed that the sections of this paper dealing with the classification and description of the fishes are in no sense a full taxonomic revision although many of the descriptions are based on larger samples than were previously available. No changes have been made in the nomenclature as at present accepted but, where personal observations indicate that changes may have to be made, notes to that effect are included.

Before describing the species of fish individually, some attempt must be made to view the East African ichthyofauna in geographical and historical perspective. Each of the five major lakes in Uganda contains numerous endemic fish species; that is to say, species which are found only within clearly circumscribed geographical limits. In a majority of cases the geographical unit is a single lake or lake basin. Not only is the number of these endemic species notable, but it is at once apparent that the lakes differ widely in the numbers of endemic species occurring within their boundaries. A further peculiarity is the absence from certain Uganda lakes of fishes which occur in many other parts of Africa. *Lates* spp. (Nile perch), *Hydrocyon* spp. (Tiger fish) and *Polypterus* spp. exemplify this chequered distribution. All three genera occur in Lake Albert and are widely distributed throughout tropical Africa (including Lakes Tanganyika and Rudolf), but are absent from Lakes Edward, George, Kyoga and Victoria. Further examples are provided by the genera *Mormyrops*, *Hyperopisus*, *Barilius*, *Auchenoglanis*, *Malapterurus*, *Heterobranchus*, *Distichodus* and *Citharinus* which are all widely distributed in Africa, but likewise missing from all the Uganda lakes except Lake Albert. The fishes of Lake Albert as compared with those of other Uganda lakes are outstandingly of genera widely distributed in Africa. Also fewer endemic species occur in Lake Albert than in the other lakes. There is, however, evidence of greater uniformity in earlier geological periods in the fish fauna of the area occupied by the modern lakes, at least as regards genera. For example, fossils from the lower Pleistocene (Kaiso) deposits on the shores of Lake Edward, show conclusively that the genera *Lates* and *Hydrocyon* were then present there; similar fossils also occur in Kaiso deposits on the shores of Lake Albert (Fuchs (1934); White (1926)). Going even further back in time, the fossil record shows that *Lates* and *Polypterus* lived during the Miocene in the area now occupied by Lake Victoria (Greenwood, 1951b).

The history of Uganda's lakes is intimately bound up with the earth movements which contributed to the formation of the Rift Valleys. Prior to their formation, Uganda was drained by a series of east-west flowing rivers which ultimately emptied into the Congo (Wayland, 1931). It was probably from these rivers that the present lakes were first populated. Little is known of the fishes which inhabited the rivers of that period.

Worthington (1954b) has suggested that the early history of the pre-rift, east-west flowing rivers was such that considerable interchange of fishes could have taken place across their more-or-less closely connected headwaters. Thus, it is not unreasonable to suppose that at first the lakes were populated by similar complexes of fishes. The basic similarity in the fish faunas of the Nile, Congo, and Niger, may be considered as evidence of contacts between these systems at an early period. It may also indicate that the fishes of the pre-rift river systems were fundamentally of the same complex, which may be geographically named, from its recent distribution, Nilotic. What few fossils have been found would seem to strengthen this argument (see above; also Greenwood (unpublished)).

The Pliocene and Pleistocene (together of about 11,000,000 years' duration) were critical phases in the development of the present-day lakes and the evolution of their fish faunas from the more widely distributed African species which first colonized them. In East Africa during this period there was considerable volcanic activity and earth movements were intense. These disturbances, together with phases of extreme rainfall and aridity, must have affected considerably the general topography, the sizes and the drainage systems of the lakes. Once spatial isolation had been effected by these agencies, the stage was set for the evolutionary processes which have led to the development of fish faunas peculiar to the several lakes and river systems.

The fishes of different lakes may be isolated by various natural barriers which efficiently prevent the interchange of species, even though the lakes may be interconnected. Predominant amongst these physical barriers are the Murchison Falls, which isolate the Lake Victoria fishes from those of Lake Albert and the Nile, and the Semliki Rapids which though less spectacular nevertheless separate the Lake Edward and the Albertine-Nilotic faunas. On the other hand, although the Ripon Falls do provide some degree of separation between Lakes Victoria and Kyoga, their efficiency is, or has been, less marked; there are only slight differences between the faunas of the two lakes (Tables I and II).

In Uganda's larger lakes, the majority of the endemic species belong to the

Cichlidae, a family which includes *Tilapia* and *Haplochromis*. This most interesting family has long attracted the attention of ichthyologists and students of evolution, and as a result there is a considerable body of literature dealing with the evolutionary aspects of the numerous cichlid 'species flocks' found in the different lakes. (For summaries see Worthington (1954a); Brooks (1950); Greenwood (1951a)). It will suffice to mention here that, from the viewpoint of specific predominance, Lakes Edward and George (with 20 endemic cichlid species) and Lakes Victoria and Kyoga (with 58 endemic cichlid species) can be classified as 'cichlid lakes'.

Faunal relationships of the fishes occurring in the larger Uganda lakes

Because of the excessive endemic speciation of the Cichlidae, faunal relationships can only be determined with certainty from the non-cichlid fishes and so discussion will first be confined to non-cichlid species.

Lake Albert. With only two exceptions, all the non-cichlid species (37) occurring in Lake Albert are found also in the Nile (Table II) and, although sixteen typically Nilotic genera are absent, there is a greater number of Nilotic genera in Lake Albert than in any other Uganda lake. Thus, if one compares the number of Nilotic genera and species in Lake Albert with the numbers present in the other lakes, it is apparent that the fish fauna of Lake Albert must be classified as Nilotic. As such, it has relationships with the faunas of Lakes Rudolf and Tana.

Lakes Victoria and Kyoga. In Lakes Victoria and Kyoga, there are slightly more endemic than non-endemic non-cichlid species (58 per cent endemism: Table II). Also, the number of typical Nilotic genera which are absent is almost twice the Lake Albert number. Of the twenty non-endemic species, eight are Nilotic and twelve East African in distribution. If percentage endemism is considered, together with the distinctiveness of endemic species, then the fishes of Lake Victoria constitute a faunal type, the Victorian. The ultimate derivation of these fishes in most probably Nilotic.

Lakes Edward and George. Worthington (1954b), on the basis of the affinities of endemic species, includes the fishes of Lake Edward in the Victorian category, but this relationship is only obvious when the Cichlidae are included. Non-cichlid species are not so readily classified. The percentage endemism of Lakes Edward and George (20 per cent) is low in relation to that of Victoria (58 per cent). Of the fifteen non-endemic species, eight are Nilotic but five of these eight Nilotic species do not occur in Lake Victoria. Divergence from the Nilotic assemblage of genera is indicated by the absence of four genera besides those which are absent also from Lake Victoria.

When the Cichlidae are considered, a somewhat different picture is obtained. The Lake Albert *Tilapia* species are with one exception Nilotic. The exceptional species, *T. leucosticta* Trewavas, occurs otherwise only in Lake Edward. In contrast, four of the five Lake Albert *Haplochromis* species are endemic, the fifth species having a fairly wide distribution in east and north Africa.

The cichlids of Lake Victoria are unique among those of Uganda lakes. Both species of *Tilapia* are endemic; fifty-eight endemic *Haplochromis* are known, and five of the six non-endemic *Haplochromis* have a relatively narrow range of distribution. In addition, there are four endemic genera allied to *Haplochromis*. This complex species flock undoubtedly deserves the status of a type fauna.

Most Lake Edward cichlids are related to Lake Victoria species. The *Tilapia* species, however, are found also in the Nile or in a single instance in Lake Albert. Although nineteen Lake Edward *Haplochromis* are considered endemic, their close affinity to similar species in Lake Victoria cannot be denied (Greenwood, 1951a). Furthermore, four *Haplochromis* species and one related genus occurring in Lake Edward are otherwise only known from Lake Victoria and the small Koki lakes. Thus, although the percentage endemism is high (71 per cent; Table II), the cichlid fauna does not warrant the separation of a Lake Edward faunal type.

Notes on the superficial anatomy of fishes

To avoid circumlocution in the keys and descriptions, it is desirable to give some notes on the superficial anatomy of fishes and the terms used.

Length. Two measures of length are used: First, total length—measured from the tip of the snout to the tip of the tail fin, and second, standard length—measured from the tip of the snout to the junction of the body and tail fin (Fig. 1). Standard length will be used exclusively in the description of genera and species.

Terms used to describe the general body form are self-explanatory.

Head. The posterior boundary of the head is formed by the bony operculum; this bone is the largest element in a series of four bones which together form the gill cover (Fig. 1). The head length is measured, with the mouth closed, from the tip of the snout to the posterior edge of the operculum, but excluding opercular spines if these are present.

In fishes, the jaws consist of a number of separate bones, *viz.* the paired premaxillae and maxillae in the upper jaw, and the paired dentaries in the lower jaw (mandible). In most of the fishes described below the premaxillae are the predominant elements in the upper jaw, the maxillae serving as levers for opening and protruding the mouth. When the mouth is shut, the premaxilla lies immediately below the upper lip, the maxilla lying above and at a slight angle to it. The greater part of the maxilla is covered by the pre-orbital bone, only its hindermost tip being visible.

Protractile and non-protractile jaws are recognized. The former term describes jaws which can be protruded and expanded away from their position at rest; non-protractile jaws are those which cannot be so protruded.

The premaxillae and dentaries carry teeth, except in the family Cyprinidae (Carps). The number and form of teeth show considerable variation within the various families.

The eye diameter is measured from the anterior to the posterior rim of the orbit. The inter-orbital width is the least distance between the upper orbital margins. Lying between the lower margin of the orbit and the maxilla is a flattened bone, the pre-orbital; the pre-orbital depth is measured from the orbit across the greatest depth of the bone (Fig. 1).

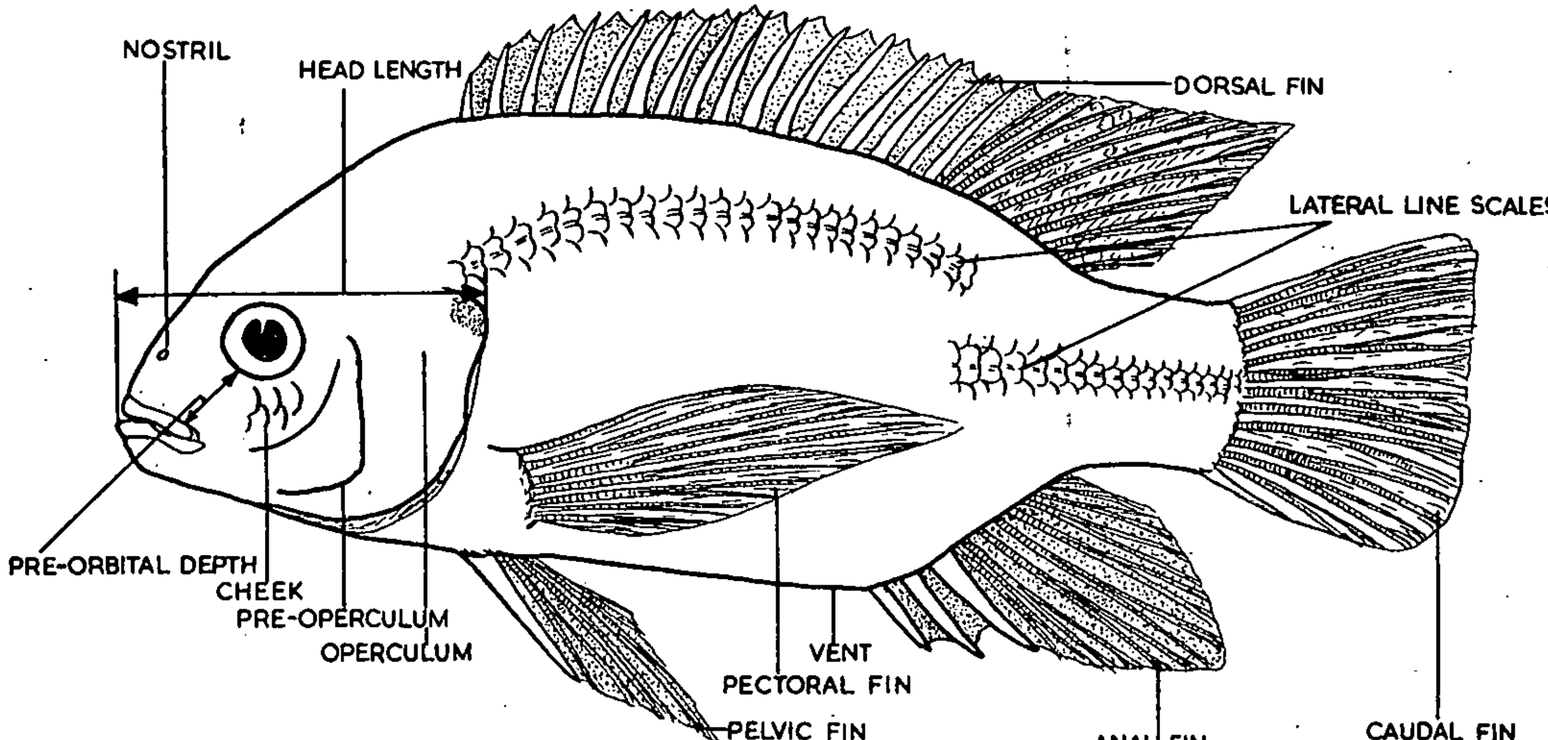

FIG. 1

Sketch showing the more important counts, measurements and characters used in the keys.

The nostrils appear as small openings lying in front of the eye and are an important character for distinguishing between the Percomorph families Cichlidae and Anabantidae. Unlike the nostrils in higher vertebrates, those of fishes do not open into the mouth, but lead into a blind sac containing the olfactory organs. An important exception is the lung-fish (*Protopterus aethiopicus* Heckel) in which there is a passage connecting the external nostrils and mouth.

The gills, carried on bony gill arches, lie in the posterior part of the 'throat' and can be examined by lifting the operculum. In most of the fishes described here, only the first four gill arches carry functional gills, the fifth arch being variously modified often bearing well developed teeth, the pharyngeal teeth.

Gill rakers sometimes afford important characters for distinguishing closely related species. The rakers are small bony projections on the anterior part of each gill arch. Inter-digitation between the gill rakers of adjacent arches provides a sieve-like mechanism which serves the double function of retaining food and protecting the delicate gill filaments from coarse objects passing out with the exhalent respiratory current. When counting gill rakers, only those lying below the angle between the upper and lower parts of the first arch are included.

Fins. Fins may be paired (the lateral pectoral and the ventral pelvic fins), or unpaired (the vertical, dorsal, anal and caudal fins). Structurally, a fin consists of a membrane supported by a number of rays, which can be either simple and spinous, or branched and soft. When describing fins, the number of rays is expressed as a formula, in which roman numerals denote spines, and arabic figures the number of rays. Thus, 'dorsal fin XVI, 8' means that the fin has sixteen spines followed by eight soft, branched, rays.

The positions of the paired fins, particularly the pelvics, afford important key characters. When the pelvic fins are situated between the pectoral and anal fins, they are described as being abdominal in position. Pelvic fins are said to be thoracic in position when situated immediately below the pectoral fins. The position of the pelvic fins reflects an underlying skeletal difference; the pelvic girdle is attached to the pectoral girdle in fishes with 'thoracic' fins, but is well separated from the pectoral girdle in those fish with 'abdominal' fins. The terms used to describe the shape of the caudal fin are self-explanatory.

Special mention must be made of the fins in the Lepidosirenidae and Polypteridae. In the former, supporting rays are not visible externally, so that the fins appear to be without rays. The paired fins in this family are unique amongst living fishes, being composed of a central, articulated axis which is flanked, at least in the pectoral fin, by short rays borne on one margin; consequently, the external form is that of an elongate and narrow filament with a variably developed membrane along one margin. The dorsal fin of the Polypteridae is distinctive; it is in the form of several separate, flag-like, finlets each composed of a spine with several small rays attached near its dorsal tip (Fig. 2). The pectoral fins of *Polypterus* show several anatomical peculiarities which need not be described, except to note the well-defined, arm-like peduncle connecting the membranous fin to the body.

An adipose dorsal fin, present in the families Characidae, Citharinidae, and in certain cat-fishes, has the general appearance of a fin but, with very few

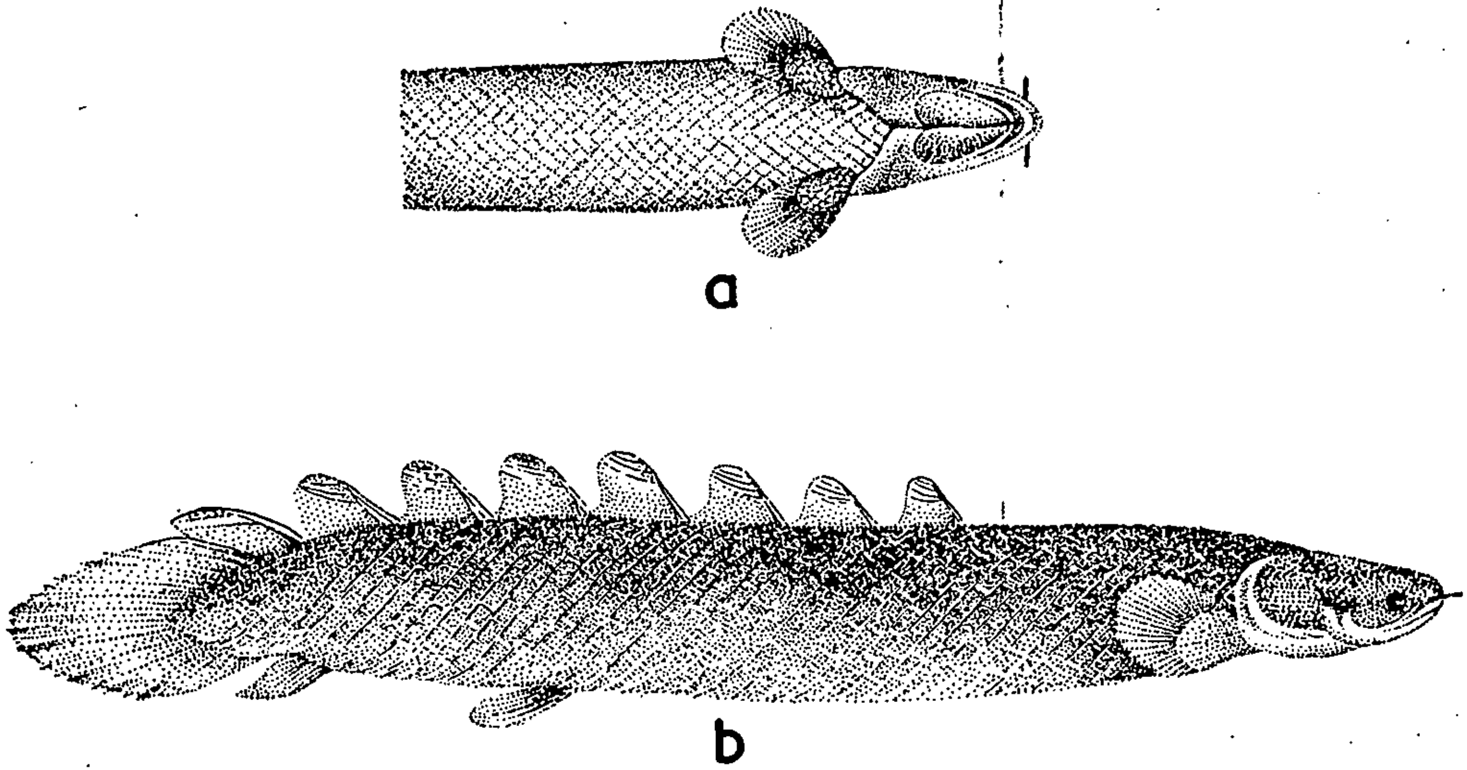

FIG. 2

Polypterus senegalus. (a) Ventral view of head, showing the characteristic gular plates and the pectoral fins. (b) Lateral view; both ×½. (Drawn by W. C. Lewis, after Boulenger.)

exceptions, is without supporting rays; it is in fact merely a flattened sheet of fatty tissue, covered by skin.

Scales. Excepting in the Lepidosirenidae (lung-fishes) and in the Polypteridae, scales are of two morphological types, *cycloid* and *ctenoid*. Cycloid scales have the exposed, visible surface, smooth, whilst ctenoid scales are covered with minute denticulations which make the scale rough to the touch. A simple test for the presence of ctenoid scales is to rub one's finger gently along the fish's flank, from tail to head; if the scales are ctenoid, the fish will feel rough. However, it is always advisable to check this character by the appearance of the scales under a low-power lens.

A longitudinal series of scales on each flank is pierced by small pores and appears as a distinct but narrow line; this is the lateral line scale series. The number of scales in the lateral line series is often of importance in separating closely related species. Beneath these perforated scales lies a series of sense organs which are in contact with the exterior through the pores in the scales.

The scales of the lung-fish *Protopterus* (Lepidosirenidae) are small, thin and deeply embedded in the skin. Thus, unless examined closely, the fish appears scaleless. On the other hand, the scales of *Polypterus* (Polypteridae) are thick and bony, with a glistening, enamel-like, surface.

Systematic list of Uganda fishes

The scheme of classification here adopted is essentially that of C. Tate Regan (1929a).

Class:	**PISCES**
Sub-class:	**CROSSOPTERYGII**
Order:	DIPNOI (Lung-fishes)
Family:	Lepidosirenidae
Genus:	*Protopterus*
Sub-class:	**PALAEOPTERYGII**
Order:	CLADISTIA
Family:	Polypteridae
Genus:	*Polypterus*
Sub-class:	**NEOPTERYGII**
Order:	ISOSPONDYLI
Sub-order:	Mormyroidea
Family:	Mormyridae (Elephant-snout fishes)
Genus:	*Mormyrus*
	Mormyrops
	Gnathonemus
	Petrocephalus
	Marcusenius
	Hyperopisus

Order:	OSTARIOPHYSI
Sub-order:	Cyprinoidea
Family:	Characidae (Tiger-fishes)
Genus:	*Hydrocyon*
	Alestes
Family:	Citharinidae (Moon-fishes)
Genus:	*Citharinus*
	Distichodus
Family:	Cyprinidae (Carps)
Genus:	*Barbus*
	Labeo
	Engraulicypris
	Discognathus
	Barilius
Sub-order:	Siluroidea (Cat-fishes)
Family:	Bagridae
Genus:	*Bagrus*
	Auchenoglanis
Family:	Schilbeidae
Genus:	*Schilbe*
	Eutropius
Family:	Clariidae
Genus:	*Clarias*
	Heterobranchus
Family:	Mochocidae
Genus:	*Synodontis*
Family:	Amphiliidae
Genus:	*Amphilius*
Family:	Malapteruridae (Electric cat-fishes)
Genus:	*Malapterurus*
Order:	MICROCYPRINI
Family:	Cyprinodontidae (Mosquito-fishes)
Genus:	*Aplocheilichthys*
	Notobranchus
	Cynopanchax
Order:	PERCOMORPHI
Sub-order:	Percoidea (Perch-like fishes)
Family:	Centropomidae (Nile perches)
Genus:	*Lates*

Family:	Cichlidae
Genus:	*Tilapia*
	Haplochromis
	Hoplotilapia
	Platytaeniodus
	Macropleurodus
	Schubotzia
	Astatoreochromis
Sub-order:	Anabantoidea
Family:	Anabantidae (Climbing perches)
Genus:	*Ctenopoma*
Order:	OPISTHOMI
Family:	Mastacembelidae (Spiny eels)
Genus:	*Mastacembelus*

KEY TO THE FAMILIES OF UGANDA FISHES

(NOTE on the use of keys. In this key, some of the more obvious external characters are presented as a series of contrasting couplets, one or other of which will be applicable to the fish being identified. A fish is first examined to determine the form of its fins, which are contrasted in the first pair of couplets. One of these couplets leads straight to the family of Lepidosirenidae: the other is followed by a figure in this instance 1. The figure indicated to which pair of couplets (numbered in the left-hand margin) one next proceeds. Having located these, it is then necessary to eliminate one possibility; the number associated with the other group of characters then shows to which succeeding pair one must proceed. This procedure is repeated until a group of characters associated with a family is reached.

Subsequent keys will be of a similar type.)

	Paired fins expanded, not filamentous, with distinct rays supporting the membrane; dorsal, anal and caudal fins separate (except in the family Mastacembelidae)	1
	Paired fins slender and filamentous; dorsal, anal and caudal fins confluent	Lepidosirenidae
1	Dorsal fin not divided into a series of separate finlets; scales present or absent; when present, thin and overlapping	2
	Dorsal fin divided into a number of separate finlets, each composed of a spine with several rays supporting the membrane; scales thick and bony, rhomboidal in outline	Polypteridae
2	Scales present	8
	Scales absent, circum-oral barbels present and well-developed (Sub-order Siluroidea)	3
3	Rayed dorsal fin present	4
	Rayed dorsal fin absent, well-developed adipose dorsal fin present	Malapteruridae
4	Dorsal fin short	5
	Dorsal fin long, extending almost to the caudal fin	Clariidae
5	Anal fin short, with 6-10 branched rays, equal to or somewhat shorter than the dorsal fin	6
	Anal fin long, with 54-70 rays	Schilbeidae

6 Dorsal fin with the first ray spinous 7
Dorsal find with the first ray soft Amphiliidae
7 Mandibular barbels not branched Bagridae
Mandibular barbels branched Mochocidae
8 Anal fin without spines. Ventral fins abdominal in position, without spines and usually with more than five rays 9
Anal and dorsal fins with spines supporting their anterior portions. Ventral fins (when present) thoracic in position, with one spine and five rays 13
9 Jaws with teeth 10
Jaws without teeth Cyprinidae
10 Adipose dorsal fin absent 12
Adipose dorsal fin present 11
11 Teeth fine and slender Citharinidae
Teeth large and fang-like or, if short, with stout bases and three-pointed crowns Characidae
12 Opercular bones hidden beneath skin; no scales on the head; caudal fin forked, mouth not protractile Mormyridae
Opercular bones not hidden beneath skin; scales present on the head; caudal fin rounded; mouth protractile, oblique. Dorsal surface of head flattened Cyprinodontidae
13 Ventral fins present 14
Ventral fins absent. Soft dorsal and anal fins confluent with caudal; spinous part of dorsal fin represented by numerous separate spines. Body eel-like Mastacembelidae
14 Dorsal fin undivided. Lateral line divided posteriorly into upper and lower portions 15
Dorsal fin deeply notched, so as to give the appearance of two fins, the anterior part completely spinous, the posterior with one spine and several rays Centropomidae
15 One nostril on each side of the head. Edge of operculum smooth Cichlidae
Two nostrils on each side of the head. Edge of the operculum serrated Anabantidae

Systematic Description of Species

Family POLYPTERIDAE

Polypterus Geoffr., 1802.

Since only one species of this genus occurs in Uganda waters, a combined description of the genus and species can be given.

Polypterus senegalus Cuvier, 1829.

Bichir (English); Mtonta (Lugungu); Otell (Alur).

Polypterus senegalus is immediately recognizable by the form of its dorsal fin which is composed of 8-11 separate finlets, each consisting of a single spine with several articulated rays supporting the membrane. The first finlet is widely separated from the tip of the pectoral fin. Further diagnostic characters are the thick bony, rhombic scales, with an enamel-like covering, the paired gular plates which lie between the rami of the lower jaw, and the distinct, scaly peduncle of the pectoral fins. In young fish, there is developed a true external gill which lies immediately behind and above the operculum.

Coloration: Adult fish, uniform olive-grey, almost khaki. Boulenger (1909) states that very young fish are conspicuously marked with dark longitudinal bands, which disappear at an early age.

Size: The total length of the largest recorded specimen from Uganda was 42 cm.

Distribution: Uganda; Lake Albert, Victoria Nile below the Murchison Falls, Albert Nile. Elsewhere; Lake Rudolf, the White Nile, the Senegal, Gambia and Niger and Lake Chad. During the Miocene (about 25,000,000 years ago) *Polypterus* occurred within the Lake Victoria basin. Fossil remains of the genus have been found in the Kavirondo Province of Kenya (Greenwood, 1951b).

Biology: Surprisingly little is known of the ecology of *P. senegalus*. From existing records it would appear to live in the marginal regions of lakes and rivers, particularly where there is emergent vegetation. Likewise, there are few data on the food of this species; in the few specimens examined (length-range 30-50 cm.) fish and small frogs apparently predominated as food.

Budget (1901) records *P. senegalus* as ready to spawn during the rainy season, July to September, but nothing is known as to the place or mode of spawning. Since cement glands—which secrete an adhesive mucus—occur on the head of larval fishes, it would seem likely that the young are attached to submerged plants.

Polypterus is of no economic value, but has excited considerable scientific interest. When first described, the Polypteridae were placed in the order Crossopterygii, an ancient group which has attracted great interest recently through the discovery of a living representative, the Coelacanth, *Latimeria*. Further research on the Polypteridae, however, has revealed that the resemblances between *Polypterus* and the Crossopterygii were only superficial; *Polypterus* appears to be more closely related to another fish group of great antiquity, the Palaeoniscoidea. The Palaeoniscoids are thought to be near the ancestor of all modern bony fishes.

The anatomy and skeleton of *Polypterus*, show a combination of archaic and specialized characters. The air-bladder which in most bony fishes functions as a hydrostatic device, in *Polypterus* serves also as an accessory respiratory organ.

Bibliography: Boulenger (1909); Bridge (1904); Daget (1950); Worthington (1929a).

Family LEPIDOSIRENIDAE

Protopterus Owen, 1839.

A single species, *P. aethiopicus*, occurs in Uganda.

Protopterus aethiopicus Heckel, 1851. (Fig. 3.)

Lung-fish (English); Mamba (Lunyoro, "Swahili"); Lut (Jonam, Lango).

Description: Body elongate, sub-cylindrical, the tail pointed and confluent with the long dorsal and anal fins. Dorsal fin originating at an equal distance from occiput and vent, or nearer the latter. Pectoral and pelvic fins slender and filamentous. There are no individual teeth in the jaws, the dentition consisting of upper and lower tooth-plates, in the form of sharp cutting ridges. Scales, thin

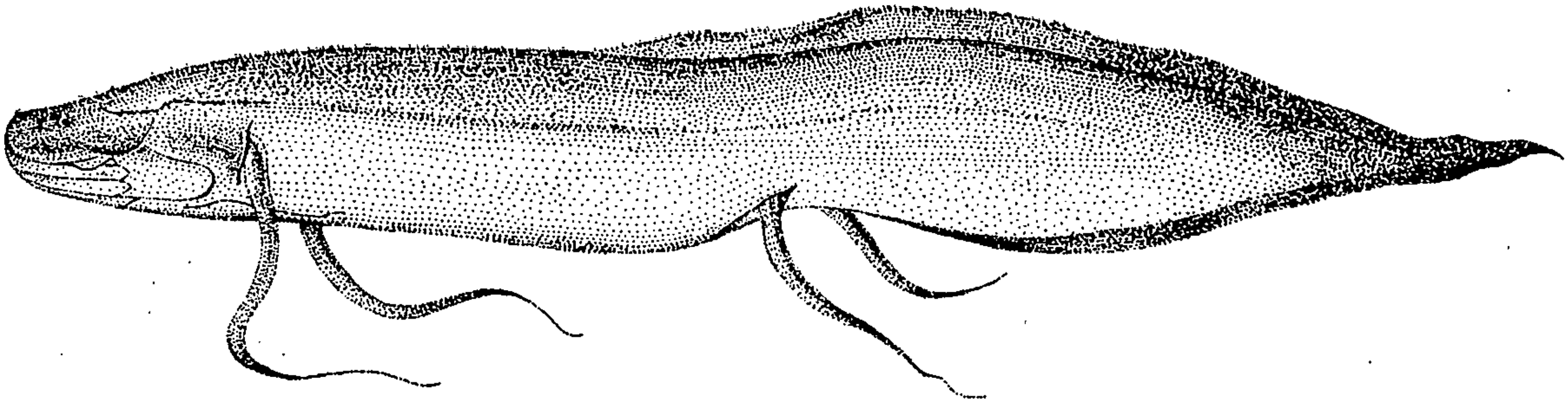

Fig. 3
Protopterus aethiopicus, lateral view, ×¼. (Drawn by W. C. Lewis, after Boulenger.)

and deeply embedded in the skin; 55-70 scales can be counted in a longitudinal series from immediately behind the head to above the vent. Ribs, 37-40 pairs.

True external gills occur in young fishes, but are usually absent in fishes over 15 cm. length.

Length: The largest recorded specimen was seven feet (2 m.) long; most individuals caught by commercial fishermen are in the size range 100-130 cm.

Coloration: Dark slaty-grey above, yellowish grey or pinkish below; often with numerous dark spots or flecks on the fins and body. The sensory canals on the head and body are conspicuously outlined in black.

Distribution: Uganda; Lakes Victoria, Nabugabo, Albert, Edward and George; the Victoria and Albert Niles, small streams and swamps associated with the major rivers and lakes; it is apparently absent from Lakes Nakavali, Kachira and Kijanebalola. Elsewhere; the Nile, the Sudan, Lake Tanganyika, Katanga, Lake No.

Biology: As the common name implies, *Protopterus* breathes by means of well-developed, paired lungs, as well as by its rather degenerate gills. In fact it would seem that, except in the youngest stages, these fishes are entirely dependent on atmospheric oxygen, since *Protopterus* kept in aquaria are asphyxiated if prevented from rising to the surface. In Lake Victoria on calm days large numbers of fish may be seen surfacing to breathe. The movements following surfacing are characteristic; the fish remains with the snout protruded for some seconds before flipping the greater part of its tail out of the water and plunging downwards.

Passing mention may be made of the known aestivating habits of *Protopterus*, although dormant lung-fish encased in their mud-cocoons have not been recorded from Uganda or neighbouring territories. With the onset of a dry season, and before the exposed mud has hardened, the fish burrows into the mud to a depth of between six inches and two feet. There it coils itself into a sac-like enlargement at the bottom of the burrow. This enlargement is lined by a capsule of hardened mucus secreted from glands in the skin. The fish is protected from extreme dehydration by the copious mucus secretion which fills the capsule. Breathing is apparently effected through a funnel-like opening in the chamber, one end of which is inserted into the fish's mouth. Although mud cocoons have not been found around the lake shores, despite fairly intensive searches (Poll and Damas, 1939; Poll, 1946) it seems probable that *Protopterus* living in isolated and temporary bodies of water may pass the dry-season in this manner. Some attempts to induce aestivation in laboratory-kept fishes have failed.

In Lakes Victoria, Nabugabo, Kyoga, Albert, Edward and George, *P. aethiopicus* occur most abundantly in the shallow inshore regions, especially in the vicinity of swamps, but they have been seen occasionally in deep water. As the lung-fish must surface for breathing at fairly frequent intervals, depth of water is probably an important factor determining its distribution within a lake. In Lake Victoria, young *P. aethiopicus* from 5-30 cm. long are very common in the matted roots of papyrus (Graham, 1929 and personal observations), although Poll and Damas (1939) record that in a similar habitat in Lake Edward (the large papyrus swamps at the mouth of the Luka River) . . . "La recherche fut vaine". In Lake Kyoga, Worthington (1929a) records that "the lung-fish is present throughout the swampy lakes and rivers, but was not observed to be nearly so abundant as in the shallow gulfs of Lake Victoria".

Food: Numerous references to the food of P. *aethiopicus* indicate that molluscs (both gastropods and bivalves) predominate in the diet. Small fish are also eaten —*Haplochromis* and young *Clarias, Synodontis* and *Bagrus* (Graham (1929); Worthington (1932); Poll (1939); unpublished records of East African Fisheries Research Organization). Poll (1952) lists crabs among the food of *P. aethiopicus* in Lake Tanganyika.

Breeding: The breeding sites of *P. aethiopicus* are found in the margins of swamps. The male fish prepares a crude nest by cleaning an area within the rooted vegetation, and later guards the eggs and young. A full account is given by Jackson (1916). Graham (1929) suggests that young lung-fish pass through a quiescent period, buried in the matted papyrus roots. The duration of this period, and the age at which it is entered, are still unknown. There is no positive information on breeding seasons of the Uganda lung-fish. By inference from the gonadal state of adult fishes, and from the occurrence of young amongst the papyrus roots it may be inferred that breeding occurs most frequently during the rains (Graham (1929); Poll (1939)).

Economic Value: The economic importance of the lung-fish in Uganda waters is considerable, but varies from lake to lake. In Lakes George and Kyoga—particularly Lake George—it forms an important element in the fisheries (Uganda Government, 1947-53), whilst in Lakes Victoria, Edward and Albert, the species contributes only slightly to the total catch. By destroying fish already caught in gill-nets, lung-fish may be of indirect importance, although much of the damage attributed to them may actually be caused by otters.

Protopterus, like *Polypterus*, is a living representative of a fish group which attained pre-eminence during the Palaeozoic (about 300,000,000 years ago). The Crossopterygii, with which this fish is classified, are of particular interest to the student of evolution as from them the terrestrial vertebrates apparently arose. Broadly speaking, the Crossopterygii are divisible into three major orders, the Dipneusti (lung-fishes), Coelacanthini (coelacanths, represented by a single living species, *Latimeria chalumnae* Smith), and the extinct Rhipidista. It is from the last order that terrestrial vertebrates are ultimately derived. Although the living lung-fishes retain many characteristics peculiar to the now almost extinct order Dipneusti, they must be considered as a relatively specialized end-point in evolution. Anatomically and osteologically, *Protopterus* shows considerable divergence from the typical bony-fishes. Special mention may be made of the well developed lungs and the consequent specialization of the blood-vascular system, which foreshadows the condition found in the Amphibia; the almost completely cartilaginous skeleton, particularly the incomplete vertebrae and persistent notochord; and the urino-genital system, which like the blood-vascular system, approaches the amphibian level of organization.

Bibliography: Boulenger (1909, 1916); Poll (1939, 1946, 1952a); Poll and Damas (1939); Jackson (1916); Graham (1929); Worthington (1929a, 1932b); Bridge (1904); Young (1950); Uganda Government (1947-1952); Johnels and Svensson (1954); Trewavas (1954).

TABLE I

Distribution of families of fishes in the five major Uganda lakes. A=absent. For each lake the number of genera within a family is given, followed below by first, the number of non-endemic species belonging to the various genera, and, second, the number of endemic species, indicated by the suffix 'e'. Lakes Victoria and Kyoga are considered together and species indicated 'e' occur in both lakes; those endemic to Lake Victoria are suffixed 'eV', and those known only from Lake Kyoga 'eK'. Figures for the Cichlidae are provisional until taxonomic studies on all five lakes are completed. The table is compiled from the data of Graham (1929), Worthington (1929a, b; 1932a, b), Trewavas (1933,1938), Poll (1939) and from reports of the East African Fisheries Research Organization.

Family		Lakes Victoria and Kyoga	Lakes Edward and George	Lake Albert
Lepidosirenidae ..	Genus Species	1 1	1 1	1 1
Polypteridae	Genus Species	A	A	1 1
Mormyridae	Genera Species	4 2+4e+1eV+1eK	1 2	5 7
Characidae ..	Genera Species	1 1+1e	A	3 5
Citharinidae	Genera Species	A	A	2 4
Cyprinidae	Genera Species	4 5+11e+3eK	2 4	4 5
Bagridae	Genera Species	1 1+1eV	1 1	2 3
Schilbeidae	Genera Species	1 1	A	2 2
Clariidae	Genera Species	1 5+1e+1eV	1 4	2 2
Mochocidae	Genus Species	1 2e	A	1 3
Amphiliidae	Genus Species	A	1 1	A
Malapteruridae ..	Genus Species	A	A	1 1
Cyprinodontidae ..	Genera Species	3 2+1eV	1 2+2e	1 1 or 2
Centropomidae ..	Genus Species	A	A	1 2e
Cichlidae	Genera Species	3+4eV 6+14e+43eV+2eK	4+1e 3+20e	2 5+4e
Anabantidae ..	Genus Species	1 1	1 1+1e	A
Mastacembelidae ..	Genus Species	1 1e	A	A

TABLE II

Analyses of data of Table I.

Lakes		Victoria and Kyoga	Edward and George	Albert
	Families	12	9	14
Non-cichlids ..	Genera Endemic genera	19 Nil	9 Nil	26 Nil
	Species Endemic species Percentage endemism	48 28 58	20 4 20	37 2 5
Cichlidae	Genera Endemic genera	6 3	5 1	2 0
	Species Endemic species Percentage endemism	64 58 90	28 20 71	9 4 44

TABLE III

Distribution of fishes in the small lakes of Uganda. Worthington's investigation (1931), and subsequent collections indicate that there are no indigenous fishes in Lake Bunyoni; of the three *Tilapia* species introduced, only one, *T. nilotica*, has apparently survived. The fishes of Lake Nabugabo are essentially those of Lake Victoria, from which the lake was separated by a sand-spit of recent geological age. The table is compiled from the data of Worthington (1929b), Trewavas (1933), Uganda Government (1947, 1948), and of collections made by the East African Fisheries Research Organization and by Makerere College Biology Department (1954).

Family	Lakes Kachira, Nakavali and Kijanebalola	Lake Nabugabo	Lake Bunyoni
Lepidosirendiae ..	Absent	*Protopterus aethiopicus*	Absent
Mormyridae	Absent	*Gnathonemus longibarbis* *Petrocephalus degeni* *Marcusenius nigricans*	Absent
Characidae	Absent	*Alestes nurse*	Absent
Cyprinidae	Absent	*Barbus* sp. *Engraulicypris argenteus*	Absent
Bagridae	Absent	*Bagrus docmac*	Absent
Clariidae	*Clarias mossambicus* *C. werneri*	*Clarias mossambicus* *C. werneri*	*Clarias carsoni* (introduced)
Schilbeidae	Absent	*Schilbe mystus*	Absent
Mochocidae	Absent	*Synodontis afro-fischeri*	Absent
Cyprinodontidae ..	*Aplocheilichthys pumilis*	Absent	Absent
Cichlidae	*Tilapia nilotica* (introduced) *T. esculenta* (introduced, Lake Kijanebalola only) *Haplochromis nubilis* *H. multicolor* *Astatoreochromis alluaudi*	*Tilapia esculenta* *T. variabilis* *Haplochromis* spp. (1+3 endemic)	*Tilapia nilotica* (Introduced) *T. nigra* ,, ,, *Haplochromis* spp. ,, ,,
Mastacembelidae ..	Absent	*Mastacembelus victoriae*	Absent

REFERENCES

Boulenger, G. A. (1909-1916). *Catalogue of the fresh-water fishes of Africa.* 1-4. London.

Brooks, J. L. (1950). Speciation in Ancient Lakes. *Q. Rev. Biol.*, **25**, 158-60.

Bridge, T. W. (1904). In "Fishes, Ascidians, etc.," Cambridge Natural History, London. (2nd edition, 1932.)

Budget, J. S. (1901). On the breeding habits of some West African Fishes. *Trans. zool. Soc. London*, **16**, 115-32.

Carpenter, G. D. H. (1920). *A Naturalist on Lake Victoria.* London.

Copley, H. (1952a). *The game fishes of Africa.* London.

(1952b). The Tilapias of Kenya Colony. *E. A. Agric. J.*, **18**, 30-34.

Daget, J. (1950). Revision des affinites phylogenetiques des Polypterides. *Mem. Inst. Franc. Afr. noire*, No. 11, 1-178.

East African Fisheries Research Organization (1950 et seq.) Annual Reports. Nairobi: East Africa High Commission.

Fish, G. R. (1955). The food of *Tilapia* in East Africa. *Uganda J.*, **19**, 85-9.

Fuchs, V. E. (1934). Geological work of the Cambridge Expedition to the East African lakes, 1930-31. *Geol. Mag. London*, **71**, 108, 147 and 157.

Graham, M. (1928). *Tilapia esculenta. Ann. Mag. nat. Hist.* (*10*,) **2**, 209.

(1929). *The Victoria Nyanza and its fisheries. A report on the fishing survey of Lake Victoria 1927-1928.* London: Crown Agents for the Colonies.

Greenwood, P. H. (1951a). Evolution of the African cichlid fishes; the *Haplochromis* species-flock in Lake Victoria. *Nature*, **167**, 19-20.

(1951b). Fish remains from Miocene deposits of Rusinga Island and Kavirondo Province, Kenya. *Ann. Mag. nat. Hist.*, (2), **4**, 1192-1201.

Jackson, Sir F. (1916). African lung-fish. *J. E. Afri. Ug. nat. Hist. Soc.*, **5**, 3.

Johnels, A. G., and Svensson, S. O. (1954). On the biology of *Protopterus annectens* (Owen). *Ark Zool.*, 1 (2), **7**, 131-64.

Lowe, R. H. (1955). Species of Tilapia in East African dams, with a key for their identification. *E. A. Agric. J.*, **20**, 256-62.

Norman, J. R. (1928). Two new fishes from Lake Victoria. *Ann. Mag. nat. Hist.*, (*10*), **2**, 104.

Percy, Lord Richard, and Ridley, M. W. (1955). On a few fish from Bwamba. *Uganda J.*, **19**, 96-101.

Poll, M. (1939). *Poissons. Exploration du Parc National Albert, Mission G. F. de Witte (1933-1935).* Fasc. 24, 1-81.

(1946). Revision de la fauna ichthyologique du Lac Tanganika. *Ann. Mus. Congo, C. Zool.*, (1), Fasc. 3.

(1952a). Poissons non Cichlidae. Exploration Hydrobiologique du Lac Tanganika (1946-1947). *Inst. roy. Science nat. de Belgique*, 3, Fasc. 5a.

(1952b). Notes sur les Cyprinodontidae du Musée du Congo belge; deuxième partie: les *Aplochlilichthyini* et les *Lamprichthyini. Rev. Zool. Bot. Afr.*, **45**, 293-305.

Poll, M., and Damas, H. (1939). *Poissons. Exploration du Parc National Albert, mission H. Damas (1935-1936).* Fasc. 6, 1-73.

Regan, C. T. (1921). The Cichlid fishes of Lakes Albert, Edward and Kivu. *Ann. Mag. nat. Hist.*, (9), **8**, 632.

Regan, C. T. (1922). The Cichlid fishes of Lake Victoria. *Proc. zool. Soc., London*, 157-91.

(1929a). "Fishes, Selachians, etc." in the Encyclopaedia Britannica; 14th edition.

(1929b). New cichlid fishes from Lakes Victoria, Kioga and Albert. *Ann. Mag. nat. Hist.* (*10*), **3**, 388.

Regan, C. T., and Trewavas, E. (1928). Four new Cichlid fishes from Lake Victoria. *Ann. Mag. nat. Hist.* (*10*), **2**, 224.

Trewavas, E. (1928). Descriptions of five new Cichlid fishes of the genus *Haplochromis* from Lake Victoria. *Ann. Mag. nat. Hist.* (*10*), **2**, 93.

(1933). Scientific results of the Cambridge expedition to the East African lakes, 1930-1.—II. The Cichlid fishes. *J. linn. Soc.* (*Zool.*), **38**, 309-41.

(1938). Lake Albert fishes of the genus *Haplochromis*. *Ann Mag. nat. Hist.* (*1*), **1**, 435-49.

(1954). The presence in Africa east of the Rift Valleys of two species of *Protopterus, P. annectens and P. amphibius. Ann. Mus. Congo Tervuren, in-4, Zool., 1,—Miscellanea Zoologica* H. Schouteden.

Uganda Government (1946 et seq.). Annual Reports of the Game and Fisheries Department. Entebbe, Govt. Printer.

Wayland, E. J. (1931). *Summary of progress of the Geological Survey, Uganda.* Entebbe.

Worthington, E. B. (1929a). *A report on the fishery survey of Lakes Albert and Kyoga.* London: Crown Agents for the Colonies.

(1929b). New species of fish from the Albert Nyanza and Lake Kyoga. *Proc. zool. Soc. London*, Pt. 3, 429-40.

(1932a). Scientific results of the Cambridge expedition to the East African lakes, 1930-1.—2. Fishes other than Cichlidae. *J. linn. Soc.* (*Zool.*), **38**, 121-34.

(1932b). *A report on the fisheries of Uganda.* London: Crown Agents for the Colonies.

(1954a). Speciation of fishes in the African lakes. *Nature*, **173**, 1064-67.

(1954b). "Fresh water organisms" in A discussion on the problems of distribution of animals and plants in Africa. *Proc. linn. Soc., London*, **165**, Pt. 1, 68-74.

Young, J. Z. (1950). *The life of vertebrates.* Oxford.

(*To be continued*)