

# A REVISION OF THE *HAPLOCHROMIS* AND RELATED SPECIES (PISCES : CICHLIDAE) FROM LAKE GEORGE, UGANDA

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## INTRODUCTION

LAKE GEORGE, smallest of the African 'Great Lakes' (text-fig. 1), occupies a virtually square basin of about 270 km<sup>2</sup> area in the western Rift valley (0°55' N to 0°05' S, and 30°02' E to 30°18' E). Water depth over much of the lake rarely exceeds 2.5 m, although there are some circumscribed areas with depths of up to 4.0 m.

Most of the lake is bordered by flat savannah-bush, but to the north and east there are areas of papyrus swamp extending, albeit as narrow fingers, for some 15 km from the lake edge. The principal affluent rivers enter Lake George through



these papyrus swamps. The Rivers Sibwe, Nsonge and Mubuka arise in the Ruwenzori mountains; the Mpanga, however, is a westward flowing tributary of the Katonga, a river which also flows eastward to enter Lake Victoria. The shared headwater of this river is a swamp divide (Doornkamp & Temple 1966), apparently impenetrable to all but air-breathing fishes.

Much of the shore line is simple, but there are a few deeply indented bays and one steep-sided bay formed from a volcanic crater.

Considerable areas of the lake bottom are covered by thick (*ca* 3 m) deposits of flocculent organic ooze, overlying a firm clay substrate. In some places, both in- and offshore, a sandy substrate is exposed or is but thinly overlaid by mud.

Two large islands (Kankurunga and Akika) lie close to the western lake shore; a third (Irangara Island), on the north-western shore, almost occludes the entrance to the lake's largest and most sheltered bay, Hamukunga Bay. The island shore-lines are varied and include slightly indented muddy bays, short stretches of sandy beach and extensive but narrow fringes of papyrus.

For a more detailed description of the lake and a brief outline of its limnological features, reference should be made to Dunn, Burgis, Ganf, McGowan & Viner (1969).

In addition to its small size and extreme shallowness, Lake George also differs from the other 'Great Lakes' in being directly linked with another water body, Lake Edward. Connection between Lakes Edward and George is effected through the Kazinga Channel, a 36 km long, river-like passage uninterrupted by swamps or rapids. There is a definite net outflow of water from Lake George into Lake Edward but the current is slight, and on occasion, undergoes wind-induced reversal of flow, at least in the upper layers of water.

To what extent the Kazinga Channel allows an actual exchange of fishes between the lakes (or of gene flow between populations of fishes in the lakes) has yet to be determined. Certainly many species of cichlid and non-cichlid fishes are present in both lakes, and the apparent endemism of some Lake George *Haplochromis* species may well be just a reflection of inadequate collecting in Lake Edward. Nevertheless, some habitats in Lake Edward are not represented in Lake George, and it is almost certain that a few Edward species are absent from Lake George. These absentees include not only species from deep-water habitats but also several from inshore habitats as well. Their absence from Lake George is hardly attributable to inadequate sampling because that lake has been intensively collected during the past six years.

Fairly comprehensive fish collections have been made recently along the whole length of the Kazinga Channel (*see* Appendix II). These collections indicate that the *Haplochromis* species of the channel are exclusively those common to both Lake Edward and Lake George. Surprisingly, even as close to Lake Edward as the Mweya Peninsula none of the inshore-living and apparently endemic Lake Edward species was found in the channel. Clearly, detailed ecological studies will have to be made (particularly at the Lake Edward end of the channel) before this situation is understood. For the moment, however, there seem to be good *a priori* grounds for believing that, for many species, there is continuity of populations between the lakes.



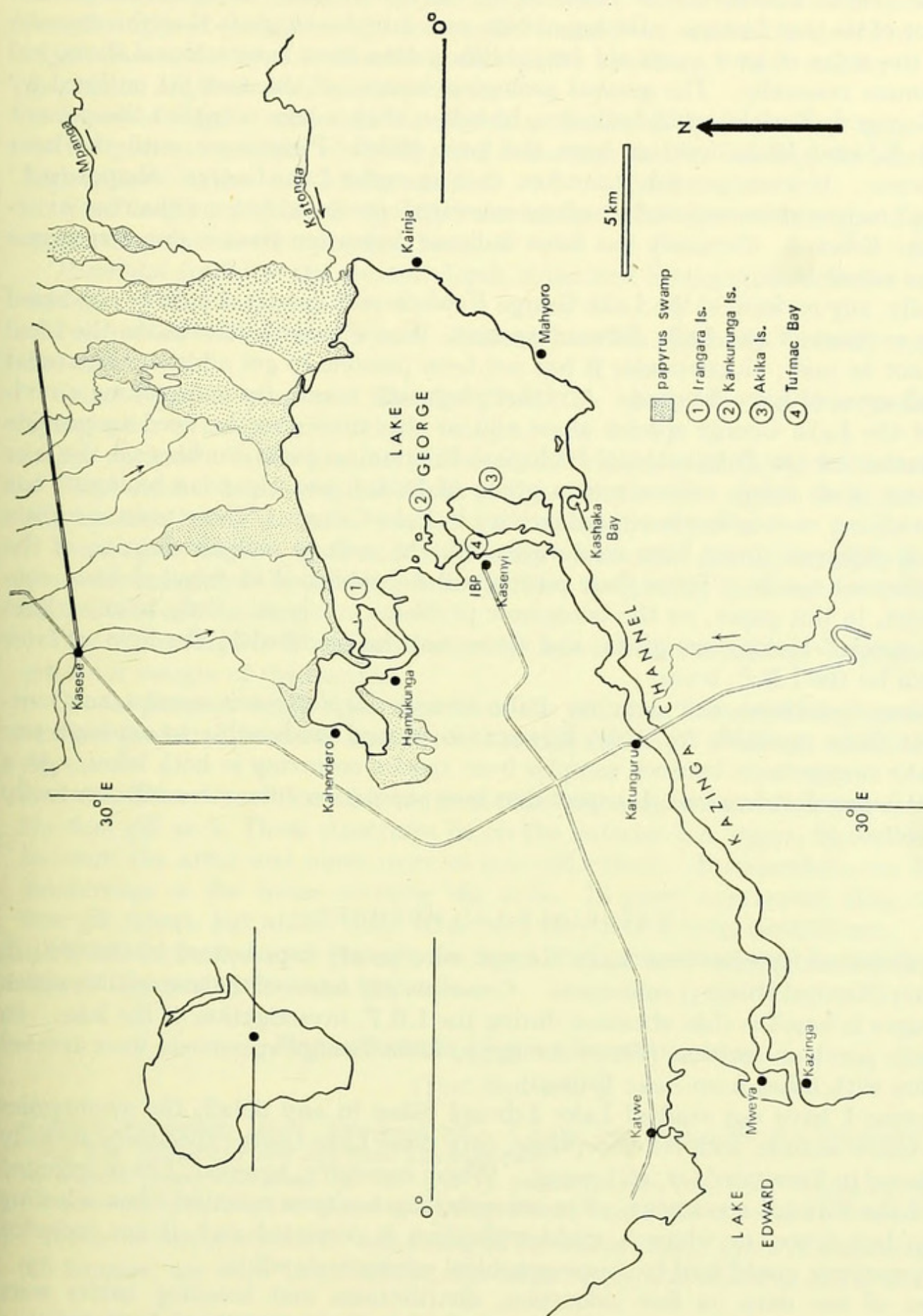


FIG. 1. Lake George and its major affluent rivers. Inset shows geographical position of the lake. Modified after Dunn *et al.* (1969).



Little precise information is available on the age of Lake George in its present form, or of its past history. Dating of lake core samples suggests that the deposits are in the order of 3500 years old (unpublished data from International Biological Programme research). The general geological history of the area (as outlined by Doornkamp & Temple 1966) indicates, however, that a lake occupied the present George-Edward basin from at least the later Middle Pleistocene until the later Pleistocene. It seems possible, therefore, that an earlier Lake George 'disappeared' (through causes unknown) and was later recreated, presumably from the then existing Lake Edward. Certainly the fishes indicate derivation from a common source at some recent time.

Ideally, any revision of the Lake George *Haplochromis* species should be combined with a revision of the Lake Edward species. For a variety of reasons the ideal could not be met; in particular it has not been possible to get additional material from all areas of Lake Edward. A rather pragmatic reason for undertaking a revision of the Lake George species alone and at this time was the need to provide information for the International Biological Programme team working on the lake (see Dunn *et al.* 1969). Since 1967 a group of British and Ugandan biologists has been studying various levels of productivity in Lake George. Three team members have, at different times, been concerned with the ecology and distribution of the *Haplochromis* species. Since their results will be published in detail, I have concentrated, in this paper, on the taxonomic problems involved. Only brief outlines of the species' biology are given, and these may be modified in the light of later research by the I.B.P. team.

Because specimens and data for Lake George *Haplochromis* species now outnumber those available for Lake Edward, it seemed inadvisable to attempt any interlake comparisons between samples from species occurring in both lakes. As a general impression, however, I suspect that interpopulation differences will eventually be detected.

#### MATERIALS AND METHODS

*Haplochromis* species from Lake George were poorly represented in the British Museum (Natural History) collections. Consequently, most of the material on which this paper is based is that obtained during the I.B.P. investigation of the lake. In the only previous revision (Trewavas 1933), Lake George specimens were treated together with fishes from Lake Edward.

Because I have not studied Lake Edward fishes in any detail, the synonymies given below include, with few exceptions, only those Lake George specimens actually mentioned in Trewavas' (*op. cit.*) paper. Where necessary, however, I have included some Lake Edward specimens. For example, this has been essential when selecting certain lectotypes, or where a misidentification is corrected and, if not included in a synonymy, could lead to zoogeographical misunderstanding.

Most of the data on live coloration, distributions and breeding habits were collected personally during several visits to the lake. A lot of this information has been supplemented and refined by the observations of Dr Ian Dunn and Mr James



Gwahaba, the fish biologists of the I.B.P. team. Both these workers have given unstintingly of their time and information, and I am extremely indebted to them.

*Measurements* used in describing the species are those I have employed in other papers on *Haplochromis* species, viz. :

*Standard length* : measured directly<sup>1</sup> from the snout tip (including the premaxilla) to the posterior margin of the hypural bones (located by bending the caudal fin at right angles to the body's long axis).

*Head length* : measured directly<sup>1</sup> across the head from snout tip to the most posterior point on the opercular bone.

*Preorbital depth* : is the greatest depth of the first infraorbital bone (= lachrymal bone).

*Interorbital width* : is the least distance between the bony (frontal) margins of the orbit.

*Snout length* : measured directly<sup>1</sup> from the snout tip (i.e. the premaxillary symphysis) to the anterior orbital margin.

*Eye diameter* : is the greatest diameter of the bony orbit in the horizontal plane.

*Cheek depth* : is the greatest depth of the muscular part of the cheek (even when this extends below the scale rows) and is measured vertically.

*Lower jaw length* : is measured directly<sup>1</sup> from the dentary symphysis to the posterior margin of the articular bone (located by opening the lower jaw and finding its point of articulation).

*Upper jaw length* : is measured directly<sup>1</sup> from the premaxillary symphysis to the posterior margin of the maxilla.

*Caudal peduncle length* : is taken from the posterior margin of the hypurals to a vertical projected from the insertion of the last anal ray. *Peduncle depth* is the least depth.

A character I have used for the first time concerns the so-called *pseudorakers* on the first gill arch. These structures lie on the anterior (i.e. upper) face of the arch, between the inner and outer rows of true gill rakers. Pseudorakers are localized thickenings of the tissue covering the arch. In gross appearance they resemble true gill rakers, but unlike those structures they lack a bony central core.

*Vertebral counts* do not include the fused first preural and ural vertebrae (which support the parhypural and hypurals).

### *Haplochromis elegans* Trewavas, 1933

(Text-figs. 2 & 3)

*Haplochromis nubilus* (part) : Trewavas, 1933, *J. Linn. Soc. (Zool.)*, **38** : 329 (specimens BMNH reg. nos. 1933.2.23 : 288–295 from Lake George).

*H. elegans* (part) Trewavas, *op. cit.* : 332 (3 paralectotypes, reg. nos. 1933.2.23 : 387–389, supposedly from Lake George, and 4 other specimens, 1933.2.23 : 390–393, also from that lake).

NOTE ON THE SYNONYMY. According to Trewavas (1933), three *H. elegans* syntypes (all females) are from Lake George, the other syntypical material being from Lake

<sup>1</sup> In a direct measurement, one tip of the dividers or calipers is placed at one of the points specified and the other tip is placed on the second point; the distance measured may thus run across the long axis of the fish (as, for example, in snout and head lengths).



Edward. I have examined the three syntypes (reg. nos. 1933.2.23 : 387–389) and agree with Trewavas' identification. However, the bottle label, and the Museum register, give the locality for these fishes as Lake Edward and not Lake George.

Trewavas (*op. cit.*) also refers seven specimens from the hypodigm (reg. nos. 1933.2.23 : 390–395) to this species, giving their localities as Worthington's (1932) stations 522 (Lake Edward) and 613 (Lake George). Six fishes (reg. nos. 1933.2.23 : 390–395) are in a bottle now labelled 'Lake George' but without any station number quoted. I take these to be the fishes from station 613. Of these specimens, three are referable to *H. elegans*.

The *lectotype*, an adult male 65.5 mm standard length (BMNH 1933.2.23 : 381), is from Lake Edward.

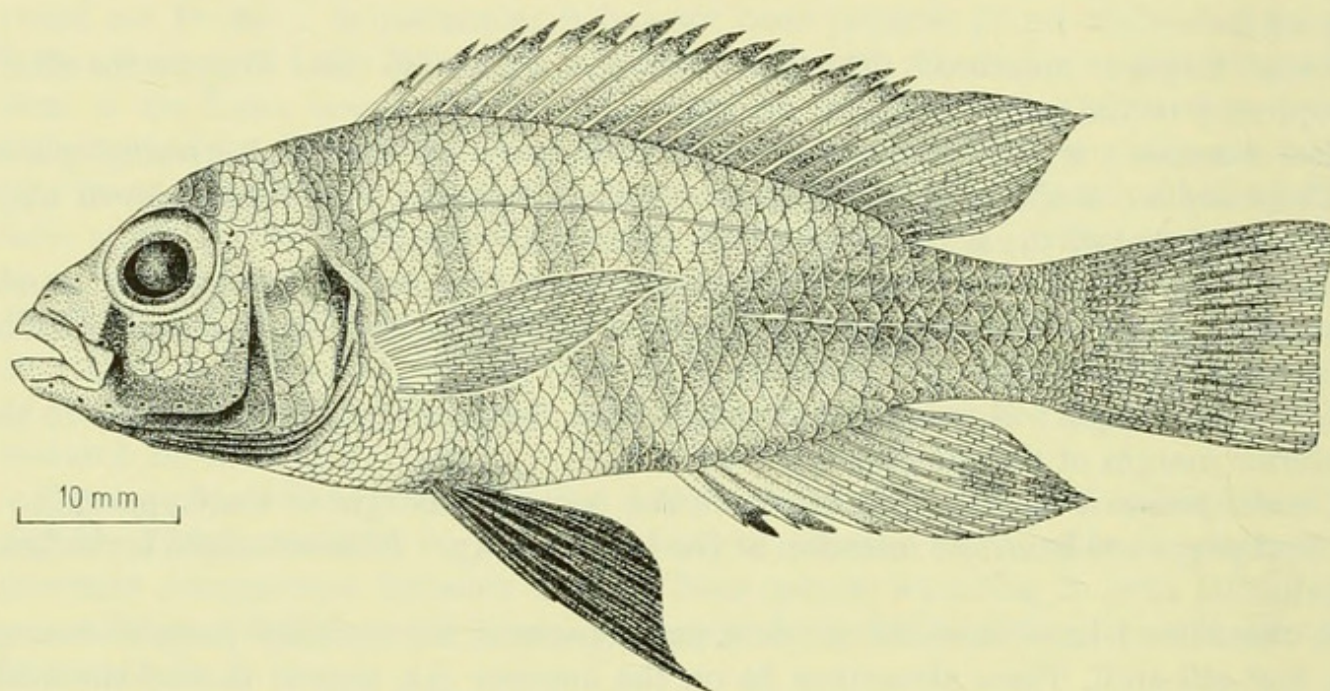


FIG. 2. *Haplochromis elegans*. Lake George specimen ; a male.

**DESCRIPTION.** Based on 34 specimens, 58.0–72.5 mm standard length (but not including the lectotype since it is from Lake Edward).

Depth of body 35.7–40.8 (mean,  $M = 37.6$ ) per cent of standard length, length of head 32.2–35.4 ( $M = 33.7$ ) per cent. Dorsal profile of head gently decurved or straight, sloping at about  $35^\circ$  to the horizontal ; dorsal margin of eye not entering the line of the profile, but clearly below it.

Preorbital depth 11.8–16.5 ( $M = 14.5$ ) per cent of head, showing very slight positive allometry. Least interorbital width 21.9–27.3 ( $M = 24.2$ ) per cent of head, length of snout 25.6–32.5 ( $M = 28.4$ ) per cent, 0.8–0.9 of its breadth. Eye diameter 28.0–37.0 ( $M = 33.5$ ) per cent of head (not showing clear-cut allometry in the size range examined), depth of cheek 18.2–24.4 ( $M = 20.8$ ) per cent.

Caudal peduncle 13.8–18.7 ( $M = 16.2$ ) per cent of standard length, 1.2–1.5 (modal range 1.2–1.3) times as long as deep.

Mouth horizontal or very slightly oblique ; lips somewhat thickened. Length of upper jaw 28.6–34.0 ( $M = 30.3$ ) per cent of head, length of lower jaw 35.0–40.2



( $M = 37.9$ ) per cent, 1.3–1.8 (mode 1.4) times as long as broad. Posterior tip of maxilla reaching the vertical through the anterior orbital margin, but not quite reaching this level in a few specimens.

*Gill rakers* variable in form but usually rather stout, the lower 1 or 2 greatly reduced; 8 or 9 rakers in the outer row on the lower part of the first gill arch. No pseudorakers are developed between the inner and outer rows of gill rakers on this arch.

*Scales*. Ctenoid; lateral line with 30 (f.2), 31 (f.15), 32 (f.15), 33 (f.1) or 34 (f.1) scales; cheek with 2 or 3 (mode) rows. Five to  $6\frac{1}{2}$  (mode  $5\frac{1}{2}$ ) scales between the upper lateral line series and the dorsal fin origin, 6–8 (mode 6) between the pectoral and pelvic fin bases.

*Fins*. Dorsal with 14 (f.2), 15 (f.24) or 16 (f.8) spinous and 8 (f.1), 9 (f.21) or 10 (f.12) branched rays. Caudal subtruncate, scaled on its basal half, or a little beyond. Pectoral 26.6–33.6 ( $M = 30.3$ ) per cent of standard length, 80.0–97.8 ( $M = 90.0$ ) per cent of head. Pelvics with the first two rays produced, especially in adult males.

*Teeth*. The *outer row* of teeth in both jaws (text-fig. 3) is composed principally of relatively stout, well-spaced, unequally bicuspid teeth; anteriorly in the lower jaw, the teeth are implanted so as to slope forward at a slight angle.

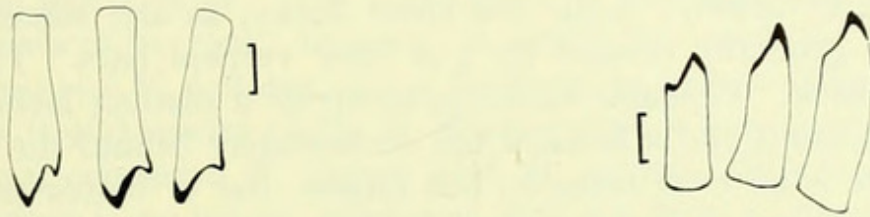


FIG. 3. *H. elegans*. (Left). Premaxillary teeth, left side, viewed from a point slightly anterior of lateral. The teeth are from an anterolateral position in the jaw. (Right). Dentary teeth (right side), lateral in position. Viewed laterally. Scale = 0.25 mm.

The major cusp is isoscelene in outline (see text-fig. 3) and very slightly incurved; the neck of the tooth is slightly flattened in cross-section. Some teeth in each jaw have one margin of the major cusp partly flattened from below the tip so that it appears as a narrow step-like flange adjacent to the minor cusp (cf. *H. aeneocolor* where the flange is present on most teeth and is more obvious).

Posteriorly in the upper jaw there may be from 1 to 5 unicuspid and dagger-shaped teeth; less often these posterior teeth are tricuspid.

There are 34–42 (mean = 38) teeth in the outer premaxillary row.

The *inner rows* (usually 2, less commonly 3 in the upper jaw, and 2 or 3 in the lower) are composed of small tricuspid teeth, often irregularly arranged (particularly in the upper jaw).

**OSTEOLOGY.** The *neurocranium* of *H. elegans* is typically that of a generalized *Haplochromis* species (see Greenwood 1962), although the preorbital profile is a little less decurved.



The lower *pharyngeal bone* is fairly stout, with its dentigerous area 1.1–1.2 times broader than long. The teeth are fine, cuspidate and compressed and are arranged in 24–26 rows. Teeth in the two median rows are somewhat coarser than the others.

Vertebral counts for the 30 specimens radiographed are : 28 (f.3), 29 (f.22) or 30 (f.5), comprising 12 (f.5), 13 (f.24) or 14 (f.1) abdominal and 15 (f.2), 16 (f.20) or 17 (f.8) caudal elements.

**COLORATION IN LIFE.** *Adult males* : ground colour smokey grey overlying bluish-silver. Snout, lips and cheek with a livid iridescence. Belly and branchiostegal membrane dark cinder grey. Dorsal fin with the spinous part sooty, the inter-spinous membrane generally darkest ; lappets black but with a narrow red streak (or spot) at the tip. Soft dorsal with maroon streaks between the rays. Caudal fin with maroon spots and blotches between the rays, and a suffuse maroon flush around the fin margin. Anal dark hyaline (or faintly grey) often dusky at its base and with a pinkish-maroon border. The pelvics are black.

*Females* : ground colour sandy green shading to silvery white on the belly and lower flanks. All fins yellowish-green. Because female *H. elegans* are not immediately identifiable in the field, these 'live' colours are in fact 'post-mortem' colours and should not be considered at all precise.

**COLORATION IN PRESERVED SPECIMENS.** *Adult males* : ground colour variable but basically grey-brown ; belly and chest dusky, as are, sometimes, the flanks. The flanks are generally crossed by 3–6 faint vertical bars. The branchiostegal membrane is black. Cephalic markings comprise a distinct lachrymal stripe, two bars across the snout and a broader bar immediately behind the orbits ; in many specimens there is an even broader, but fainter, bar or blotch transversely across the nape. The lower part of the cheek and the vertical limb of the preoperculum are sometimes dusky.

The dorsal fin is dusky, with darker streaks between the spines and rays, or the latter region maculate. Anal fin dusky or indistinctly maculate. Caudal with a dark central area and a light marginal zone. Pelvics are black, and the pectorals hyaline.

*Females* have a greyish-yellow ground coloration, and sometimes very faint traces of 3–6 vertical bars on the flanks. On the head there are slight indications (sometimes just a darker area) of two bars across the snout, and a lachrymal stripe. All the fins are hyaline, the dorsal usually darker than the others ; the caudal is often maculate.

**ECOLOGY.** *Habitat.* *Haplochromis elegans* is essentially a species of the inshore regions of the lake, especially near papyrus shores or where the bottom is sandy. It rarely occurs in open-water localities or in shallow places where the substrate is mud.

*Food.* Mostly chironomid larvae, although emergent aquatic Diptera are also eaten when available.

*Breeding.* *Haplochromis elegans* is a female mouth-brooder. All specimens, of both sexes, within the size range studied are adult ; females appear to reach a larger size than do males. In the 15 sexually active females examined, 11 have the right



ovary noticeably larger than the left, 2 have the ovaries equally developed, and 2 have the right ovary a little larger than the left one.

*Distribution.* Lakes Edward and George, and the Kazinga Channel.

**DIAGNOSIS AND AFFINITIES.** Within Lake George, *H. elegans* most closely resembles *H. aeneocolor* (see p. 150), both morphologically and in its habitat preferences. Adult males of the two species are readily distinguished by their coloration, but females and preserved specimens are differentiated chiefly by the fewer and somewhat stouter teeth of *H. elegans* (32–42,  $M = 38$ , cf. 40–58,  $M = 48$  in *H. aeneocolor*), the slightly procumbent anterior dentary teeth of *H. elegans*, the well-developed flange on the major cusp of most teeth in *H. aeneocolor* (see p. 151), the shorter upper jaw of *H. elegans* (28.6–34.0,  $M = 30.3$  per cent of head, cf. 30.0–37.8,  $M = 34.9$  per cent) and the shorter lower jaw of *H. elegans* (35.0–40.2,  $M = 37.9$  per cent of head, cf. 38.0–44.0,  $M = 41.0$  per cent in *H. aeneocolor*). In life the lips of *H. elegans* appear thicker than those of *H. aeneocolor*, but this distinction is less obvious in preserved material.

*Haplochromis elegans* shows few specializations in its dental or cranial anatomy, and must be ranked amongst the 'generalized' *Haplochromis* species. Outside the Lake Edward–Lake George species complex it resembles *H. pallidus* (Blgr.) of Lake Victoria (see Greenwood 1960). From *H. pallidus*, *H. elegans* differs in its adult male coloration, some morphometric characters (e.g. having a shorter snout) and in its overall morphology. The significance of this apparent resemblance will be discussed elsewhere (p. 230); however, it should be noted that the resemblance between *H. elegans* and *H. pallidus* cannot be shown to be more significant than that existing between it and species of the *H. bloyeti* complex (see Greenwood 1971).

Trewavas (1933) compared *H. elegans* with *H. cinereus* (Blgr.) of Lake Victoria, but this comparison is no longer valid now that we have a clearer concept of *H. cinereus* (see Greenwood 1960). In fact, *H. cinereus* shows some specialized characters (its dentition for one). These specializations would not be apparent in 1933, because at that time '*H. cinereus*' was a dumping ground for several of the generalized Lake Victoria species.

Resemblances which I noted between *H. elegans* and *H. velifer* Trewavas of Lake Nabugabo (Greenwood 1965b) are somewhat diluted by the greater amount of information now available on *H. elegans*. For example, the teeth of *H. elegans* (at least in Lake George populations) have a more acutely pointed cusp, and there are fewer teeth in the outer premaxillary row. There is, of course, a marked difference in the male breeding coloration of the two species.

Diagnostic problems arising in connection with *H. elegans* and species at present known only from Lake Edward (and then very imperfectly known) are virtually identical with those discussed in relation to *H. aeneocolor* on page 153.

#### STUDY MATERIAL

Register number BMNH	Locality: Lake George
1972.6.2 : 166–167	N.E. lake shore (papyrus)
1972.6.2 : 168–171	Papyrus shore off I.B.P. Laboratory
1972.6.2 : 172–177	Kankurunga Island



1972.6.2 : 178-179	Kankurunga Island
1972.6.2 : 180-182	Kankurunga Island
1972.6.2 : 183-206	Kankurunga Island
1972.6.2 : 207-224	Kankurunga Island
1972.6.2 : 225-230	Kankurunga Island
1972.6.2 : 231-236	Kankurunga Island
1972.6.2 : 237-238	Akika Island
1972.6.2 : 239-243	Akika Island
1972.6.2 : 244-260	Akika Island
1972.6.2 : 261-272	I.B.P. Jetty
1972.6.2 : 273-285	Kashaka Bay
1972.6.2 : 286-291	Tufmac Bay
1972.6.2 : 292	Close to shore (muddy)

*Haplochromis aeneocolor* sp. nov.

(Text-figs. 4 & 5)

*Haplochromis nubilus* (part): Trewavas, 1933, *J. Linn. Soc. (Zool.)* **38**: 329 (4 specimens, BMNH reg. nos. 1933.2.23 : 296-299).

HOLOTYPE. A male, 68.0 mm standard length, BMNH reg. no. 1972.6.2 : 43.

The specific name refers to the brassy appearance of adult males.

DESCRIPTION. Based on 36 specimens (including the holotype), 58.0-75.0 mm standard length.

Depth of body 35.7-41.1 ( $M = 37.7$ ) per cent of standard length, length of head 32.0-36.8 ( $M = 34.5$ ) per cent. Dorsal profile of head straight or slightly concave, sloping fairly steeply at *ca* 35°-40° with the horizontal; dorsal margin of orbit not entering the line of the profile but distinctly below it.

Preorbital depth 12.0-18.2 ( $M = 14.6$ ) per cent of head (not showing any clear-cut allometry), least interorbital width 22.7-29.3 ( $M = 25.5$ ) per cent, snout length 26.7-31.8 ( $M = 28.8$ ) per cent, 0.8-1.0 (mode 0.9) of its breadth. Eye diameter 28.6-35.0 ( $M = 31.4$ ) per cent of head (showing no obvious allometry), depth of cheek 19.0-25.0 ( $M = 22.8$ ) per cent.

Caudal peduncle 12.9-17.4 ( $M = 15.3$ ) per cent of standard length, 1.2-1.5 (modal range 1.2-1.3) times as long as deep.

Mouth angle ranging from horizontal to slightly oblique; lips somewhat thickened. Length of upper jaw 30.0-37.8 ( $M = 34.9$ ) per cent of head, lower jaw 38.0-44.0 ( $M = 41.0$ ) per cent of head, 1.5-2.1 (modal range 1.6-1.8) times as long as broad. Posterior tip of the maxilla reaching a vertical through the anterior part of the eye or even to a vertical through the anterior margin of the pupil.

*Gill rakers* of various shapes, from short and stout to relatively slender; the lower 1 or 2 rakers on the first gill arch are greatly reduced, the upper 2 or 3 often flattened. There are 8 or 9 rakers on the lower part of the first arch.

Pseudorakers are poorly developed.

*Scales*. Ctenoid; lateral line with 30 (f.11), 31 (f.18), 32 (f.4) or 33 (f.1) scales, cheek with 3 (rarely 2) rows. Five to 6½ (mode 5½) scales between the lateral line



and the dorsal fin origin, 6 (mode) or 7, rarely  $5\frac{1}{2}$  or 5, between the pectoral and pelvic fin bases.

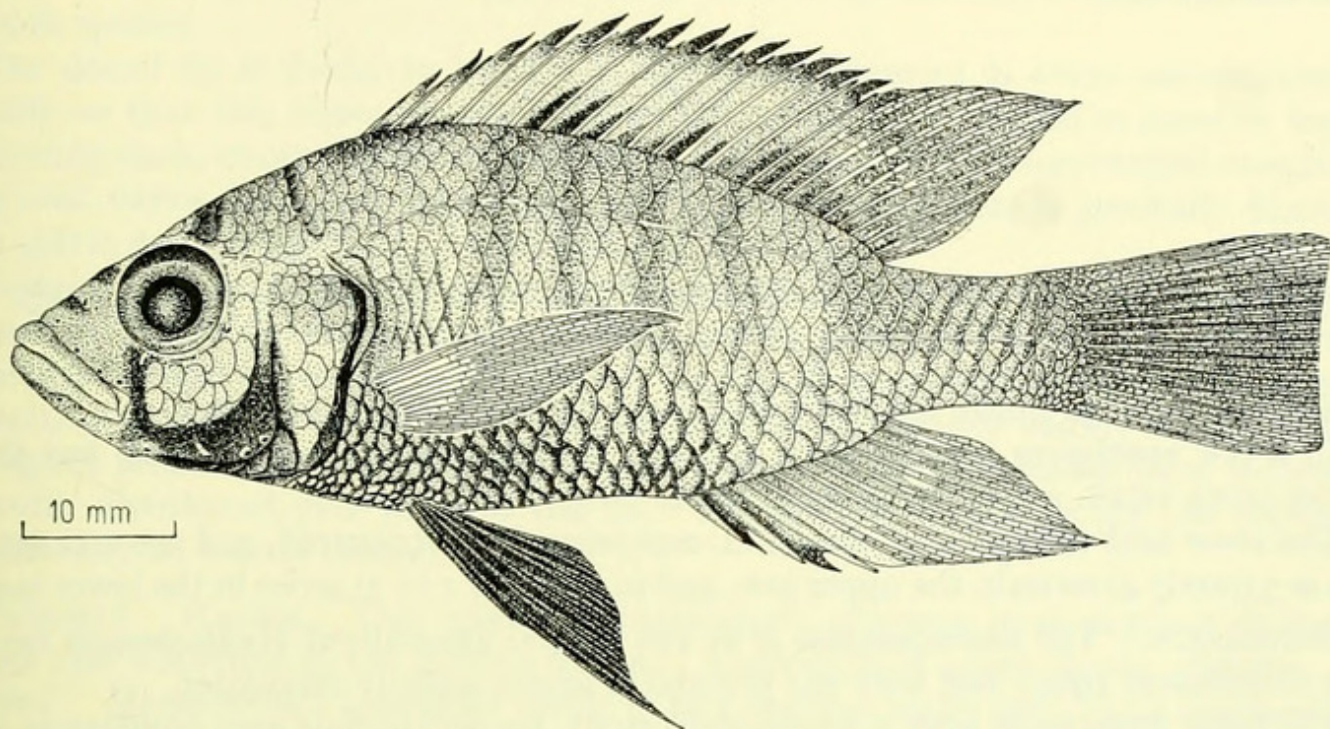


FIG. 4. *Haplochromis aeneocolor*. Holotype.

*Fins.* Dorsal with 14 (f.3), 15 (f.31) or 16 (f.2) spinous and 8 (f.3), 9 (f.25) or 10 (f.8) branched rays. Anal with 3 spines and 7 (f.1), 8 (f.9), 9 (f.20) or 10 (f.6) branched rays. Caudal subtruncate, scaled on its basal half. Pectoral 27.0–31.7 (M = 28.9) per cent of standard length, 73.8–93.5 (M = 84.5) per cent of head. Pelvics with the first and second rays produced (the first markedly so), and relatively longer in adult males than in females.

*Teeth.* The *outer teeth*, although basically of the generalized, unequally bicuspid type, are nevertheless rather distinctive. This is due to the presence of a well-developed, thin flange on that margin of the outer cusp which is adjacent to the minor cusp (see text-fig. 5). Few individuals fail to show flange development on at least the majority of anterior and lateral teeth in both jaws. The flange can be so well developed that the tooth seems to have an expanded and obliquely sloping major cusp (i.e. to be like the teeth of *H. limax*, see p. 168). Usually the flange is thin and almost transparent, so that there appears to be a dividing line between it and the more substantial body of the cusp itself. Although the flange may be continuous with the occlusal (i.e. distal) part of the cusp (thereby simulating an *H. limax*-like tooth) it is generally confined to the proximal half or two-thirds of the cusp. In this way a distinct step is developed between the flange and the occlusal tip of the cusp.

Apart from the flange, outer teeth in *H. aeneocolor* are typical bicuspids, with the major cusp having the outline of an isosceles triangle rather than of an equilateral one. The minor cusp is well developed, but its tip is not very acute. The crown of



an outer tooth has virtually no incurvature, and the neck is a slightly compressed cylinder.

The posterior 1-4 upper teeth are either compressed tricuspid or are unicuspid and caniniform.

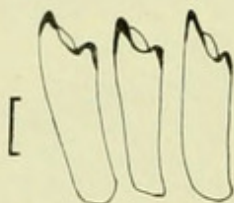


FIG. 5. *H. aeneocolor*. Dentary teeth (left side), lateral in position. Viewed laterally. Scale = 0.25 mm.

There are 40-56 (mean 48) teeth in the outer row of the upper jaw.

In a few specimens, all the outer teeth in the lower jaw are unicuspid, but the upper teeth retain a typical bicuspid form.

The *inner teeth* in both jaws are small, compressed and tricuspid, and are arranged in 2 or 3 (rarely 4) series in the upper jaw, and in 2 (rarely 1 or 3) series in the lower jaw.

**OSTEOLOGY.** The *neurocranium* is of the typical generalized *Haplochromis* type (see Greenwood 1962), but with the preorbital profile slightly straighter.

The *lower pharyngeal bone* is moderately stout, its dentigerous area equilateral or slightly broader than long. The teeth are fine, compressed and cuspidate, and are arranged in *ca* 24-26 rows; the median teeth are not noticeably larger or coarser than those of the lateral rows.

*Vertebral counts* in the 16 fishes examined are 27 (f.1), 28 (f.7) and 29 (f.8), comprising 12 (f.6) or 13 (f.10) abdominal and 15 (f.4), 16 (f.11) or 17 (f.1) caudal elements.

**COLORATION IN LIFE.** *Adult males*: the flanks, lateral aspect of the chest and belly, lower part of the head, the branchiostegal membrane and the lips are dark sulphurous yellow, with an orange overlay on the operculum. The rest of the flank (i.e. the posterior part) and the caudal peduncle are yellowish-green with a faint bluish overlay, and the ventral aspect of the chest is sooty. The dorsal body surface is dull bronze posteriorly, becoming purple above the flanks, and crimson anteriorly. The snout and anterior dorsum of the head are puce.

The overall colour impression gained from a newly caught male is one of brassiness, despite the various colour elements described above.

The dorsal fin is dark hyaline on the spinous part (the lappets black), but lighter on the soft part where the margin is crimson. The anal fin is hyaline over the basal third of the soft part, but with the spines and distal two-thirds of the soft part pinkish-crimson; the ocelli are orange-yellow. The caudal fin is pinkish to red, the colour intensified on the ventral third of the fin and at its posterior angle. The pelvic fins are black, the pectorals hyaline.

Male coloration is difficult to describe adequately because the intensity of the various colours is variable and changes rapidly after the fish is removed from water. Some fishes, for example, appear almost black a short while after capture.



**PRESERVED COLORATION.** *Males*: the ground colour is essentially like that described for *H. elegans* (see p. 148), but in *H. aeneocolor* the dark ventral pigment is more extensive; in some individuals it covers the entire caudal peduncle and the flanks to a level just below the upper lateral line. Cephalic markings are identical in both species.

The dorsal fin is dusky to black; if dusky, the pigment is often concentrated basally so that this region of the fin is almost black. The caudal is more or less uniformly dark, except for hyaline areas on the ventral and posteroventral margin. The anal varies from grey to dusky; the area over the spines is generally black. The pelvic fins are black, the pectorals hyaline.

*Females* have a greyish-silver to greyish-yellow ground colour; the head shows very faint traces of two transverse bars across the snout and an ill-defined, short, lachrymal stripe or streak. The dorsal fin has dark streaks between the rays, especially on the spinous part. The caudal is maculate, usually weakly so, and with the spots most obvious on the centre of the fin; a few specimens have intense maculae distributed over most of the fin. The anal is hyaline as are the pelvics (which may be faintly dusky).

**ECOLOGY.** *Habitat.* This species is particularly common near papyrus shores, and is rare elsewhere in the inshore region. Apparently it never occurs offshore.

*Food.* *Haplochromis aeneocolor* seems to be a detritus feeder since plant fragments and insect larvae are predominant elements of its gut contents. Adult insects are, however, also eaten.

*Breeding.* *Haplochromis aeneocolor* is a female mouth brooder. Of the 10 adult females examined, the right ovary is much larger than the left in 6 individuals, slightly larger in 3 and of equal size in 1 fish.

All specimens within the size range studied are adult and there is apparently no sexual dimorphism in the maximum size attained.

*Distribution.* Lake George and the Kazinga Channel.

**DIAGNOSIS AND AFFINITIES.** Until more is known about most Lake Edward species (and especially those not recorded from Lake George) an adequate diagnosis for *H. aeneocolor* is difficult to compile. For example, *H. eduardii* Regan superficially resembles *H. aeneocolor* but appears to differ in having stouter, non-flanged and less acutely cuspidate teeth, a shallower body and more rounded (i.e. decurved) head profile. *Haplochromis engystoma* Trewavas (known only from the holotype and one other specimen) has dental characteristics more like those of *H. aeneocolor*, but differs in several morphometric characters, especially in its higher (2.0) eye/cheek ratio, shorter lower jaw (34.8 per cent of head) and its strongly decurved head profile. *Haplochromis vicarius* Trewavas (at least as restricted to the holotype) has an overall superficial resemblance, but differs in having obliquely cuspidate outer teeth, more rows of inner teeth and a larger eye (36.0 per cent of head); Poll (1939) has synonymized *H. vicarius* with *H. eduardii* but I doubt the correctness of this decision (see Appendix I).

Regrettably, in none of these comparisons could life colours be taken into account because these are unavailable for the Lake Edward species.



Considering now those species which also occur in Lake George, *H. elegans* has the closest overall and detailed resemblances with *H. aeneocolor* (see p. 149). Male coloration is, however, very different in the two species, and there are dental and morphometric differences as well (again, see p. 147). Distinguishing between females of the species is especially difficult, although in the field the more rounded head profile of *H. elegans* does give some guidance for preliminary sorting.

*Haplochromis limax* Trewavas shows a fairly marked resemblance to *H. aeneocolor* in its superficial morphology and there is also a certain convergence in dental morphology. This arises from the peculiar flange developed on the major cusp of outer teeth in *H. aeneocolor* (see p. 152). If this flange is hypertrophied, it increases the area of the major cusp and imparts to it an oblique cutting edge. However, if such teeth in *H. aeneocolor* are closely examined, the junction between flange and main body is apparent, as is a slight indentation on the cutting edge. Furthermore, the flange is much thinner (nearly transparent) than the corresponding margin of a tooth in *H. limax*. Another distinguishing feature of *H. limax* is the broader array of inner teeth, and their larger size. Again, male breeding coloration is very different in the two species.

Beyond the confines of Lakes Edward and George, *H. aeneocolor*, like *H. elegans*, resembles the generalized *Haplochromis* species of Lake Victoria, in particular *H. pallidus*. But, in the absence of any clearly defined specializations in the species involved, little significance can be attached to these resemblances. The peculiar flange formation on the outer teeth of *H. aeneocolor* is an unusual feature for *Haplochromis* but its recognition as a specialization remains to be confirmed. Certainly it is rarely manifest among Lake Victoria species, but it does occur more frequently (if only as an individual variant) amongst the species of Lakes Edward and George.

Finally, and as if to reinforce the generalized nature of *H. aeneocolor* anatomy, the resemblance between this species and *H. nubilus* (Blgr.) should be noted. *Haplochromis nubilus* is one of the anatomically and ecologically most generalized species occurring in the Victoria-Edward drainage basin (see p. 221), and in turn shows close affinity with the fluviatile species of east Africa. On all morphometric characters *H. nubilus* and *H. aeneocolor* cannot be separated, but male coloration is markedly distinct, the caudal of *H. nubilus* has a nearly round distal outline, flanged teeth are not found (the teeth are unicuspid in large fishes) and the dorsal head profile is more concave than in *H. aeneocolor*.

#### STUDY MATERIAL

Register number BMNH	Locality : Lake George
1972.6.2 : 43 (Holotype)	N.E. shore near River Mpanga mouth
1972.6.2 : 44-50 (Paratypes)	Kankurunga Island
1972.6.2 : 52-54 (Paratypes)	Kashaka Crater
1972.6.2 : 55-63 (Paratypes)	N.E. shore
1972.6.2 : 64-67 (Paratypes)	N.E. shore
1972.6.2 : 68-72 (Paratypes)	Kashaka Bay
1972.6.2 : 73-79 (Paratypes)	Kankurunga Island
1972.6.2 : 81-84	Papyrus shore off I.B.P. Laboratory



1972.6.2 : 85-103

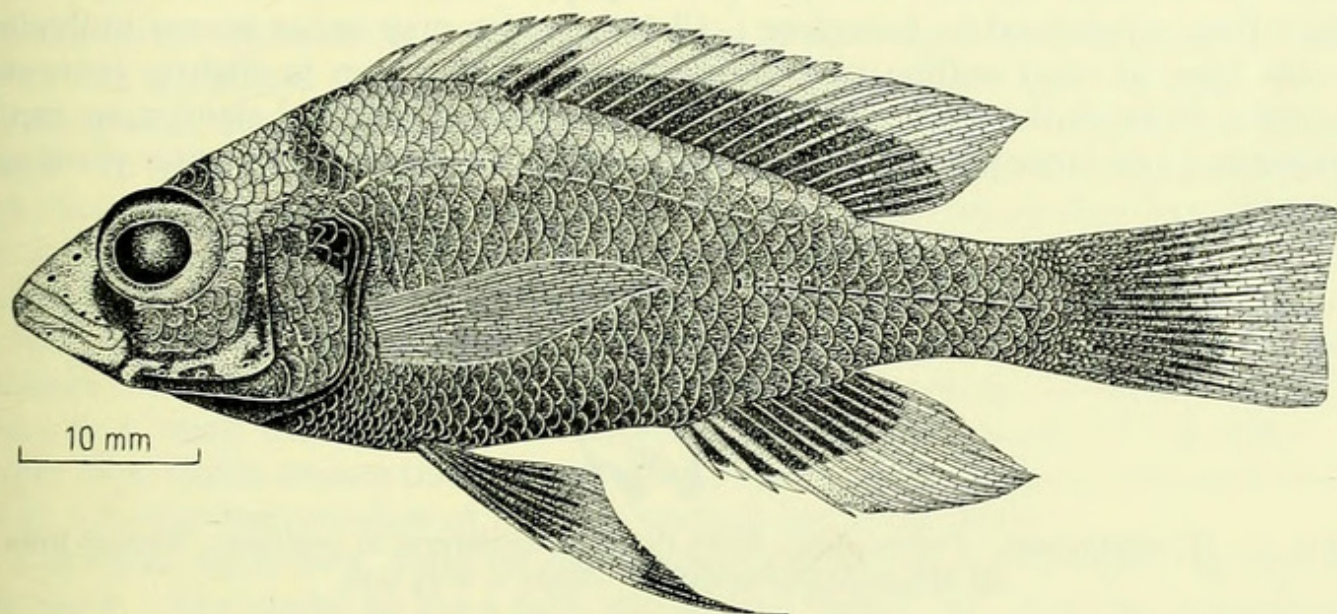
N.E. shore

1972.6.2 : 104-III

Kankurunga Island

***Haplochromis nigripinnis* Regan, 1921**

(Text-figs. 6 &amp; 7)

*Haplochromis nigripinnis* Regan, 1921, *Ann. Mag. nat. Hist.* (9) **8** : 635.*Haplochromis nigripinnis* : Trewavas, 1933, *J. Linn. Soc. (Zool.)*, **38** : 330 (refers to Lake Edward fishes only).*Haplochromis guiarti* (part) : Trewavas, 1933, *op. cit.* : 340 (1 of the 3 small fishes from Worthington's (1932) stations 613 and 618, Lake George, viz. BMNH reg. no. 1933.2.23 : 476.**HOLOTYPE.** A male (probably adult), 64.0 mm standard length from Lake Edward, BMNH reg. no. 1914.4.8 : 14.**DESCRIPTION.** Based on 36 specimens (excluding the holotype), 50.0-68.0 mm standard length.Depth of body 32.3-41.5 ( $M = 36.8$ ) per cent of standard length, length of head 31.5-35.3 ( $M = 33.6$ ) per cent. Dorsal head profile straight or gently curved, sloping at *ca* 35°-40° to the horizontal; dorsal margin of orbit barely entering the line of the head profile.Preorbital depth 10.0-14.6 ( $M = 13.0$ ) per cent of head, least interorbital width 20.7-27.5 ( $M = 24.2$ ) per cent, ratio of interorbital width to eye diameter 1.28-1.75 ( $M = 1.49$ ). Snout length 24.0-30.3 ( $M = 27.4$ ) per cent of head, 0.8-0.9 (rarely 1.0) its breadth; eye diameter 33.3-40.0 ( $M = 35.8$ ) per cent, with no detectable allometry; depth of cheek 16.3-22.9 ( $M = 19.8$ ) per cent.FIG. 6. *Haplochromis nigripinnis*. Lake George specimen; a male.Caudal peduncle 15.8-19.8 ( $M = 17.4$ ) per cent of standard length, 1.3-1.8 (modal range 1.5-1.7) times as long as deep.Mouth horizontal, lips not noticeably thickened. Length of upper jaw 30.6-36.9 ( $M = 34.0$ ) per cent of head, length of lower jaw 39.0-47.5 ( $M = 43.6$ ) per cent,



1.8–2.2 (modal range 1.9–2.0) times as long as broad. Posterior tip of the maxilla reaching a vertical through the anterior part of the eye or even to one through the anterior margin of the pupil.

A noticeable feature of the snout in *H. nigripinnis* is the size of the anterior opening to the nasal laterosensory canal. The opening is as large as (or almost as large as) the nostril. In most other *Haplochromis* species from Lake George (and apparently Lake Edward also) the opening to this canal is much smaller than the nostril, and is often difficult to locate.

The intestine in *H. nigripinnis* is long (ca 2–2½ times total length) and much coiled on itself.

*Gill rakers* on the first arch are, except for the reduced lower 1–3 and the occasional flattened and anvil-shaped upper 1–3, slender and relatively elongate. There are 8–10 (mode 9), rarely 11, rakers on the lower part of this arch. No pseudorakers are developed (see p. 145).

*Scales.* Ctenoid; lateral line with 30 (f.6), 31 (f.13), 32 (f.14) or 33 (f.3) scales, cheek with 2 or 3 (mode) rows. Five to 6½ (mode 5½) scales between the upper lateral line and the dorsal fin origin, 6 or 7 (mode), rarely 5, between the pectoral and pelvic fin bases.

*Fins.* Dorsal with 14 (f.1), 15 (f.28) or 16 (f.7) spinous and 8 (f.7), 9 (f.24) or 10 (f.5) branched rays. Caudal generally truncate but weakly emarginate in some fishes; scaled on its basal half. Pectorals 25.8–31.3 ( $M = 29.7$ ) per cent of standard length, 79.5–94.5 ( $M = 87.3$ ) per cent of head. Pelvics with the first ray slightly produced.

*Teeth.* The *outer teeth* in both jaws (except posteriorly in the upper) are slender, compressed and unequally bicuspid (text-fig. 7). The outline of the major cusp varies from equilateral to isoscelene; all intergrades may occur in one individual or one type of cusp outline may predominate. The crown is slightly incurved. Posterior teeth in the upper jaw are often either unicuspid and slender, or small, compressed and tricuspid. There are 40–60 ( $M = 52$ ) teeth in the outer premaxillary row.

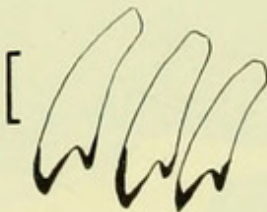


FIG. 7. *H. nigripinnis*. Premaxillary teeth (left), anterolateral in position. Viewed from an anterolateral position. Scale = 0.25 mm.

Teeth of the *inner rows* are small, compressed and tricuspid, and are arranged in 1 or 2 rows (rarely in 3) in the upper jaw, and 1 or 2 in the lower jaw. The serial arrangement of these teeth is often rather irregular.

**OSTEOLOGY.** The *neurocranium* of *H. nigripinnis* is identical with that of *H. elegans* and *H. aeneocolor*, that is, of a generalized type.



The *lower pharyngeal bone* gives an impression of being long, slender and fine (especially when compared with the bone in *H. elegans* or *H. aeneocolor*). Its denticulate surface, however, is about 1.2 times broader than long. The teeth on this bone are fine, slender and cuspidate, and are arranged in *ca* 34 rows; teeth situated on the posterolateral angles of the bone are more densely crowded than elsewhere.

*Vertebral counts* in the 13 specimens radiographed are 28 (f.1), 29 (f.9), 30 (f.2) or 31 (f.1), and comprise 12 (f.2), 13 (f.10) or 14 (f.1) abdominal and 16 (f.9) or 17 (f.4) caudal elements.

**COLORATION IN LIFE.** *Adult males*: ground colour (including that of the head) is a dark malachite green with a silvery underlay; the branchiostegal membrane is black. On the head there is a prominent lachrymal stripe and a less intense interorbital bar; both marks are intensified after death. The dorsal fin is dark grey, with black lappets, and a darker irregular line along the base; a pink suffusion is visible over the soft part of the fin. The caudal has an overall pink flush except basally, where the membrane is dark hyaline. The anal is black over the spinous part, pinkish elsewhere (the colour intensifying distally); ocelli orange-yellow. Pelvic fins are black.

*Adult females* have an overall greyish-silver coloration above a midlateral line, and are chalky white below that level. The upper half of the caudal fin is hyaline but the basal area and lower half of the fin are suffused with pale lemon-yellow; this pigmentation sometimes extends over the entire fin but even then is most intense on the lower half. Some individuals show dark rather elongate spots along the middle of the caudal. The anal has, distally, similar yellow colour to that of the caudal but it is hyaline basally. The dorsal and pelvic fins both are hyaline.

**PRESERVED COLORATION.** *Adult males*: the ground colour is dark brown to black below the midlateral line, and to varying degrees above that level as well. When dark pigment does extend dorsally it is generally less intense than on the ventral body. In some fishes up to seven dark, fairly narrow vertical bars extend across the light brown of the upper body; sometimes there is a longitudinal dark bar extending for a variable length along the upper lateral line scale row.

The ventral half of the head is dark brown, the branchiostegal membrane black. A fairly distinct lachrymal stripe is usually visible through the general dark ground coloration of the snout. Two bars (of equal thickness) cross the snout, and often there is a small median blotch above the posterodorsal margin of the orbit. A larger dark blotch crosses the nape anterior to the dorsal fin origin; this mark seems to be a medial continuation of the first vertical bar of the flank.

The dorsal fin is dark, black on its proximal half and dusky beyond; the lappets are black. The caudal fin has a dark central area basally but otherwise it is greyish. The anal is black on its basal half, and dusky or hyaline distally. The pelvics are uniformly black or blotched black and dusky, the outer half of the fin being the darker part. The pectorals are hyaline.

*Females* have a greyish-silver to greyish-brown ground colour, and are lighter ventrally. In some few specimens very faint indications of vertical bars are visible on the flanks; such marks are confined to the central flank region and do not extend



as far as the dorsal or ventral body outline. All fins are hyaline, the dorsal sometimes greyish with dark lappets.

**ECOLOGY.** *Habitat.* Although predominantly a species of offshore areas and the open central part of the lake, *H. nigripinnis* is sometimes found within a few feet of the shoreline, especially where the substrate is sandy.

*Food.* As the long and coiled intestine suggests, *H. nigripinnis* is a vegetarian species. It feeds principally on suspended phytoplankton; there is no indication from the gut contents of any bottom feeding habits. Like many *Haplochromis* species, *H. nigripinnis* is an opportunistic feeder; insect remains (of both larvae and pupae) are recorded from the gut.

*Breeding.* Female mouth brooding is practised by *H. nigripinnis*. Of the 8 adult females examined, 5 have the right ovary noticeably larger than the left, 1 has the right ovary slightly the larger and 2 show equal ovarian development.

*Distribution.* Lakes Edward and George and the Kazinga Channel.

**DIAGNOSIS AND AFFINITIES.** Trewavas (1933) compared *H. nigripinnis* with *H. cinereus* (Blgr.) of Lake Victoria. The invalidity of this comparison has been commented upon above (p. 149). It is due entirely to there being, at that time, insufficient material of either species to permit of precise comparison.

Surprisingly, neither Trewavas (*op. cit.*) nor Regan (1921) compared *H. nigripinnis* with any other species in the Edward-George complex. *Haplochromis nigripinnis* is indeed a distinctive species, especially when its coloration, fine dentition, long gut, fine gill rakers and its feeding habits are considered. But, preserved specimens (or live females) have a great similarity with specimens of *H. macropsoides*, a new taxon described on p. 162.

*Haplochromis nigripinnis* differs from *H. macropsoides* in having finer outer teeth in both jaws, fewer rows of inner jaw teeth, a longer and more slender caudal peduncle, and in having a relatively larger opening to the nasal laterosensory canal (*see above*, p. 156).

The same character combination (and especially the dental ones) serves to distinguish *H. nigripinnis* from such species as *H. elegans*, *H. aeneocolor* and *H. limax*. In all instances, of course, male breeding coloration provides the most outstanding interspecific difference.

Outside Lakes Edward and George, the greatest morpho-anatomical (and ecological) resemblances are with *H. erythrocephalus* Greenwood & Gee, of Lake Victoria (Greenwood & Gee 1969). Both species have, besides a similar gross morphology, a diet of phytoplankton, fine and numerous teeth, slender gill rakers and a long, coiled intestine; all, of course, correlated characters within each species. Male coloration is particularly different. Male *H. erythrocephalus* have a bright red head, while the head in *H. nigripinnis* is dark malachite green (*cf.* p. 157 above with p. 21 in Greenwood & Gee, *op. cit.*). There are several other interspecific differences, particularly in the pharyngeal dentition and the neurocranial shape. Skull form in *H. erythrocephalus* is more like that in the moderately specialized *Haplochromis* species, and the pharyngeal teeth are finer, more numerous and more densely arranged than in *H. nigripinnis*. *Haplochromis erythrocephalus* also has



relatively longer and more slender gill rakers. In other words, *H. erythrocephalus* shows greater specialization for phytoplankton feeding than does *H. nigripinnis*.

#### STUDY MATERIAL

Register number BMNH	Locality : Lake George
1972.6.2 : 549-554	Tufmac Bay (trawl)
1972.6.2 : 598-601	Small island north of Kankurunga Island
1972.6.2 : 602-605	Small island north of Kankurunga Island
1972.6.2 : 606	Kashaka Bay
1972.6.2 : 607-611	Kashaka Bay
1972.6.2 : 648-654	East side of Akika Island
1972.6.2 : 636-647	Mid-lake <i>ca</i> 5 miles east of Kankurunga Island
1972.6.2 : 805 (figured specimen)	Small island north of Akika Island (trawl)

### *Haplochromis oregosoma* sp. nov.

(Text-figs. 8 & 9)

**HOLOTYPE.** A female, 66.5 mm standard length, BMNH reg. no. 1972.6.2 : 141.

The specific name (from the Greek *orego* to stretch and *soma* the body) alludes to the rather elongate form of this species.

**DESCRIPTION.** Based on 20 specimens, including the holotype, 48.0-72.5 mm standard length.

Depth of body 30.3-34.3 ( $M = 32.1$ ) per cent of standard length, length of head 32.0-36.0 ( $M = 33.8$ ) per cent. Dorsal head profile gently curved, less commonly straight, sloping at an angle of *ca* 35° to the horizontal ; dorsal margin of eye entering the profile or extending slightly above it.

Preorbital depth 10.5-15.2 ( $M = 13.3$ ) per cent of head (showing ill-defined positive allometry with standard length), least interorbital width 20.0-25.0 ( $M = 22.3$ ) per cent, ratio of interorbital width to eye diameter 1.5-1.8 ( $M = 1.7$ ). Snout length 23.5-29.2 ( $M = 26.1$ ) per cent of head, 0.7-0.9 (rarely 1.0) times broader than long ; eye diameter 33.4-41.2 ( $M = 38.2$ ) per cent, depth of cheek 15.2-20.8 ( $M = 17.9$ ) per cent.

Caudal peduncle 15.9-21.1 ( $M = 17.9$ ) per cent of standard length, 1.4-2.0 (modal range 1.6-1.7) times as long as deep.

Mouth horizontal, lips not thickened. Length of upper jaw 28.6-34.7 ( $M = 31.7$ ) per cent of head, length of lower jaw 38.1-45.6 ( $M = 41.9$ ) per cent and 1.6-2.3 (mode 2.0) times as long as broad. Posterior tip of the maxilla reaching a vertical through the anterior margin of the eye.

Intestine about  $1\frac{1}{2}$  times the total length.

**Gill rakers.** The lower 1-3 on the first arch are reduced, the remainder either all slender and elongate or, less commonly, with the upper 2-4 flattened and branched. There are 9-11 (mode 10) rakers on the lower part of the first arch. No pseudorakers are developed.

**Scales.** Ctenoid ; lateral line with 30 (f.1), 31 (f.3), 32 (f.10) or 33 (f.5), cheek with 2 or 3 rows. Five to 6 (bimodal at  $5\frac{1}{2}$  and 6) scales between the upper lateral line and dorsal fin origin, 5 or 6 (mode) between the pectoral and pelvic fin bases.



*Fins.* Dorsal with 15 (f.11) or 16 (f.9) spines, and 8 (f.5) 9 (f.9) or 10 (f.6) branched rays. Anal with 3 spines and 7 (f.1), 8 (f.8) or 9 (f.11) branched rays. Caudal slightly emarginate, scaled on its basal half or a little further posteriorly. Pectoral fin 25.6–30.0 ( $M = 28.1$ ) per cent of standard length, 75.0–88.0 ( $M = 82.7$ ) per cent of head. Pelvics with the first ray slightly produced.

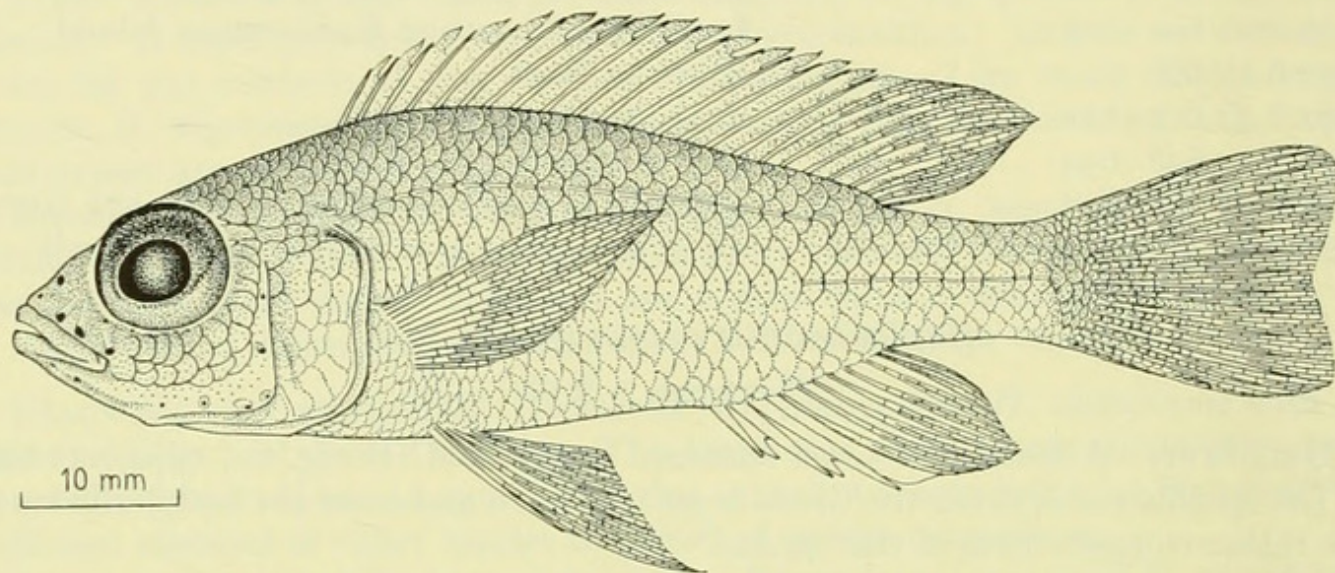


FIG. 8. *Haplochromis oregosoma*. Holotype.

*Teeth.* The predominant tooth form in the *outer row* of both jaws is a moderately slender, compressed and unequally bicuspid tooth (text-fig. 9). The major cusp in such teeth is produced, isoscelene in outline and slightly incurved. A distinct, step-like flange is sometimes developed on that margin of the cusp adjacent to the minor cusp. Some teeth may have the minor cusp greatly reduced in size. Posterolateral teeth in the upper jaw may be bicuspid like the others, slender unicuspid or compressed tricuspid. Tricuspid teeth are occasionally intercalated amongst the anteriorly situated bicuspid in either or both jaws. There are 42–60 ( $M = 50$ ) outer teeth in the premaxilla.

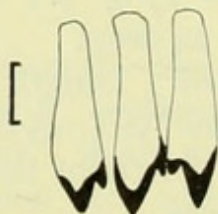


FIG. 9. *H. oregosoma*. Premaxillary teeth (left side), anterior in position. Viewed anteriorly. Scale = 0.25 mm.

*Inner* tooth rows in both jaws are composed of small tricuspid and compressed teeth, arranged in a single (rarely double) series.

*OSTEOLOGY.* Basically, the *neurocranium* of *H. oregosoma* is of the generalized *Haplochromis* type, but differs in having a low supraoccipital crest and a relatively shorter ethmo-vomerine region.



The lower pharyngeal bone is fine, its dentigerous area slightly broader than long (1.1–1.2 times). The teeth are slender and cuspidate, and are arranged in ca 26–30 rows.

Vertebral counts in the 12 specimens radiographed are 29 (f.3) or 30 (f.9), comprising 13 (f.5) or 14 (f.7) abdominal and 15 (f.1), 16 (f.8) or 17 (f.3) caudal centra.

COLORATION IN LIFE. *Adult males*: ground colour metallic purple above the midlateral line, shading through iridescent turquoise to silvery on the belly and ventral flanks; a sooty overlay spreads across the chest and belly. The dorsal fin is a dark sooty colour, as is most of the anal except for its scarlet tip; the anal ocelli are large, near circular in outline, and orange-yellow in colour. The entire caudal fin is scarlet, but the basal fifth may be sooty or solid black. The pelvic fins are uniformly black.

*Adult females* are an overall greyish-silver. The dorsal fin is hyaline, the anal pale yellow, the caudal dark hyaline and the pelvics greyish.

PRESERVED COLORATION. *Adult males*: ground coloration black or intensely dusky, with a silvery underlay; the chest and midventral aspects of the belly are light dusky. No distinct markings are visible on the head (probably they are obscured by the general dark coloration). Dorsal fin dusky to black, the pigment most intense between the rays. Anal black over its distal two-thirds, dusky beyond. Caudal with variable coloration but always dark over the proximal third; distally the fin is usually yellowish with a dusky overlay that intensifies between the middle rays. The pelvic fins are black, the pectorals hyaline.

*Adult females* are silvery-grey, shading to silver on the chest and belly; the dorsum and snout are dark grey. No cephalic markings are visible. All fins are greyish-hyaline.

BIOLOGY. Very little is known about the biology of *H. oregosoma*. Apparently the species is confined to offshore areas of the lake, and it does not occur close to papyrus or other shores. Specimens have been caught over both sand and mud substrata.

The breeding habits are unknown; of 9 adult females examined, 4 have the right ovary considerably larger than the left one, 4 have the ovaries equally developed and 1 has the left ovary larger than the right one. Individuals less than 55 mm standard length are immature, although males of 56 mm standard length are ripening. Fishes, of both sexes, are fully adult at 60 mm standard length.

*Haplochromis oregosoma* seems to feed on phytoplankton, but as yet too few specimens have been examined to establish whether the food is taken in suspension or from bottom deposits.

*Distribution.* Lake George and the Kazinga Channel.

DIAGNOSIS AND AFFINITIES. From all other *Haplochromis* species in Lake George, *H. oregosoma* is distinguished by the following character combination: large eye, numerous and slender gill rakers, slender and elongate body form. Perhaps the species showing most superficial similarity with *H. oregosoma* is *H. nigripinnis*; the characters listed above, together with a difference in eye/interorbital ratio (1.5–1.8, mean 1.7, cf. 1.3–1.8, mean 1.5 for *H. nigripinnis*) serve to distinguish the species.



The totality of characters (including skull and jaw form) suggest that *H. nigripinnis* and *H. oregosoma* are probably not very closely related.

Among the Lake Edward species not recorded from Lake George, there is some resemblance between *H. oregosoma* and *H. engystoma* Trewavas. Unfortunately, *H. engystoma* is known only from the holotype (now in a poor state of preservation) and another, much smaller specimen which may not be a member of the species. Comparing *H. engystoma* holotype with *H. oregosoma*, the latter differs in having more gill rakers (10 or 11, cf. 8), straighter teeth, longer lower jaw (38.1–45.6,  $M = 41.9$  per cent head, cf. 34.8 per cent in *H. engystoma*), and a slightly larger eye (33.4–41.2,  $M = 38.2$  per cent head, cf. 34.8 per cent).

No known species from Lake Victoria shows any close resemblance to *H. oregosoma*.

#### STUDY MATERIAL

Register number BMNH	Locality : Lake George
1972.6.2 : 141 (Holotype)	North end of Kankurunga Island
1972.6.2 : 142–146 (Paratypes)	North end of Kankurunga Island
1972.6.2 : 147 (Paratype)	Northern tip Kankurunga Island
1972.6.2 : 148–152 (Paratypes)	Northern tip Kankurunga Island
1972.6.2 : 153 (Paratype)	Kankurunga Island
1972.6.2 : 154 (Paratype)	Tufmac Bay
1972.6.2 : 165 (Paratype)	In sandy shallows
1972.6.2 : 155–160	Tufmac Bay
1972.6.2 : 161–164	Tufmac Bay

### *Haplochromis macropsoides* sp. nov.

(Text-figs. 10–12)

*H. vicarius* (part) Trewavas, 1933, *J. Linn. Soc. (Zool.)*, **38**: 330–331 (1 of the paratypes, BMNH reg. no. 1933.2.23 : 353 from Worthington's station 613, Lake George. Trewavas incorrectly lists this station as '... East shore of Lake Edward', but *vide* Worthington 1932).

**HOLOTYPE.** A male, 76.0 mm standard length, BMNH reg. no. 1972.6.2 : 718.

The trivial name refers to the overall similarity between this species and *H. macrops* (Blgr.) of Lake Victoria (and, so it was once thought, of Lake Edward as well).

**DESCRIPTION.** Based on 30 specimens (including the holotype, and the paratype of *H. vicarius*, see above), 59.0–77.0 mm standard length.

Depth of body 34.9–41.0 ( $M = 36.5$ ) per cent of standard length, length of head 32.2–37.2 ( $M = 34.3$ ) per cent. Dorsal head profile straight or very slightly curved, sloping at an angle of ca 35°–40° to the horizontal; dorsal margin of the eye entering the line of the profile or extending slightly above it.

Preorbital depth 12.0–15.2 ( $M = 13.5$ ) per cent of head, least interorbital width 20.5–25.0 ( $M = 23.1$ ) per cent. Snout length 25.0–30.5 ( $M = 27.6$ ) per cent, 0.8–0.9 times broader than long, eye diameter 33.3–39.1 ( $M = 36.0$ ) per cent, showing very slight negative allometry with standard length, depth of cheek 17.5–23.8 ( $M = 21.4$ ) per cent.



Caudal peduncle 13.6–19.3 ( $M = 15.8$ ) per cent of standard length, 1.0–1.5 (modal range 1.2–1.3) times as long as deep.

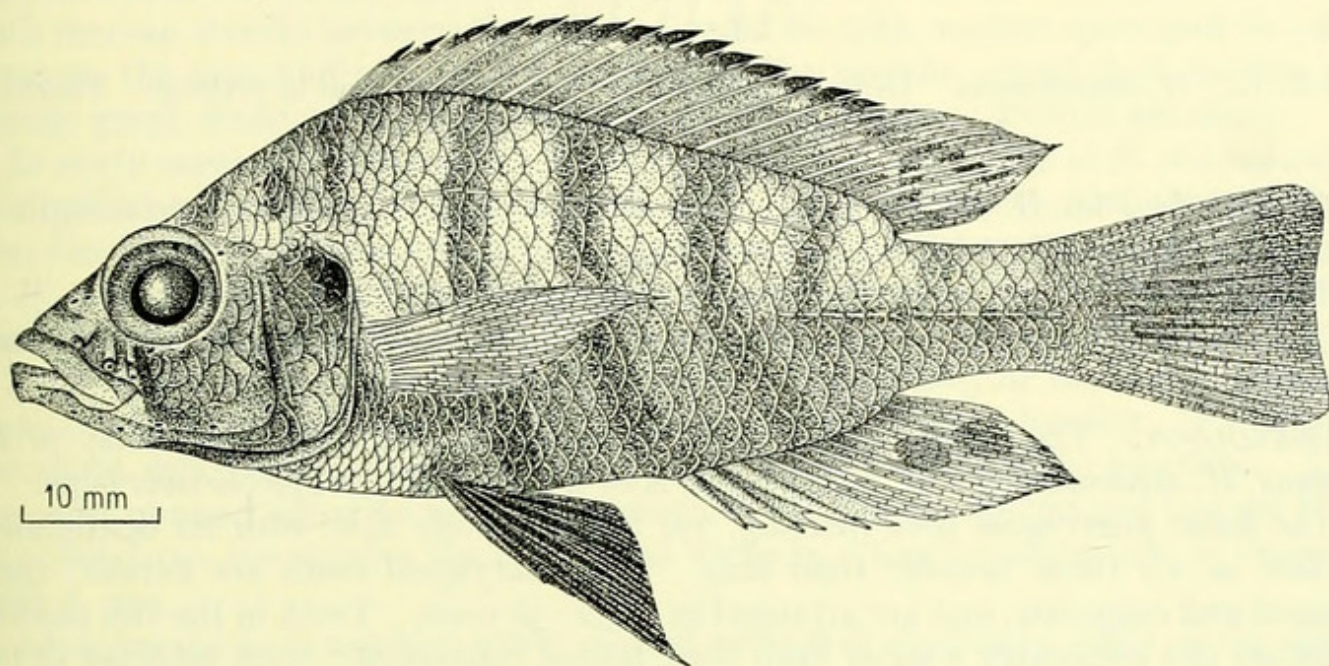


FIG. 10. *Haplochromis macropsoides*. Holotype.

Mouth horizontal, lips not thickened. Length of upper jaw 31.3–41.5 ( $M = 34.2$ ) per cent of head, length of lower jaw 39.2–45.4 ( $M = 41.0$ ) per cent, 1.7–2.2 (modal range 1.7–1.9) times as long as broad. Posterior tip of the maxilla reaching a vertical through the anterior margin of the eye or somewhat behind that level.

The anterior opening to the nasal laterosensory canal is much smaller than the nostril (*cf. H. nigripinnis*), and indeed, can be difficult to locate.

The intestine is  $1\frac{1}{3}$ – $1\frac{1}{2}$  times the total length.

*Gill rakers.* Except for the reduced lower 1 or 2 rakers, others on the first gill arch are relatively slender, although some of the uppermost ones may be flat and some lower ones stout. There are 8–10 (mode 9) rakers on the lower part of this arch. Pseudorakers are present, but are poorly developed and small.

*Scales.* Ctenoid; lateral line with 30 (f.2), 31 (f.9), 32 (f.15) or 33 (f.4) scales, cheek with 2 or 3 (bimodal) rows. Five to  $6\frac{1}{2}$  (mode 6) scales between the upper lateral line and the dorsal fin origin, 6 or 7 (rarely 5) between the pectoral and pelvic fin bases.

*Fins.* Dorsal with 14 (f.4), 15 (f.20) or 16 (f.6) spinous and 8 (f.4), 9 (f.10) or 10 (f.16) branched rays. Anal with 3 spines and 8 (f.7), 9 (f.22) or 10 (f.1) branched rays. Caudal truncate or, less frequently, weakly emarginate; scaled on its basal half. Pectorals 25.7–32.3 ( $M = 29.4$ ) per cent of standard length, 73.0–95.5 ( $M = 85.0$ ) per cent of head. Pelvics with the first ray slightly produced.

*Teeth.* The majority of the *outer teeth* in both jaws are relatively stout, compressed and very unequally bicuspid; the larger cusp is isoscelene in outline and the crown slightly incurved (text-fig. 11). Posteriorly in the upper jaw the last few teeth are often slender and unicuspid. Some tricuspid teeth may be intercalated amongst the bicuspids anteriorly in either or both jaws.



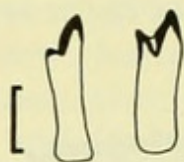


FIG. 11. *H. macropsoides*. Dentary teeth (right side), anterolateral in position. Viewed anteriorly. Scale = 0.5 mm.

As described for *H. elegans* (see p. 147), some bicuspid can have one margin of the major cusp produced into a narrow flange.

There are 42–60 ( $M = 52$ ) teeth in the outer premaxillary series.

The *inner tooth rows* (2 or 3 in both jaws) are composed of tricuspid, compressed teeth.

**OSTEOLOGY.** The *neurocranium* of *H. macropsoides*, identical with that of *H. elegans*, *H. aeneocolor* and *H. nigripinnis*, is of a generalized *Haplochromis* type.

The *lower pharyngeal bone* (text-fig. 12) is moderately fine, with its dentigerous surface *ca* 1.2 times broader than long. The pharyngeal teeth are slender, compressed and cuspidate, and are arranged in *ca* 32–36 rows. Teeth in the two median rows are not noticeably coarser than their lateral congeners; teeth situated in the posterolateral corners of the bone are more closely set than elsewhere.

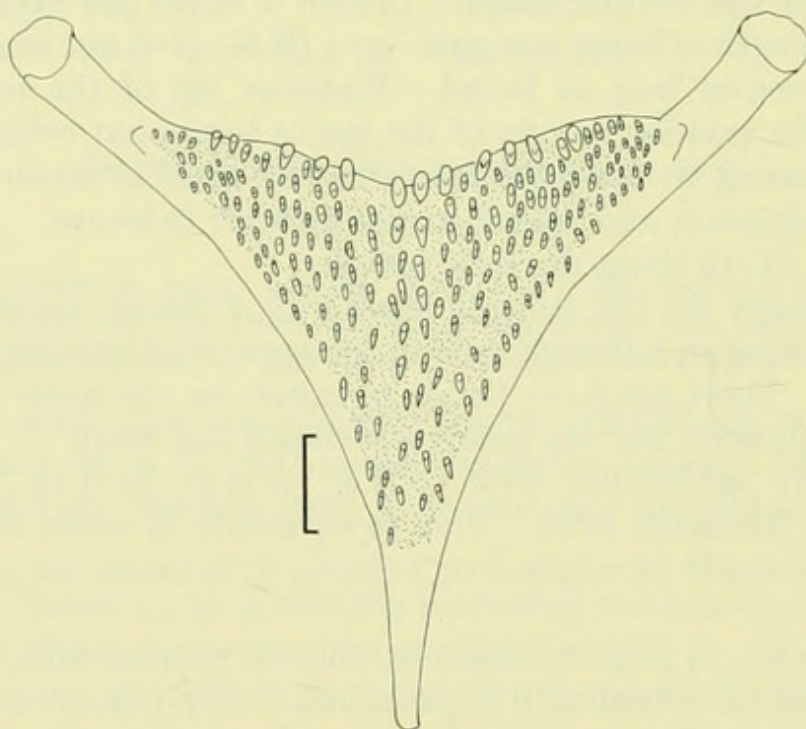


FIG. 12. *H. macropsoides*. Lower pharyngeal bone, occlusal view. Scale = 1.0 mm.

*Vertebral counts* in the 7 specimens examined are: 29 (f.6) or 30 (f.1), comprising 13 abdominal and 16 (f.6) or 17 (f.1) caudal centra.

**COLORATION IN LIFE.** *Adult males*: ground colour smokey grey overlying bluish-silver; snout, cheeks and lips a muted iridescent blue-green. Shortly after death, six faint vertical bars appear on the flanks; the first and second bars are separated



by a greater distance than that between any of the succeeding bars. Dorsal fin with the spinous part sooty, the interspinous membrane generally darkest in colour; lappets black but with a narrow red streak or spot at the tip. Soft part of dorsal with maroon streaks between the rays. Caudal fin with maroon spots and blotches between the rays and a maroon flush around the margin. Anal dark hyaline (or faintly grey), dusky at the base but with a pinkish border. Pelvics are black.

In every major detail the adult, sexually active male coloration of *H. macropsoides* is identical with that of *H. elegans*. The sole colour difference, and that a subtle one, lies in the less brilliantly iridescent blue colour of the snout, cheeks and lips; in *H. macropsoides* the colour is more blue-green. More vertical stripes (9) appear after death in *H. elegans*.

I have been able to compare live fishes, of both species, in the same advanced state of sexual activity (i.e. ripe-running) and from the same locality. Except for the slight differences noted, I would consider the coloration to be identical. This is a most unusual situation amongst syntopic *Haplochromis* species and has not been recorded from the species flock of Lake Victoria. Further comment is reserved until p. 229.

*Adult females* have a golden-silver ground coloration shading to white on the belly. The dorsal fin has sooty lappets and an overall dark coloration except for reddish vertical stripes between the spines. The caudal fin is fairly dusky, with dark red streaks between the middle rays, and traces of red on the upper posterior margin. The anal is pale yellow, with a prominent orange spot occupying the position of an ocellus in a male fish. The pelvics are pale yellow.

**PRESERVED COLORATION.** *Adult males* have a generally dusky ground colour, darkest on the ventral aspects of the flanks and belly, but greyish-silver on the chest. At least 5 dark vertical bars are visible on the flanks; each bar extends from the dorsal to the ventral body outline. The head is dusky overall, with a distinct lachrymal stripe. Paired trans-snout bars are rarely visible, and then but faintly. No other cephalic markings can be detected (cf. *H. elegans*, p. 148). The branchiostegal membrane is black. The dorsal fin is dark grey to dusky, sometimes with a narrow black band along the entire base; the lappets are black, and the soft part of the fin is darkly maculate. Caudal fin greyish (darkest basally) and maculate but sometimes only weakly so. The anal is black or dark grey along its basal half, hyaline to light grey distally. The pelvics are dusky to black, the pectorals hyaline.

*Adult females* are greyish-silver, the ventral half of the body more silver than grey. No distinct cephalic markings are present. The dorsal and caudal fins are greyish hyaline, the margin of the dorsal often dusky. The caudal is immaculate, but has dark, ill-defined streaks between its rays. All other fins are hyaline.

**ECOLOGY. Habitat.** Not a great deal of information is available for this species, probably because in the field it is easily confused with *H. nigripinnis* and *H. elegans*. The specimens of *H. macropsoides* at my disposal are either from lake areas close to the fringing papyrus of islands (especially Kankurunga and Akika) or from more exposed areas offshore from these islands. In all localities the substrate is either sand with a thin mud overlay or organic mud.



*Food.* Only 6 of the specimens I have examined contained ingested material in the guts; in all, this comprised dipteran larvae and pupae. As no other material was present (and particularly no phytoplankton or sand grains) the fishes may have been feeding away from the bottom.

*Breeding.* *Haplochromis macropsoides* is a female mouth brooder. All 7 of the adult, sexually active females examined have the right ovary much larger than the left one.

*Distribution.* Definitely recorded from Lake George and the Kazinga Channel (where it is scarce). The species probably occurs in Lake Edward as well since some specimens in the British Museum (Natural History), misidentified as *H. macrops* (Blgr.), a Lake Victoria endemic, are probably referable to *H. macropsoides*.

DIAGNOSIS AND AFFINITIES. As noted above (p. 165) the male reproductive coloration of *H. macropsoides* is virtually identical with that of *H. elegans*. However, the species clearly differ in a number of characters, including dentition (more outer teeth and more inner tooth rows in *H. macropsoides*) and the larger eye and longer upper and lower jaws of *H. macropsoides*.

From *H. nigripinnis*, *H. macropsoides* is distinguished by its deeper caudal peduncle (length/depth ratio 1.0–1.5, modal range 1.2–1.3, cf. 1.3–1.8, modal range 1.5–1.7 for *H. nigripinnis*), broader and more numerous inner tooth rows (3 in both jaws, cf. 1 or 2) and in having the anterior opening to the nasal laterosensory canal much smaller than the nostril (equal to it in *H. nigripinnis*). The species also differ in male coloration and, apparently, in their feeding habits (the intestine of *H. nigripinnis* is much longer and more coiled than that of *H. macropsoides*, and the former species is known to be a specialized phytoplankton eater).

From *H. oregosoma*, another large-eyed Lake George species, *H. macropsoides* differs in body form (depth 30.3–34.3,  $M = 32.1$  per cent of standard length in *H. oregosoma*, cf. 34.9–41.0,  $M = 36.5$  per cent; also the caudal peduncle is more slender in *H. oregosoma*, namely 1.4–2.0, modal range 1.6–1.7 times longer than deep, cf. 1.0–1.5 modal range 1.2–1.3), in dentition (2–3 inner tooth rows in *H. macropsoides* cf. 1 in *H. oregosoma*), in neurocranial shape and in adult male coloration.

At first glance, *H. macropsoides* resembles *H. macrops* (Blgr.) of Lake Victoria. Closer inspection shows that the species differ in several characters. For example, the interorbital width is less in *H. macropsoides* (20.5–25.0,  $M = 23.1$  per cent of head, cf. 26.6–32.2,  $M = 29.7$  per cent in *H. macrops*), the eye is larger (33.3–39.1,  $M = 36.0$  per cent of head, cf. 28.6–35.4,  $M = 33.0$  per cent in *H. macrops*), the lower jaw is longer (39.2–45.4,  $M = 41.0$  per cent head, cf. 38.0–42.5,  $M = 39.5$ ) and the outer jaw teeth are fewer (42–60,  $M = 52$ , cf. 46–66,  $M = 60$  in *H. macrops*). Male breeding coloration differs (cf. p. 164 above with p. 237 in Greenwood 1960). The supposed occurrence of *H. macrops* in Lakes Edward and George is discussed on p. 232.

*Haplochromis velifer* Trewavas of Lake Nabugabo resembles *H. macropsoides* in several respects. However, the species may be differentiated by the shallower preorbital of *H. macropsoides* (12.0–15.2,  $M = 13.5$  per cent head, cf. 13.8–18.5,  $M = 16.3$  per cent), the shorter snout (25.0–30.5,  $M = 27.6$  per cent head, cf.



29.1–33.4,  $M = 31.3$  per cent for *H. velifer*) and larger eye (33.3–39.1,  $M = 36.0$  per cent head, cf. 26.3–33.4,  $M = 30.6$  per cent); male coloration is also quite different in the two species (compare p. 164 above with pp. 321–322 in Greenwood, 1965b).

## STUDY MATERIAL

Register number BMNH	Locality: Lake George
1972.6.2 : 718 (Holotype)	Kankurunga Island
1972.6.2 : 723–728 (Paratypes)	Small island north of Kankurunga Island
1972.6.2 : 734–738 (Paratypes)	East side of Akika Island
1972.6.2 : 739–744 (Paratypes)	East side of Akika Island
1972.6.2 : 746–752 (Paratypes)	East side of Akika Island
1972.6.2 : 753 (Paratype)	Kankurunga Island
1972.6.2 : 754 (Paratype)	Kankurunga Island
1972.6.2 : 802–803 (Paratypes)	Kankurunga Island
1933.2.23 : 354 (Paratype)	Worthington collection
1972.6.2 : 719–722	Small island north of Kankurunga Island
1972.6.2 : 729–733	Small island north of Kankurunga Island
1972.6.2 : 755–756	Kankurunga Island
1972.6.2 : 757–765	East side of Akika Island
1972.6.2 : 766–772	Small island north of Kankurunga Island
1972.6.2 : 773–777	Small island north of Kankurunga Island
1972.6.2 : 778–783	Small island north of Kankurunga Island

*Haplochromis limax* Trewavas, 1933

(Text-figs. 13 &amp; 14)

*H. elegans* (part) Trewavas, 1933, *J. Linn. Soc. (Zool.)*, **38**: 332 (1 specimen, BMNH reg. no. 1933.2.23 : 395, collected by Worthington from Lake George [no other locality data given]).  
 ? *H. nubilus* (part) : Trewavas, 1933, *op. cit.* (2 specimens BMNH reg. nos. 1933.2.23 : 301–302 from Lake George, are tentatively referred to *H. limax*).

**HOLOTYPE.** A male 80 mm standard length (BMNH reg. no. 1933.2.23 : 243) from Lake Edward.

**DESCRIPTION.** Based on 22 specimens (excluding the holotype), 61.0–84.0 mm standard length.

Depth of body 35.4–40.3 ( $M = 37.9$ ) per cent of standard length, length of head 31.8–34.4 ( $M = 33.0$ ) per cent. Dorsal head profile straight (rarely with a slight concavity or a slight convexity), sloping fairly steeply at an angle of *ca* 40°–45° with the horizontal.

Preorbital depth 13.6–18.2 ( $M = 15.4$ ) per cent of head, least interorbital width 23.3–30.5 ( $M = 26.0$ ) per cent. Snout 26.5–31.8 ( $M = 29.0$ ) per cent, 0.8–0.9 (rarely 1.0) times broader than long; eye diameter 28.2–34.1 ( $M = 31.6$ ) per cent, cheek depth 21.1–26.2 ( $M = 23.9$ ) per cent. Caudal peduncle 13.6–18.1 ( $M = 15.3$ ) per cent of standard length, 1.0–1.4 (mode 1.1) times as long as deep.

Mouth slightly oblique, lips a little thickened. Length of upper jaw 29.2–36.0 ( $M = 33.1$ ) per cent of head (showing slight positive allometry with standard



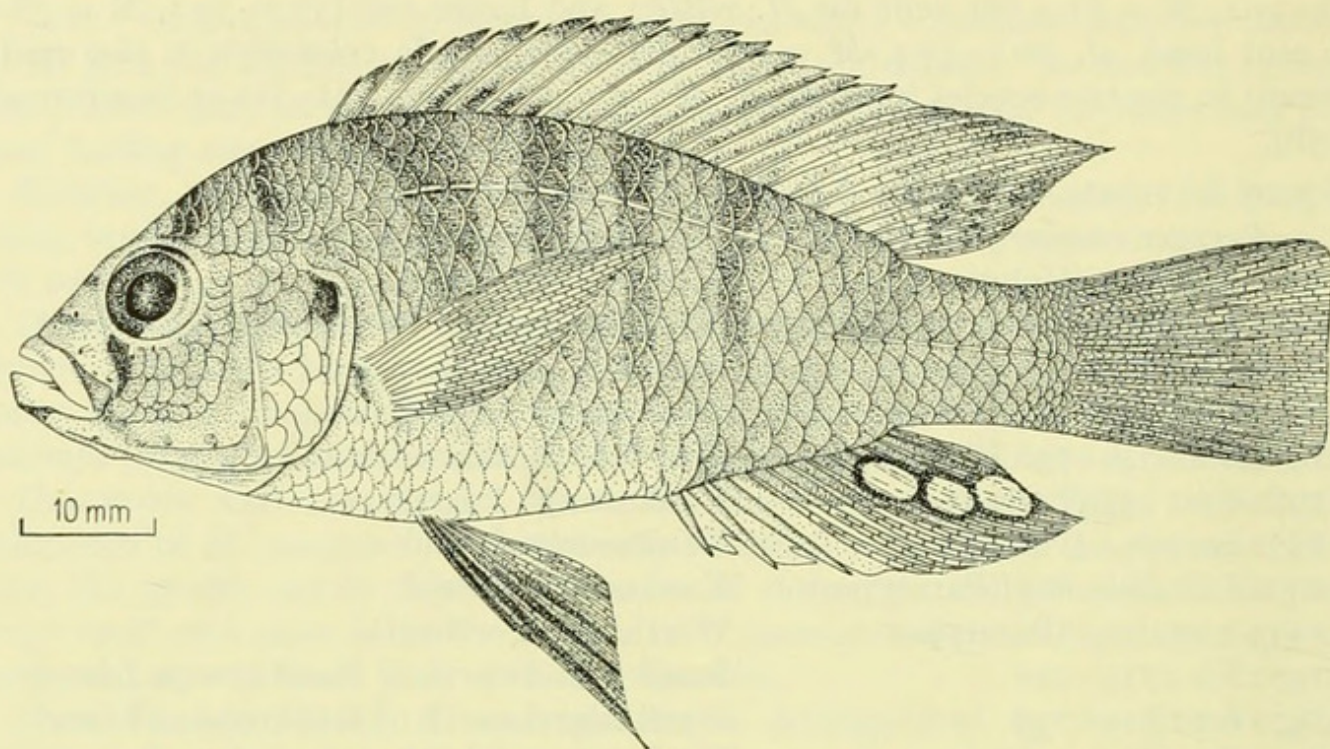


FIG. 13. *Haplochromis limax*. Lake George specimen ; a male.

length), length of lower jaw 36.0–40.9 ( $M = 38.3$ ) per cent, 1.3–1.9 (modal range 1.4–1.6) times as long as broad. Posterior tip of maxilla reaching or almost reaching a vertical through the anterior margin of the eye.

Intestine long, *ca*  $1\frac{1}{2}$  to  $1\frac{3}{4}$  times total length, and much coiled.

*Gill rakers*. Lower 1 or 2 rakers reduced, the remainder relatively slender or with 1 or 2 lower rakers short and stout. (One individual has no reduced rakers, but in this fish the total count is only 7 rakers.) There are 7 (rare) to 10 (mode 9) rakers on the lower part of the first gill arch.

The pseudorakers are well developed and are directed medially so that they overlies the true gill rakers of the inner row.

*Scales*. Ctenoid ; lateral line with 29 (f.1), 30 (f.9), 31 (f.8) or 32 (f.4) scales ; cheek with 2 or 3 (mode) rows. Five to 7 (rarely), mode  $5\frac{1}{2}$ , scales between the upper lateral line and the dorsal fin origin, 5–6 $\frac{1}{2}$  (mode 6) between the pectoral and pelvic fin bases.

*Fins*. Dorsal with 14 (f.4), 15 (f.15) or 16 (f.3) spinous and 8 (f.1), 9 (f.12) or 10 (f.9) branched rays. Anal with 3 spines and 8 (f.1), 9 (f.18) or 10 (f.3) rays. Caudal subtruncate, scaled on its basal half. Pelvics with the first ray produced. Pectoral 26.4–31.0 ( $M = 29.3$ ) per cent of standard length, 80.0–98.0 ( $M = 89.1$ ) per cent of head.

*Teeth*. Although basically the form of *outer row* jaw teeth is that of an obliquely cuspidate bicuspid, there is some individual variability, especially in the upper jaw (text-fig. 14). This variability concerns the angle of the cutting edge to the major cusp. In all specimens examined, this edge is most acute in teeth situated posterolaterally on the premaxilla ; teeth more anteriorly placed sometimes have the cusp so obliquely truncate that the cutting edge is almost horizontal. The modal



condition, however, is one where the edge is at an angle of about  $60^\circ$  with the vertical. It may be noted that, in this respect, the Lake George fishes differ from the holotype whose teeth are of the more acute type.

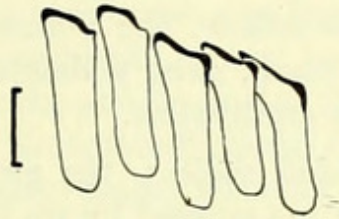


FIG. 14. *H. limax*. Dentary teeth (left), anterolateral in position. Viewed from a slightly ventrolateral position. Scale = 0.5 mm.

In the lower jaw, teeth tend to be more uniform with regard to cusp shape, and are like the modal upper jaw teeth already described. The minor cusp, in teeth of both jaws, is very small irrespective of major cusp shape. Posterior premaxillary teeth (usually the last 1-4 of the series) are generally unicuspid or are of the generalized bicuspid type, that is, with an acutely pointed major cusp.

There are 30-54 ( $M = 46$ ) teeth in the outer premaxillary row.

Teeth of the *inner series* are invariably tricuspid and compressed. There are 4 or 5 (rarely 3) rows anteriorly in the premaxilla, and 3 or 4 (mode) anteriorly in the dentary; laterally and posteriorly the number of rows, in both jaws, decreases to 1. A very distinct interspace separates the outermost row of the inner series from the outer row.

**OSTEOLOGY.** The *neurocranium* is of a generalized *Haplochromis* type but with the preorbital region more noticeably decurved than in *H. macropsoides* and *H. elegans*. Also, when compared with these fishes, the premaxilla of *H. limax* is more robust; the dentary, however, is similar in all three species.

Comparison of *H. limax* syncranium with that in Lake Victoria species of similar feeding habits (i.e. scraping epilithic and epiphytic algae) shows that *H. limax* is more like *H. obliquidens* Hildg. and *H. lividus* Greenwood than *H. nigricans* (Blgr.). In the latter species the preorbital face of the skull is more strongly decurved and the dentary is deeper and more robust.

The lower *pharyngeal bone* in *H. limax* is moderately stout; the dentigerous area is *ca* 1.2 times broader than long. The pharyngeal teeth are fine, compressed and cuspidate, and are arranged in *ca* 28-30 rows.

*Vertebral counts* in the 6 specimens radiographed are: 28 (f.5) and 29 (f.1), comprising 12 (f.1) or 13 (f.5) abdominal and 15 (f.4) or 16 (f.2) caudal elements.

**COLORATION IN LIFE.** *Adult males*: ground colour greyish, with a faint overlay of lime on the caudal peduncle and ventrally on the flanks as far forward as the anal fin. Laterally on the flanks and ventrally on the belly there is a scarlet flush, the intensity and area of which vary with sexual state. In quiescent fishes the flush is the colour of dried blood but it is bright scarlet in sexually active individuals. A similarly coloured flush is developed on the operculum and cheek.

The dorsal fin is dark hyaline with deep scarlet streaks between the spines; between the branched rays the streaks are more precisely demarcated as scarlet



lines. Anal fin is hyaline with a pink flush ; the ocelli are small and yolk-yellow in colour. The pelvic fins are dusky overall.

*Adult females* have a golden-grey ground colour, shading through silver to white on the lower flanks, belly and chest. The dorsal fin is hyaline but is somewhat dusky along its base. Caudal greyish-yellow, the yellow predominating basally. Anal fin also pale grey-yellow, with small, deep yellow spots in the position of ocelli in males. Pelvic and pectoral fins are hyaline.

**PRESERVED COLORATION.** *Adult males* : the ground coloration is silvery grey. The flanks and caudal peduncle are crossed by up to seven faint vertical bars, none of which extends ventrally below the level of the pectoral fin insertion. In some individuals a faint midlateral band is visible on the caudal peduncle, and extending forward to about a vertical through the origin of the soft dorsal fin. The chest, in some fishes, is sooty ; the branchiostegal membrane, in all, is black. A pair of parallel bars (of variable intensity) cross the snout ; a faint transverse bar extends across the head immediately behind the orbit, but in most specimens only that part of the bar immediately above the orbit is at all intense and discrete.

The dorsal fin is always dark, sometimes sooty, sometimes almost solid black between the rays ; the lappets are black. The caudal fin is greyish, becoming yellow on its ventral third ; in a few specimens there are concentrations of melanophores between the middle rays. The anal is greyish basally, yellowish distally. The pelvics are dusky to black on the outer (i.e. anterior) half, but yellowish elsewhere.

*Adult females* have a coloration similar to that of males, but the ground coloration is somewhat lighter and the pelvic fins are hyaline.

**ECOLOGY.** *Habitat.* The distribution of *H. limax* is closely correlated with the presence of emergent rooted vegetation, or of other places suitable for the growth of aufwuchs. *Haplochromis limax* has never been recorded far from the shore line, but the substrata over which it occurs are varied.

*Food.* Aufwuchs, its associated microfauna and macerated phanerogam tissue are the commonest types of ingested matter recorded from the gut. Little of the higher plant tissue is digested ; its occurrence in the gut is probably accidental and associated with the plant-scraping feeding habits of the species. Since sand grains and other inorganic bottom material are sometimes found in the gut, it is presumed that *H. limax* also feeds by scraping suitable food items from the lake bottom.

*Breeding.* *Haplochromis limax* is a female mouth brooder. Of the 6 adult females examined, 5 have the right ovary much larger than the left and 1 has the ovaries equally developed. One of the 2 smallest fishes available (both 61.0 mm standard length) is a juvenile, the other is a male with indications of early sexual development. At a standard length of 64 mm, fishes of both sexes are adult.

*Distribution.* Lakes Edward and George. The absence of this species from samples made in apparently suitable areas of the Kazinga Channel is noteworthy and inexplicable (see Appendix II).

**DIAGNOSIS AND AFFINITIES.** No other *Haplochromis* species in Lake George shows the dental characteristics of *H. limax* ; the male coloration is also highly diagnostic. In Lake Edward, on the other hand, there are two species, *H. serridens*



Regan and *H. fuscus* Regan, both with multiseriate inner tooth rows, and obliquely cuspidate outer teeth. *Haplochromis limax* is distinguished from *H. serridens* by its straighter dorsal head profile (distinctly curved in *H. serridens*), the fewer rows of inner teeth anteriorly in the jaws (3-5, cf. 5-8 in *H. serridens*) and by the presence of a distinct space between the outer tooth rows and the inner series of teeth. From *H. fuscus*, *H. limax* is distinguished primarily by the outer teeth having a broader and more obliquely truncate cusp, by the smaller size of the minor cusp on these teeth and by having a truncate (as opposed to rounded) caudal fin. In addition, preserved male *H. fuscus* are uniformly dark (nearly black) whereas *H. limax* males are silvery grey.

With so few specimens of *H. fuscus* and *H. serridens* available for comparison with *H. limax* it is impossible to evaluate the apparent interspecific differences in some morphometric characters. Data on live colours are not available for *H. serridens* or *H. fuscus*.

From the little information available, it seems reasonable to consider the three species closely related, with *H. serridens* the most specialized (at least in its oral dentition).

Trewavas (1933) noted similarities between *H. limax* and *H. vicarius*. Certainly the outer teeth in many of the *H. vicarius* specimens available do resemble the *H. limax* type. But, they are equally like those of *H. fuscus* (see above). It will be necessary to examine further samples of *H. vicarius*, and get information on live male coloration, before more definite conclusions can be reached on this possible interspecific relationship.

I have compared *H. limax* with those Lake Victoria species having a similar diet and dental specializations (viz. *H. lividus*, *H. nigricans* and *H. obliquidens*). All three species can be distinguished from *H. limax* by various characters or character combinations.

Tooth form and dental pattern in *H. limax* is most like that of *H. lividus*, but it is by no means identical. The teeth of *H. lividus* are more slender, their crowns are relatively less expanded, have curved not straight vertical margins, and are more movably implanted. On these characters, *H. lividus* would seem more specialized than *H. limax*.

The subequally, or almost subequally, bicuspid teeth of *H. nigricans*, coupled with the strongly decurved preorbital skull profile, and the relatively massive dentary of this species, all suggest that it belongs to a different lineage from that of the other Lake Victoria algal grazers. These same characters also serve to distinguish *H. nigricans* from *H. limax*.

The extreme modification of the teeth in *H. obliquidens* (see Greenwood 1956b) immediately distinguishes this species from *H. limax* but does not necessarily rule out a fairly close relationship between the species. The teeth in *H. obliquidens* seem to be the ultimate expression of a specialization already apparent in *H. lividus* and *H. limax* (see Greenwood, *op. cit.*, and above).

A fourth Lake Victoria species, *H. nuchisquamulatus* (Hildg.), has feeding habits similar to those discussed above. However, its teeth retain the basic, unequally bicuspid crown, and are not closely like those of *H. limax* (see Greenwood, *op. cit.*, and above).



Except for *H. nuchisquamulatus*, where it is not known, the breeding coloration of these species is clearly different.

Finally, comparison should be made with *H. annectidens* Trewavas of Lake Nabugabo. This species has about the same degree of resemblance to *H. limax* as does *H. lividus*. The same can probably be said of *H. astatodon* Regan of Lake Kivu, but far less is known about intraspecific morphological and dental variability in this species.

In brief, *H. lividus*, *H. limax*, *H. astatodon* and, despite its highly specialized teeth, *H. obliquidens* could well be members of a phyletic lineage.

#### STUDY MATERIAL

##### Registered number BMNH

##### Locality

1933.2.23 : 243 (Holotype)	Lake Edward (collected by Worthington)
1933.2.23 : 395	Lake George (collected by Worthington)
1972.6.2 : 112-118	Lake George, various localities
1972.6.2 : 119-123	Lake George, various localities
1972.6.2 : 124	Lake George, Akika Island
1972.6.2 : 125	Lake George, papyrus edge
1972.6.2 : 126-128	Lake George, Kankurunga Island
1972.6.2 : 129-135	Lake George, Kankurunga Island
1972.6.2 : 136-139	Lake George, Kankurunga Island
1972.6.2 : 140	Lake George, no locality
1972.6.2 : 808 (Figured specimen)	Lake George, Kankurunga Island

#### *Haplochromis mylodon* sp. nov.

(Text-figs. 15 & 16)

*Haplochromis ishmaeli* (non Boulenger) : Trewavas, 1933, *J. Linn. Soc. (Zool.)*, **38** : 334 (both specimens identified as *H. ishmaeli* are from Lake Edward).

**HOLOTYPE.** A male, 85.0 mm standard length, BMNH reg. no. 1972.6.2 : 656.

The trivial name, from the Greek, refers to the mill-like crushing dentition of the pharyngeal bones.

**DESCRIPTION.** Based on 21 specimens (including the holotype), 68.0-115.0 mm standard length.

Depth of body 36.0-40.5 ( $M = 38.6$ ) per cent of standard length, length of head 31.0-35.8 ( $M = 33.1$ ) per cent. Dorsal head profile with some size correlated variation in outline, being more decurved in larger individuals and almost straight in smaller fishes ; sloping at an angle of  $40^{\circ}$ - $45^{\circ}$  with the horizontal at all sizes.

Preorbital depth 13.3-20.8 ( $M = 15.9$ ) per cent of head, least interorbital width 24.1-28.6 ( $M = 26.6$ ) per cent. Snout length 28.0-32.2 ( $M = 30.1$ ) per cent of head, 0.8-0.9 (rarely 1.0) times its breadth, eye diameter 26.0-34.0 ( $M = 29.8$ ) per cent, cheek depth 20.7-26.3 ( $M = 22.8$ ) per cent. Caudal peduncle 14.7-18.4 ( $M = 17.9$ ) per cent of standard length, 1.1-1.5 (mode 1.3) times as long as deep.

Mouth horizontal, lips not thickened. Length of lower jaw 35.2-40.5 ( $M = 37.6$ ) per cent of head, 1.2-1.8 (modal range 1.5-1.6) times as long as broad. Posterior



tip of premaxilla reaching a vertical through the anterior margin of the orbit or a little further posteriorly.

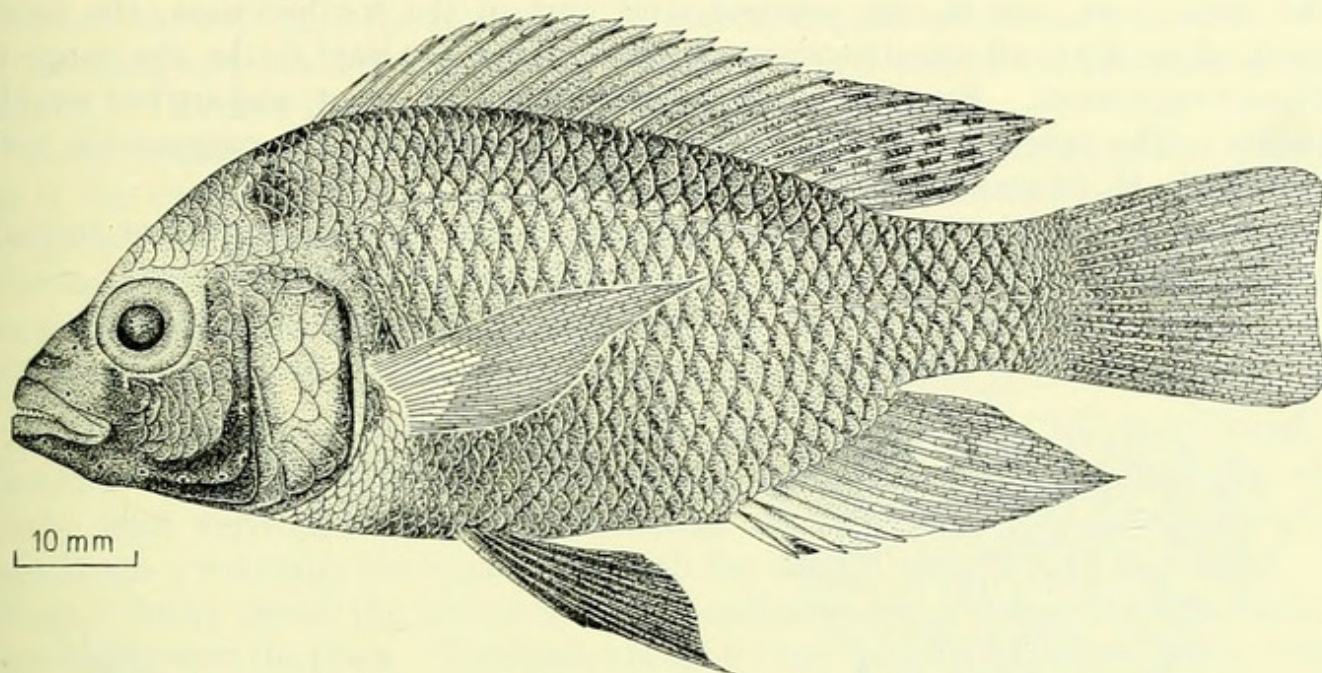


FIG. 15. *Haplochromis mylodon*. Holotype.

*Gill rakers* short and stout, the lower 1 or 2 reduced; 7-9 (mode 7) rakers on the lower part of the first gill arch. The median row of pseudorakers on the first arch is well developed but individual pseudorakers are low.

*Scales*. Ctenoid; lateral line with 31 (f.11), 32 (f.9) or 34 (f.1) scales, cheek with 3 (rarely 2) rows. Five to 7 (mode 5½) scales between the upper lateral line and the dorsal fin origin, 6-8 (mode 7) between the pectoral and pelvic fin bases.

*Fins*. Dorsal with 14 (f.2), 15 (f.10), 16 (f.8) or 17 (f.1) spinous and 8 (f.5), 9 (f.13) or 10 (f.3) branched rays. Caudal subtruncate, scaled on its basal half. Pectoral 27.6-33.3 (M = 29.5) per cent of standard length, 82.0-96.5 (M = 84.1) per cent of head. Pelvics with the first ray slightly produced.

*Teeth*. Except for 1 to 3 unicuspid posteriorly in the upper jaw of most fishes, the *outer teeth* in both jaws are stout and unequally bicuspid; the major cusp is almost equilateral in outline, moderately protracted and barely incurved. There are 32-46 (M = 40) teeth in the outer premaxillary row.

The *inner teeth* are small and tricuspid, and are arranged in 1 or 2 rows in the upper jaw, and a single (rarely double) row in the lower one.

**OSTEOLOGY.** The neurocranium of *H. mylodon* is virtually identical with that of *H. ishmaeli* (or *H. pharyngomylus*) of Lake Victoria (see Greenwood 1960). The shape and size of the facet for the upper pharyngeal bones is strictly comparable in all three species, as is the relative contribution to this facet of the basioccipital and parasphenoid bones.

The *lower pharyngeal bone* is a massive structure (text-fig. 16). Compared with this bone in *H. ishmaeli* and *H. pharyngomylus*, that of *H. mylodon* is slightly less massive. The difference is not nearly so marked, however, as that between the bone



in Lake Victoria and Lake George populations of *Astatoreochromis alluaudi* (see Greenwood 1959a, 1965b). The dentigerous area of the lower pharyngeal bone in *H. mylodon* is slightly smaller than in *H. ishmaeli* or *H. pharyngomylus*. Except in the outer rows, and in the posterolateral part of the toothed area, the lower pharyngeal teeth are all massive, stout and molariform (at least in the size range of specimens examined). Even the non-molariform teeth are stout, and are but weakly cuspidate. The extent of 'molarization' in *H. mylodon* is thus comparable with that found in *H. ishmaeli* and *H. pharyngomylus*.

Vertebral counts in the 8 specimens radiographed are : 28 (f.1), 29 (f.6) or 30 (f.1), comprising 13 (f.8) abdominal and 15 (f.1), 16 (f.6) or 17 (f.1) caudal centra.

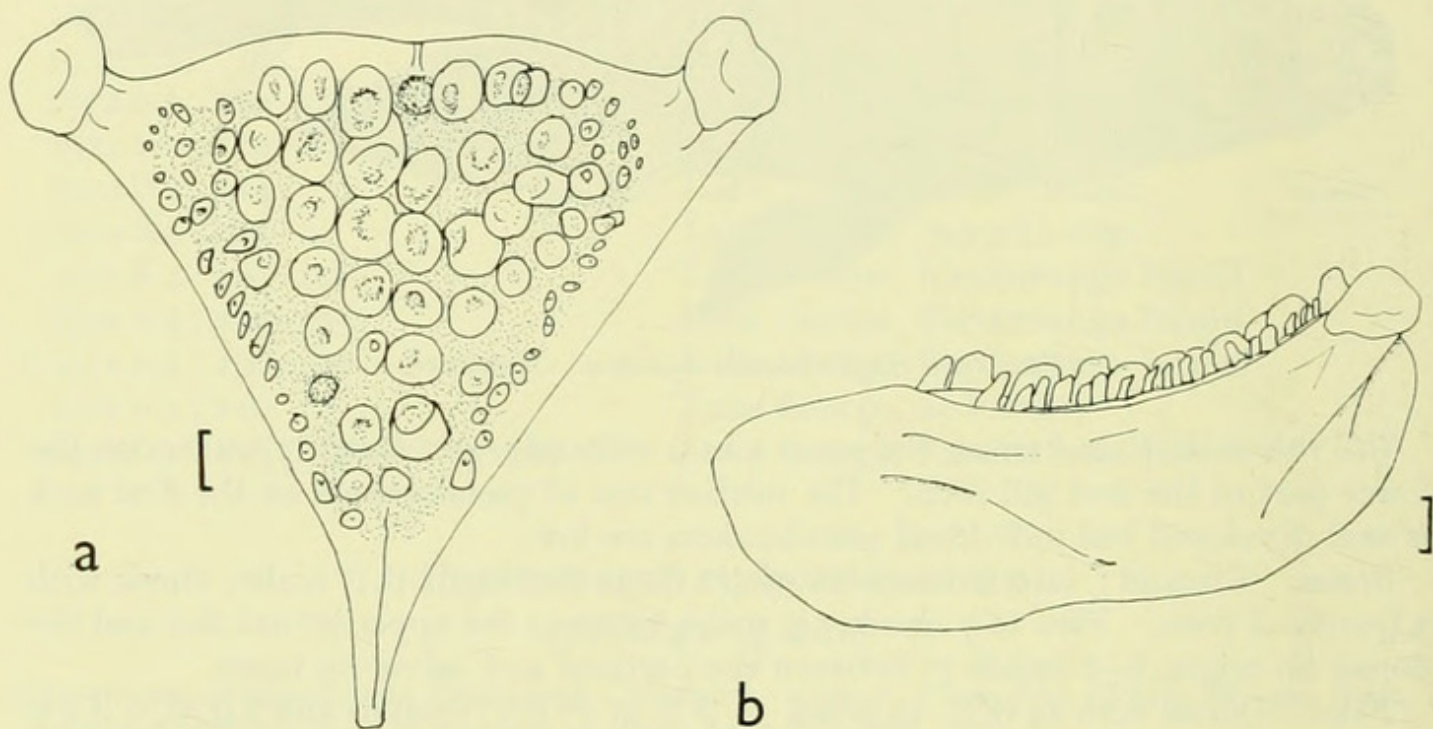


FIG. 16. *H. mylodon*. Lower pharyngeal bone. (a) In occlusal view. (b) In lateral view. From a specimen 110 mm standard length. Scale = 1.0 mm.

**COLORATION IN LIFE.** *Sexually active males* have a blue-grey ground colour with an iridescent turquoise sheen that is particularly concentrated around the margin of flank scales; the belly is silvery grey, the chest and branchiostegal membrane are charcoal-grey. The head is blue-grey but the interorbital region is iridescent blue and is crossed by 2 dark bars. A prominent and dark lachrymal stripe continues to above the eye, where it expands to form a dark blotch. The dorsal fin is greyish-hyaline, the lappets are dusky, the soft dorsal has an orange-red to red margin, and there are dark red streaks between the rays. The caudal is dark over its proximal third, the remainder being rather dusky but with a red (crimson-lake) margin; this red colour tends to extend forward onto the lower half of the fin, resulting in a dusky-pink coloration. The anal varies from dark hyaline to dusky pink on the spinous part (the lappets are black); the soft part is dark hyaline proximally, crimson to pink distally (the darker shades found nearest the middle of the fin). The anal ocelli are deep yellow. The pelvic fins are uniformly dusky.



In general, all colours are more intense in the sexually more active individuals.

*Sexually quiescent and starting males* have a light brassy ground colour with a pale-lime overlay, and are white on the chest and belly. The dorsal fin is dark hyaline, the soft part the darker. The caudal is yellowish basally, hyaline on the distal half, and has a bright orange-red margin that widens on the ventral half of the fin. The anal is pinkish, the pelvics dusky.

*Adult females* are silvery, shading to white on the belly. The dorsal fin is hyaline, as is the caudal which, however, has a yellowish flush on the ventral half and a bright scarlet posterior margin. The distal part of the ventral half of the caudal is also light scarlet. The anal fin is yellowish with a pinkish to scarlet overlay that is particularly intense along the margin of its soft part; two orange spots occur in the position of the ocelli in males. The pelvic fins are hyaline or faintly yellow.

**PRESERVED COLORATION.** *Adult males* are brown above the midlateral line, shading to dark brown (almost bitter chocolate) below. Up to 8 rather narrow and fairly faint vertical bars are visible across the lighter part of the flank in some specimens; ventrally the bars merge with the darker ventral flank coloration. The chest is dusky silver, the branchiostegal membrane dusky below the operculum but lighter between the jaws. The head, except for the operculum, is dark yellow-brown; the operculum is even darker (i.e. it is comparable with the ventral flanks). There is a well-defined and broad lachrymal stripe, and two narrow transverse bars across the snout; a broad, rather ill-defined band crosses the head behind the posterodorsal margin of the orbits, while another broad but more diffuse band or blotch extends across the nape immediately before the dorsal fin origin. The dorsal fin is dark grey, with short black blotches or streaks between the spines (at least basally). The soft part of this fin is darkly maculate. The caudal is greyish, becoming darker over its basal half. Proximally the anal is dark grey to dusky, the dark area becoming more extensive posteriorly and may occupy as much as the basal half of the fin. The rest of the fin is light yellowish-brown. The pelvics are dusky to black, the pectorals are hyaline.

*Adult females* are yellowish-brown to light greyish-brown dorsally, shading to silvery yellow on the belly and lower flanks. The dorsal and caudal fins are greyish, the anal, pelvics and pectorals are yellowish-hyaline.

**ECOLOGY.** *Habitat.* *Haplochromis mylodon* occurs near the shoreline over mud and mud-sand substrata. A few specimens have been caught in more open-water localities over a sandy bottom.

*Food.* Within the size range sampled, the diet of *H. mylodon* seems to consist mainly of gastropods, particularly *Melanoides tuberculata*. Chironomid larvae are also eaten.

*Breeding.* *Haplochromis mylodon* is a female mouth brooder. Individuals, of both sexes, less than 75 mm standard length are immature, and a few larger fishes (80 mm standard length) also show no signs of gonadal activity. Females may reach a larger size than the males; the largest male recorded is 90 mm standard length, whereas the largest female is 115 mm standard length.

*Distribution.* Lakes Edward and George and the Kazinga Channel.



DIAGNOSIS AND AFFINITIES. Amongst the *Haplochromis* species of Lake George (and, apparently, also of Lake Edward), *H. mylodon* is immediately recognizable by its massive pharyngeal bones and dentition.

On the basis of purely anatomical characters, Trewavas (1933) very reasonably identified Lake Edward specimens of *H. mylodon* as *H. ishmaeli*, a species otherwise known only from Lake Victoria. Certainly on such characters it is difficult to distinguish between the two species. However, in life the coloration of adult, sexually mature males is very different (compare p. 174 above with p. 277 in Greenwood 1960).

When Lake George specimens are compared with *H. ishmaeli* from Lake Victoria (see Greenwood 1960) there are, in fact, some slight anatomical differences as well. For example, the cheek is a little shallower in *H. mylodon*, there are fewer teeth in the outer premaxillary tooth row than in *H. ishmaeli* and the chest scales are smaller.

A shallower cheek but larger chest scales and a longer pectoral fin distinguish *H. mylodon* from *H. pharyngomylus*, the other Lake Victoria species with a similar crushing pharyngeal dentition. Once again, adult male coloration provides a ready interspecific difference when live fishes are compared. But, in this instance the coloration is rather less different than in the case of *H. ishmaeli* and *H. mylodon*.

In brief, *H. mylodon*, *H. ishmaeli* and *H. pharyngomylus* are alike in nearly all morphometric characters and in most anatomical ones as well, but each species has a characteristic male coloration. It is chiefly because of the differences in coloration that I place *H. mylodon* in a distinct species (and do not include it with *H. pharyngomylus*). The importance of male coloration in cichlid courtship and species recognition is such that it would be biologically unsound to consider *H. mylodon* as anything other than specifically distinct.

Poll (1959) described three species (one from Lake Edward and two from nearby localities) with enlarged pharyngeal bones and molariform pharyngeal teeth. Of these species, one, *H. malacophagus* (from Lake Kibuga, ca 50 km south of Lake Edward), need not be considered in detail. Its pharyngeal bones and dentition are but slightly enlarged and there are other characters which differentiate it from *H. mylodon*.

The second species, *H. placodus* (from the Molindi River, near Lake Kibuga), has a greatly enlarged lower pharyngeal bone and an almost completely molariform pharyngeal dentition; in both characters it is comparable with *H. mylodon*. In overall appearance, too, *H. placodus* is rather like *H. mylodon*. The holotype and only specimen (101 mm standard length) differs from *H. mylodon* in its larger pectoral and nuchal scales ( $4\frac{1}{2}$  between upper lateral line and dorsal origin, 5 between pectoral and pelvic fin bases, cf. 5–7 [mode  $5\frac{1}{2}$ ] and 6–8 [mode 7] in *H. mylodon*), in having a much smaller eye (22.2 per cent of head, cf. 26–34.0, mean = 29.8 per cent) and a shorter pectoral fin (72.3 per cent head length, cf. 82.0–96.5, mean 84.1 per cent). When more specimens of *H. placodus* are available, its relationships with *H. mylodon* can be reviewed more critically. But, unless *H. placodus* holotype is an aberrant individual, it seems unlikely that the two species will prove to be conspecific.

The third species, *H. pharyngalis*, is from the western shore of Lake Edward, at Bugazia. In two of the three syntypes, the pharyngeal mill exhibits a degree of development almost comparable with that of *H. mylodon* and *H. placodus*. In the third specimen, however, the bones are not greatly enlarged and only the median



rows of the lower pharyngeal teeth are molariform. Body form in *H. pharyngalis* is unlike that of *H. mylodon*, being elongate and slender. The thickened lips and slightly shorter lower jaw of *H. pharyngalis* give to the face a most distinctive appearance. Several other characters serve to distinguish this species from *H. mylodon* (and the other species considered here). Outstanding among these diagnostic features are the minute nuchal and chest scales. I count, in the three *H. pharyngalis* syntypes, 8 or 9 scales between the upper lateral line and the dorsal fin origin, and about the same number between the pelvic and pectoral fin bases; furthermore, scales lower on the chest are so small and thin that, at first sight, this area seems naked. Other diagnostic characters are the low number of gill rakers (5 or 6), the longer snout (34.5 and 35.0 per cent head, *cf.* 28.0–32.2, mean 30.1 per cent in *H. mylodon*) and deeper cheek (26.7 and 29.3 per cent of head, *cf.* 20.7–26.3 per cent, mean = 22.8 per cent in *H. mylodon*). Because the two *H. pharyngalis* syntypes measured (82.5 and 88.0 mm standard length) are within the size range of the *H. mylodon* sample, these morphometric differences are unlikely to be the results of allometric growth. (The third syntype is rather distorted and was, therefore, not measured.)

There do not seem to be any grounds for assuming a close or even distant relationship between *H. pharyngalis* and *H. mylodon* (or, indeed, between that species and *H. placodus* or *H. malacophagus*). The peculiarly small nuchal and thoracic squamation of *H. pharyngalis* is, however, characteristic of a species recently discovered in Lake George (*see p.* 209). The two species also have a similar body form and physiognomy, but the new Lake George species does not have a hypertrophied pharyngeal mill; their possible relationship is considered below (*p.* 213).

#### STUDY MATERIAL

Register number BMNH	Locality: Lake George
1972.6.2 : 656 (Holotype)	Small island north of Kankurunga Island
1972.6.2 : 655 (Paratype)	N.E. corner of the lake
1972.6.2 : 657 (Paratype)	Over sandy shallows
1972.6.2 : 661–667 (Paratypes)	Various localities
1972.6.2 : 668–676 (Paratypes)	Various localities
1972.6.2 : 799–801 (Paratypes)	Small island north of Kankurunga Island
1972.6.2 : 658	Sandy shallows
1972.6.2 : 677–678	Locality unknown
1972.6.2 : 679–680	50–70 m from bush shore
1972.6.2 : 681	Locality unknown
1972.6.2 : 682	Locality unknown

#### *Haplochromis angustifrons* Blgr., 1914

(Text-figs. 17–19)

SYNONYMY. Trewavas (1933) gives a full synonymy for *H. angustifrons*, a species which Regan (1921) had previously synonymized with *H. schubotzi* Blgr.

Trewavas' redescription of the species (and her synonymy for it) was based entirely on Lake Edward specimens in the B.M.(N.H.) collections, which include 5



of Boulenger's syntypes (see Boulenger 1914 and 1915). One of the latter specimens was referred to *H. schubotzi* by Trewavas (*op. cit.*), and only 3 of the remaining 4 syntypes were included in her redescription of *H. angustifrons*. I have examined the fourth and neglected specimen, and can confirm its identity as *H. angustifrons*. The 4 syntypical specimens have the B.M.(N.H.) register numbers, 1914.4.8 : 25-28.

Through the courtesy of Dr K. Deckert (Berlin Museum) I was able to examine 48 syntypes of this species (including the specimen figured in Boulenger 1914 and 1915). It should be noted that there are apparently 53 syntypes in existence, although Boulenger (1914) originally recorded 56 specimens.

As far as I can tell without detailed knowledge of *H. angustifrons* in Lake Edward, all except 2 of the Berlin syntypes can be referred to this species. I do, however, have some reservations about the identity of a few small specimens in this series.

The 2 specimens which I do not consider to be *H. angustifrons* provide something of a puzzle that may only be solved when a large-scale revision of the Lake Edward *Haplochromis* species is carried out. Both these fishes are from the Berlin Museum lot number 19778. One, a female 71 mm standard length, appears to be of an *H. elegans*-like species. The other, a female, 86.0 mm standard length, I am tentatively referring to a new species described below (p. 188).

In his original description of *H. angustifrons*, Boulenger (1914) mentions some females as having '... einem breite, dunklen, braunen Seitenband vom kiemendeckel zur Schwanzflosse, ...'. The 86 mm female mentioned above is the only syntype I examined with such a midlateral band. *Haplochromis angustifrons* females do not exhibit this colour pattern which is, however, a characteristic of the new species to which this syntypical fish is now tentatively referred (see p. 190 below).

As *lectotype* of *H. angustifrons* I have chosen the figured specimen, a male 91.0 mm standard length, Berlin Museum number 19118, collected by Schubotz from Lake Edward.

At least with respect to Lake George populations of *H. angustifrons*, the lectotype is unusual in being a male of such large size. In Lake George, adult males are generally much smaller than females. Despite this size discrepancy, the lectotype is a modal *H. angustifrons* in all morphological characters.

Trewavas' (1933) synonymy of *H. angustifrons* must now be expanded to include :

*H. elegans* (part) Trewavas, 1933, *J. Linn. Soc. (Zool.)*, **38** : 333 (1 specimen from Lake George, BMNH reg. no. 1933.2.23 : 394).

*H. vicarius* (part) Trewavas, 1933, *op. cit.* : 331 (1 of the 2 paratypes from Lake George, [Worthington's (1932) station 613], BMNH reg. no. 1933.2.23 : 353).

*H. schubotzi* (part) : Trewavas, 1933, *op. cit.* : 337 (the 5 small specimens from Lake George, BMNH reg. nos. 1933.2.23 : 409-413, from Worthington's stations 613 and 627).

*H. nubilus* (part) : Trewavas, 1933, *op. cit.* : 329 (2 specimens, BMNH reg. nos. 1933.2.23 : 287 and 300, from Worthington's stations 613 and 618, Lake George).

*H. guarti* (part) : Trewavas, 1933, *op. cit.* : 339 (1 specimen, BMNH reg. no. 1933.2.23 : 477, collected by Worthington from Lake George but no station number was given).

**DESCRIPTION.** Based on 41 specimens, 40.0-90.0 mm standard length, all from Lake George.

Depth of body 34.3-40.5 ( $M = 36.2$ ) per cent of standard length, length of head 34.5-38.3 ( $M = 36.4$ ) per cent. Dorsal head profile straight or very weakly convex,



sloping at an angle of *ca*  $35^{\circ}$ – $40^{\circ}$  to the horizontal; premaxillary pedicels prominent and breaking the dorsal head outline to give the fish a very characteristic 'Roman nose' profile. The upper margin of the orbit just enters the line of the head profile.

Preorbital depth 12.5–18.9 ( $M = 16.6$ ) per cent of head, least interorbital width 17.3–24.0 ( $M = 20.5$ ) per cent, snout length 25.0–34.0 ( $M = 29.5$ ); all three proportions show slight positive allometry with standard length. The snout varies from slightly broader than long to a little longer than broad (0.8–1.1), but modally is as long as broad.

The eye diameter and the cheek depth both show marked allometry with standard length, the former negatively allometric, the latter positively so. Thus, for these measurements two figures are given, first for fishes < 60 mm standard length ( $N = 12$ ), and second for larger fishes ( $N = 29$ ). Eye 32.3–37.6 ( $M = 35.1$ ) per cent head, and 27.8–33.4 ( $M = 31.0$ ) per cent; cheek 15.3–23.7 ( $M = 21.3$ ) per cent, and 22.7–29.6 ( $M = 25.7$ ) per cent.

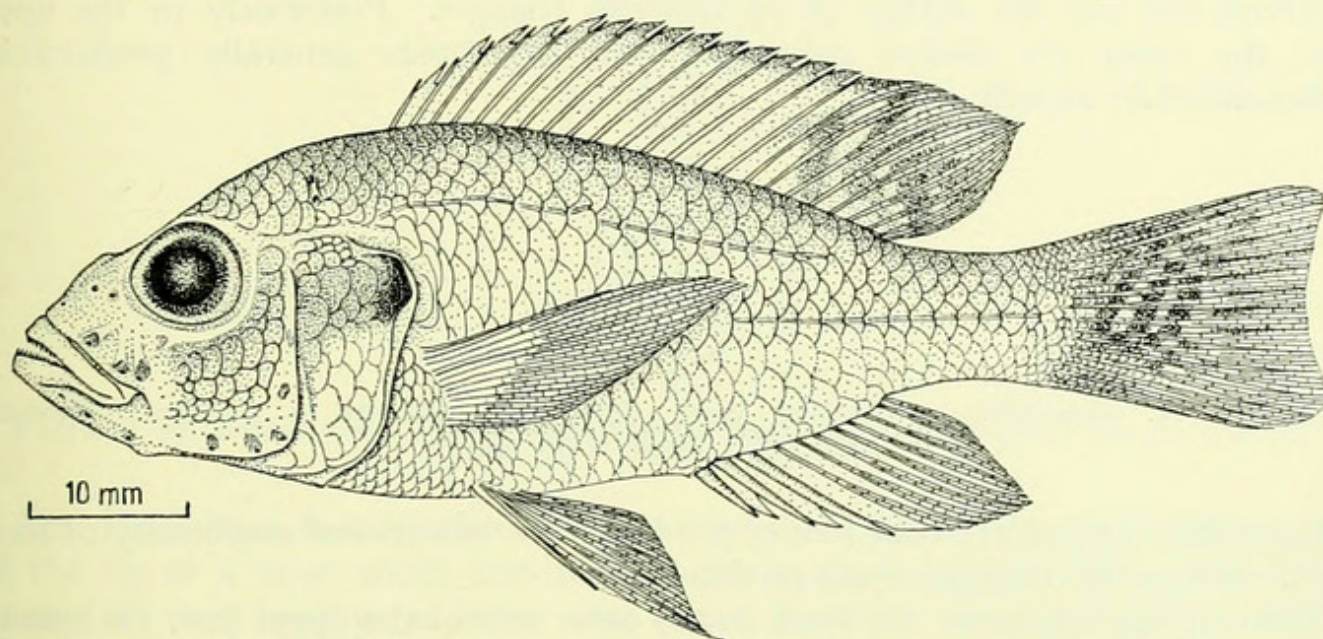


FIG. 17. *Haplochromis angustifrons*. Lake George specimen; a female.

Caudal peduncle 15.6–20.0 ( $M = 17.5$ ) per cent of standard length, 1.2–1.8 (modal range 1.3–1.5) times as long as deep.

Mouth slightly oblique, or horizontal; lips not thickened. Length of upper jaw 30.2–37.5 ( $M = 34.4$ ) per cent of head, length of lower jaw 38.8–45.8 ( $M = 42.5$ ) per cent, 1.5–2.3 (modal range 2.0–2.2) times as long as broad. Posterior tip of the maxilla reaching a vertical through the anterior part of the eye or even through the pupil.

*Gill rakers.* The lower 1 or 2 rakers are reduced, the remainder relatively slender and elongate, although the rakers immediately above the reduced ones may be short and stout. There are 7 or 8 (rarely 10) rakers on the lower part of the first gill arch.

Pseudorakers are barely developed; the tissue between the inner and outer rows of true rakers is slightly thickened and thrown into low and barely discrete projections.



*Scales.* Ctenoid; lateral line with 30 (f.13), 31 (f.22) or 32 (f.6) scales, the cheek with 2 (rare)–4 (mode 3) rows. Four and a half to  $5\frac{1}{2}$  (rarely  $6\frac{1}{2}$ ), mode 5, scales between the upper lateral line and the dorsal origin, 5–7 (rarely 8), mode 6, between the pectoral and pelvic fin bases.

*Fins.* Dorsal with 14 (f.15) or 15 (f.26) spinous and 8 (f.3), 9 (f.29) or 10 (f.9) branched rays. Anal with 3 spines and 7 (f.2), 8 (f.29) or 9 (f.10) branched rays. Caudal truncate to very weakly emarginate, scaled on its basal half or a little further posteriorly. Pectoral 27.4–33.7 ( $M = 30.4$ ) per cent of standard length, 74.0–89.9 ( $M = 83.1$ ) per cent of head. Pelvics with the first and second rays somewhat produced.

*Teeth.* The *outer row* in the upper jaw usually is composed of both unicuspid and bicuspid teeth (text-fig. 18) the latter sometimes showing every gradation from fully and unequally bicuspid to weakly bicuspid (with the minor cusp virtually absent). As far as I can ascertain, this variability is not size correlated. All bicuspids, like the unicuspids, are slender and compressed; the major cusp is protracted, slightly incurved and has the outline of an isosceles triangle. Posteriorly in the upper jaw, the teeth are always unicuspid, and unicuspids generally predominate posterolaterally as well.

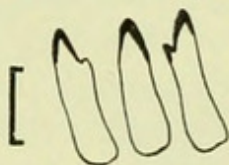


FIG. 18. *H. angustifrons*. Dentary teeth (left), anterolateral in position. Viewed laterally. Scale = 0.5 mm.

In general, the outer tooth row of the lower jaw has greater uniformity of tooth type. Unequally bicuspid teeth predominate.

There are 44–66 (mean 56) teeth in the outer row of the upper jaw, the number showing a slight positive correlation with size.

Tricuspid teeth predominate in the inner tooth series of both jaws, but many individuals have an admixture of tricuspid and weakly tricuspid teeth, or of unicuspids and weakly tricuspids. There are 1 or 2 (rarely 3) rows in both jaws.

**OSTEOLOGY.** The *neurocranium* closely resembles that in *H. schubotzi* and the new taxon, *H. schubotziellus* (see p. 190). It represents a somewhat specialized departure from the basic *Haplochromis* type; the preorbital region is relatively elongate and gently sloping, and there is an overall reduction in neurocranial width.

The *lower pharyngeal bone* is fine, its outline noticeably elongate and narrow (text-fig. 19), especially in comparison with the pharyngeal bone of other species in the Lake George flock. The dentigerous area is a little longer than broad (*ca* 1.1 times), the teeth fine, compressed and cuspidate and are arranged in *ca* 24–28 rows. Some teeth in the median rows are a little stouter than those situated laterally.

*Vertebral counts* for the 10 specimens radiographed are 28 (f.4) or 29 (f.6), comprising 12 (f.9) or 13 (f.1) abdominal and 16 (f.5) or 17 (f.5) caudal elements.



**COLORATION IN LIFE.** *Adult males*: the dorsum of the head and body is an iridescent violet which shades to turquoise on the midflank and greenish-golden on the belly. Chest and lower jaw are sooty, the branchiostegal membrane dusky to black, and the cheeks greenish-turquoise. Cephalic markings are not always visible, but when developed consist of a prominent, saddle-shaped nuchal bar and two parallel stripes across the snout.

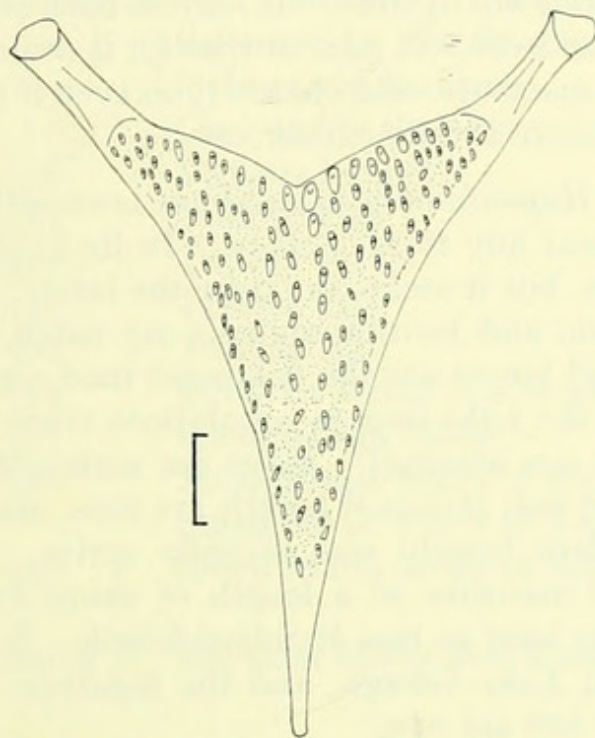


FIG. 19. *H. angustifrons*. Lower pharyngeal bone, in occlusal view. Scale = 1.0 mm.

The dorsal fin is dark hyaline with a sinuous black band running the entire length of the fin at a level about one-third of the distance between margin and base. Caudal fin dark hyaline, as is the anal which, however, is black basally and along its margin, and may show a faint pink flush; the anal ocelli are orange. The pelvic fins are black.

Shortly after death, traces of 7-10 vertical bars may appear on the flanks and caudal peduncle.

*Adult females* are metallic grey dorsally, shading through silver on the flanks to whitish on the belly. All fins are hyaline or faint yellow; the caudal is densely and clearly maculate, the spots dark grey and very obvious. (Indeed, this feature is diagnostic for the species in Lake George.)

**PRESERVED COLORATION.** *Males*: the ground colour is dark brown to black, the dark pigment most concentrated on the snout, cheeks, operculum, belly and lower half of the flanks. The lips are usually lighter than the cheeks, and the thoracic region is lighter than the flanks and belly. Traces of up to 6 narrow, fairly close-set vertical bars are often visible on the flanks. The bars are most distinct dorsally because ventrally they merge with the overall dark coloration for that region. Cephalic markings are not always visible, but when present consist of 2 bars across



the snout, a lachrymal stripe, a large posteriorly directed triangular blotch on the posterior interorbital region, and a broad band across the nape.

The dorsal, pelvic and anal fins are dusky to black, the dorsal lappets intensely black; the pigment on the dorsal and anal fins may be concentrated along the fin base. The caudal is lighter than the others, and has its pigment concentrated between the middle rays.

*Females* are silvery brown, some with faint traces of about 6 ill-defined vertical bars on the flanks. All fins are hyaline, but narrow dark streaks occur between the spines of the dorsal fin, and the soft part of that fin is sometimes weakly maculate. The caudal is invariably maculate, and distinctly so even if the spots are rather pale. (As in live fishes, this feature is a diagnostic one.)

**ECOLOGY.** *Habitat.* *Haplochromis angustifrons* is essentially an offshore species, and is rarely captured near any type of shore. In its habitat it occurs over both mud and sand substrates, but it seems to prefer the latter.

*Food.* Both planktonic and benthic animals are eaten, of which, respectively, chaoborid and chironomid larvae are the dominant food organisms.

*Breeding.* At least in the Lake George populations there is a very marked sexual dimorphism in the adult size attained. Males are noticeably smaller than females, individuals more than 65 mm standard length are rare, and the smallest male fish examined (40 mm standard length) was sexually active. Females, on the other hand, only reach sexual maturity at a length of about 63–65 mm, and attain a maximum adult size of at least 90 mm standard length. Some males do reach this size (one is known from Lake George, and the holotype, from Lake Edward, is 91 mm standard length) but are rare.

In addition to this sexually correlated size disparity, there also appears to be a marked imbalance in sex ratio at all times, but especially during daylight hours when males are particularly scarce (about 1 in 20 adult fishes). This problem of diurnal sex ratio change (with the concomitant problem of male 'migration'), and the apparently real predominance of females at all times and all places, is under active research by the I.B.P. team on Lake George. No further comments can be made at this time.

Of the 25 sexually active females sampled, 12 have the right ovary considerably larger than the left one, 6 have the left slightly larger and 7 have both ovaries equally developed.

*Distribution.* Lakes Edward and George, and the Kazinga Channel.

**DIAGNOSIS AND AFFINITIES.** *Haplochromis angustifrons* is immediately distinguishable from other Lake George *Haplochromis* species by its deep body, distinctive 'Roman nose' profile and, at least in females, by the clearly maculate caudal fin. The distinctive coloration and small adult size of males are further diagnostic features.

*Haplochromis angustifrons* does not appear to be closely related to any other species in Lake George, nor, as far as can be estimated from known collections, to any species in Lake Edward. The dentition, narrow and elongate lower pharyngeal bone and the body form (especially head shape) distinguish this species from, on



the one hand, the *H. elegans-macropsoides* complex, and on the other hand, from *H. schubotzi* and related species.

These same characters give *H. angustifrons* a superficial resemblance to *H. empodisma* Greenwood of Lake Victoria (see Greenwood 1960), and to *H. simpsoni* Greenwood of Lake Nabugabo (Greenwood 1965b). These two species are, however, distinguished from *H. angustifrons* by several morphometric and colour differences.

#### STUDY MATERIAL

Register number BMNH	Locality : Lake George
1933.2.23 : 287	Collected by Worthington, station no. 618
1972.6.2 : 412	Over sandy shallows
1972.6.2 : 414	Over sandy shallows
1972.6.2 : 420-428	Various localities
1972.6.2 : 432-433	Tufmac Bay
1972.6.2 : 434-437	Tufmac Bay
1972.6.2 : 438-440	Tufmac Bay
1972.6.2 : 441-500	Tufmac Bay
1972.6.2 : 512-515	Between Akika and Kankurunga Islands
1972.6.2 : 516-518	Kankurunga Island
1972.6.2 : 519-526	Small island north of Kankurunga Island
1972.6.2 : 531	Small island north of Kankurunga Island
1972.6.2 : 542-548	Small island north of Kankurunga Island
1972.6.2 : 804 (figured specimen)	Between Akika and Kankurunga Islands

#### *Haplochromis schubotzi* Blgr., 1914

(Text-figs. 20 & 21)

*Haplochromis schubotzi* (part) : Trewavas, 1933, *J. Linn. Soc. (Zool.)*, **38** : 337 (the 2 specimens 107 and 110 mm standard length, collected by Worthington. These specimens were not previously registered in the B.M. [N.H.] collection and are now given the reg. nos. 1972.2.24 : 1-2).

The five small specimens (52-80 mm standard length) from Lake George which Trewavas (*op. cit.*) mentions in her description of *H. schubotzi* are now identified as *H. angustifrons* (see above, p. 178).

The type series of *H. schubotzi* consists of 5 large males, all from Lake Edward (see Boulenger 1914). One of these fishes (reg. no. 1914.4.8 : 18) is in the collections of the British Museum (Nat. Hist.), the others are in the Berlin Museum. Through the courtesy of Dr K. Deckert I have been able to examine these specimens and thus to select a lectotype for the species.

**LECTOTYPE.** A male, 118.0 mm standard length, collected by Schubotz from Lake Edward (Berlin Museum number 19116). The three paralectotypes from that museum (also *ex* Lake Edward) have the lot number 22699.

**DESCRIPTION.** Based on 30 specimens from Lake George, 69.0-125.0 mm standard length.



Depth of body 33.7–39.3 ( $M = 36.4$ ) per cent of standard length, length of head 32.5–37.8 ( $M = 34.9$ ) per cent. Dorsal head profile straight or, less commonly, gently curved, sloping at an angle of *ca*  $35^{\circ}$ – $40^{\circ}$  with the horizontal.

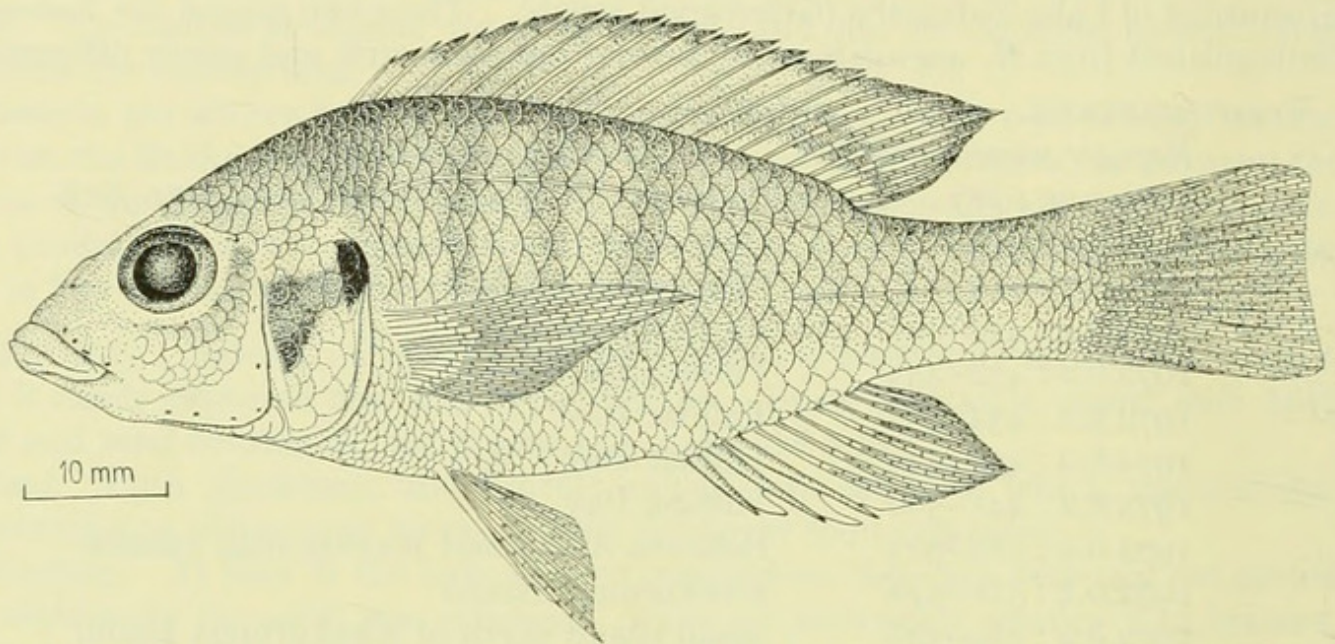


FIG. 20. *Haplochromis schubotzi*. Lake George specimen; a juvenile female.

Preorbital depth 16.4–20.9 ( $M = 19.0$ ) per cent of head, least interorbital width 19.2–25.0 ( $M = 22.4$ ) per cent; snout length 30.4–39.6 ( $M = 33.4$ ) per cent, its breadth equal to (mode) or slightly greater than its length. Eye diameter 25.5–32.0 ( $M = 28.4$ ) per cent of head, depth of cheek 20.7–26.0 ( $M = 22.8$ ) per cent.

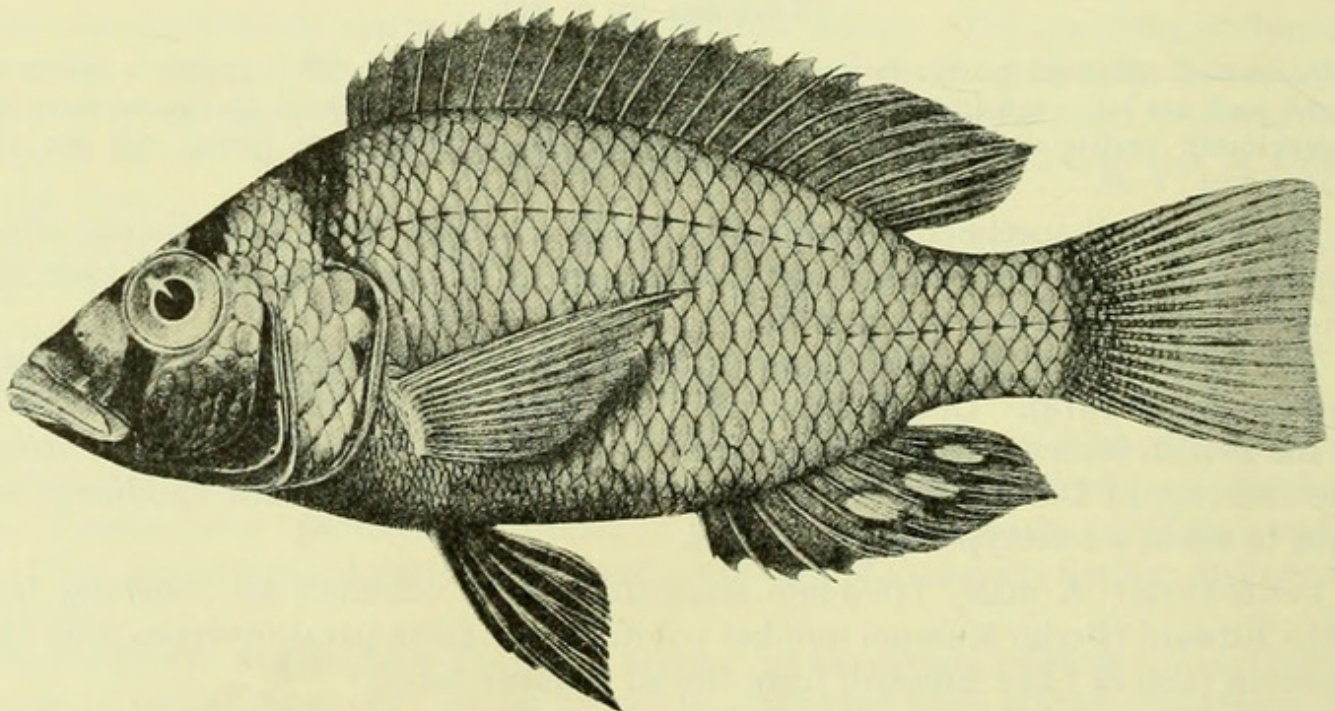


FIG. 21. *Haplochromis schubotzi*. A Lake Edward specimen (the lectotype). From Boulenger, *Cat. Afr. Fishes* (1915).



Caudal peduncle 16.2–19.2 ( $M = 17.7$ ) per cent of standard length, 1.2–1.7 (modal range 1.3–1.5) times as long as deep.

Mouth horizontal, lips slightly thickened. Length of upper jaw 27.0–33.3 ( $M = 30.5$ ) per cent of head, length of lower jaw 35.8–44.0 ( $M = 39.2$ ) per cent, 1.4–2.0 (modal range 1.6–1.7) times as long as broad. Posterior tip of the maxilla usually reaching a vertical slightly anterior to the orbital margin, but reaching that level in a few fishes.

*Gill rakers.* A characteristic feature of the first gill arch in *H. schubotzi* is the well-developed papillose area of tissue immediately preceding the first (i.e. lowermost) gill raker. This raker, and usually the next one, is reduced; the others are well developed and range in form from relatively stout to relatively slender. The pseudo-rakers on this arch are especially well developed.

There are 7 or 8 (mode) rarely 9 gill rakers on the lower part of the first arch.

*Scales.* Ctenoid; lateral line with 31 (f.10), 32 (f.14), 33 (f.5) or 34 (f.1) scales; cheek with 3 rows (rarely 2 or 4), the scales deeply embedded in the skin. Five to 6½ (mode 5½) scales between the upper lateral line and the dorsal fin origin; 6 or 7 (deeply embedded) scales between the pectoral and pelvic fin bases.

*Fins.* Dorsal with 13 (f.1), 15 (f.17) or 16 (f.11) spinous and 8 (f.8), 9 (f.19) or 10 (f.2) branched rays; anal with 3 spines and 8 (f.15) or 9 (f.15) branched rays. Caudal weakly emarginate, scaled on its basal half. Pectoral 25.6–30.0 ( $M = 27.6$ ) per cent of standard length, 73.0–87.0 ( $M = 79.4$ ) per cent of head. Pelvics with the first ray produced in adults, proportionately longer in males.

*Teeth.* Tooth form is loosely correlated with body size. In fishes less than 71 mm standard length, the *outer teeth* are clearly, but unequally bicuspid, the major cusp is produced and isoscelene in outline. In larger individuals the disparity in cusp size is more marked so that the inner cusp is virtually invisible; the major cusp seems to be even more protracted and slender. At all sizes, the outer teeth are slender and compressed, with the crown slightly incurved. Irrespective of the fish's size the posterior and some posterolateral teeth in the upper jaw are relatively more slender than the others and are usually unicuspid or very weakly bicuspid. Elsewhere in this jaw (and particularly in larger fishes) there is usually an admixture of clearly bicuspid teeth, weakly bicuspid and, to a lesser extent, unicuspid.

Tooth form in the lower jaw is, on the whole, more uniform.

There are 46–62 ( $M = 52$ ) teeth in the outer series of the premaxilla; the number of teeth does not show any clear-cut correlation with standard length, but the two largest fishes (123 and 125 mm standard length) do have the two highest numbers of teeth recorded (60 and 62 for the fishes respectively).

The *inner series* in most fishes less than 90 mm standard length are composed of slender tricuspid, but in larger individuals there may be an admixture of tricuspid, weakly tricuspid and weakly bicuspid. All inner teeth are slender, and are generally implanted so as to lie horizontally. There are 3 rows (less frequently 2 or 4) in the upper jaw and 2 or 3 in the lower jaw.

**OSTEOLOGY.** The *neurocranium* of *H. schubotzi* shows many of the characters seen in the skull of *H. riponianus* (Blgr.) from Lake Victoria (see Greenwood 1960). In other words, it is a slightly specialized derivative of the generalized skull-type



seen in, for example, *H. elegans*. The principal differences lie in the more elongate preorbital region of *H. schubotzi* skull, and in its straighter and less steeply sloping dorsal profile.

The *lower pharyngeal bone* is relatively slender, with its dentigerous area almost equilateral. The teeth are fine, compressed and cuspidate, and are arranged in from 26 to 30 rows. Some fishes have the teeth in the median rows slightly coarser than the others.

*Vertebral counts* in the 6 fishes radiographed are 29 (f.5) or 30 (f.1) comprising 12 (f.2) or 13 (f.4) abdominal and 16 (f.3) or 17 (f.3) caudal elements.

**COLORATION IN LIFE.** *Adult males*: the dorsum of the head, snout and body, the operculum and the anterolateral aspects of the flanks have a pinkish to orange-red flush; the remainder of the body is blue-grey except for the sooty chest, and yellow tinge on the upper part of the caudal peduncle. Lips, lower margin of the preoperculum, the lower jaw and the lateral aspects of the snout are bright iridescent blue, or the cheek may be orange-red. Branchiostegal membrane is black but with traces of iridescent blue over its anterior half.

Dorsal fin dark but with reddish to orange streaks between the rays and a faint overall reddish-orange flush on the soft part; the lappets are black. The caudal is hyaline with a faint red tinge between the rays, especially noticeable on the upper half of the fin. Anal bluish to dusky, the ocelli yolk-yellow. Pelvics dusky to black.

*Immature males* are basically silver-grey, with a faint rose flush on the operculum and anterior flanks, and some iridescent blue on the cheek and lips. Dorsal and anal fins are hyaline, the former with reddish streaks between the spines and rays; caudal hyaline with a faint pink flush on its ventral half.

*Adult females* have a silvery-grey ground colour, shading to white on the belly. The dorsal, caudal and anal fins are hyaline with a faint yellowish to yellowish-grey flush, the pigment being most concentrated basally. The pelvic fins are hyaline.

**PRESERVED COLORATION.** *Adult males*: ground colour greyish-brown or greyish-silver above the midlateral line, becoming dusky silver ventrally. Lateral aspects of the belly and the entire thoracic region are dusky. The snout, cheeks and most of the opercular region are dusky or at least darker than the dorsum. Cephalic markings are of variable intensity depending on the basic tone of the head coloration. The lachrymal stripe is generally intense; the snout is crossed by 2 bars, the upper of which is the wider and is often interrupted medially. On either side of the midline behind the level of the orbits is a dark, near-triangular blotch extending ventrally to the upper orbital margin; an ill-defined black blotch crosses the nape, anterior to the dorsal fin origin.

The dorsal and anal fins are dark grey to greyish-brown, the margin of the soft part pale, the lappets of the dorsal black. The caudal is greyish, either darkest over its basal third or almost uniformly grey-brown. The pelvic fins are black or dusky, the pectorals hyaline.

*Females* are greyish to brown over a silvery underlay, silvery on the lower flanks and belly. Some individuals have very faint traces of transverse barring on the upper part of the body. Cephalic markings apparently are not developed save for a



very faint lachrymal blotch. The dorsal and caudal fins are greyish, the soft dorsal sometimes maculate. The anal is hyaline to yellowish, the pelvics and pectorals are hyaline.

**ECOLOGY.** Virtually nothing is known about the feeding and breeding habits of *H. schubotzi*, and little is known of its distribution within Lake George.

Most of the specimens described above came from offshore localities, over sand or muddy sand substrates. Some localities are exposed, others relatively protected. Certainly the species is rarely caught in nets set close to a papyrus margin or close to other emergent aquatic plants; nevertheless it does sometimes occur in such habitats. Apparently the species is absent from the open waters of the centre lake.

The few available records of gut contents suggest that *H. schubotzi* is insectivorous, but the extent of its dependence on this food source requires confirmation.

It is still not known whether or not *H. schubotzi* is a mouth brooder. Fishes, of both sexes, less than 75 mm standard length are immature, as are some larger fishes (up to 80 mm standard length). Of the 8 adult females studied, 5 have the right ovary considerably larger than the left one and 3 have both ovaries equally developed.

**Distribution.** Lakes Edward and George and the Kazinga Channel.

**DIAGNOSIS AND AFFINITIES.** Probably the species from Lake George most like *H. schubotzi* is the new taxon *H. schubotziellus*. This species is described on p. 188, and its relationship with *H. schubotzi* is discussed on p. 192.

Superficially, *H. schubotzi* also resembles *H. mylodon* but is readily distinguished from that species by its unmodified pharyngeal bones, narrower interorbital (19.2–25.0,  $M = 22.4$  per cent head, cf. 24.1–28.6,  $M = 26.6$  per cent for *H. mylodon*), and by the presence of the extensive papillose area on the lower part of the first gill arch. In life, male breeding coloration is distinctive.

Rather less similar in its overall morphology is *H. angustifrons*, although small individuals of *H. schubotzi* could be confused with members of that species. *Haplochromis schubotzi* differs from *H. angustifrons* in having the inner jaw teeth horizontally aligned, in its shorter upper jaw (27.0–33.3,  $M = 30.5$  per cent head, cf. 30.2–37.5,  $M = 34.4$  per cent head), in possessing a papillose area preceding the first gill raker (see above), and in the failure of the posterior tip of the maxilla to reach the anterior orbital margin. Again, male coloration is diagnostic.

Considering species from outside Lakes Edward and George, *H. cinereus* (Blgr.) of Lake Victoria shares several characteristics with *H. schubotzi*. As pointed out before (Greenwood 1960), *H. cinereus* is, in fact, not the generalized species it was once thought to be by many workers. Its dentition and skull are relatively specialized when compared with the generalized *Haplochromis* type (Greenwood *op. cit.*). In these particular characters *H. cinereus* resembles *H. schubotzi*, as it also does in having well-developed pseudorakers and a papillose area before the lower gill raker (characters not previously recorded for *H. cinereus*). *Haplochromis cinereus* differs from *H. schubotzi* principally in having rather more unicuspid teeth in the jaws (at least when equal-sized fishes are compared) and in having the median teeth of the lower pharyngeal bone noticeably enlarged. The possible relationship of these two species will be considered again later in this paper (p. 233).



Gross morphology, neurocranial shape and dental characters are also similar in *H. schubotzi* and two other Lake Victoria species, *H. riponianus* (Blgr.) and *H. saxicola* Greenwood (see Greenwood 1960). The slender lower pharyngeal bone (lacking enlarged median teeth) of *H. schubotzi* is more like that of *H. saxicola* than that of *H. riponianus*. As usual, the coloration of adult males is different and there are morphometric characters distinguishing *H. schubotzi* from the two Lake Victoria species.

#### STUDY MATERIAL

Register number BMNH	Locality : Lake George
1972.6.2 : 683-685	Bay at the north end of Akika Island
1972.6.2 : 687-692	Bay at the north end of Akika Island
1972.6.2 : 697-698	Bay at the north end of Akika Island
1972.6.2 : 699	Bay at the north end of Akika Island
1972.6.2 : 700-701	Bay at the north end of Akika Island
1972.6.2 : 702-703	Off east shore of Akika Island
1972.6.2 : 704-705	Off papyrus edge of Akika Island
1972.6.2 : 706-707	Locality unknown
1972.6.2 : 708	Locality unknown
1972.6.2 : 709	1 m offshore from papyrus edge
1972.6.2 : 710	Over sandy shoal
1972.6.2 : 711-712	Locality unknown
1972.6.2 : 713	Northeast of Kankurunga Island
1972.6.2 : 714-715	Off Kankurunga Island
1972.6.2 : 716	Tufmac Bay
1972.6.2 : 717	Tufmac Bay
1972.6.2 : 807	
(figured specimen)	Tufmac Bay

#### *Haplochromis schubotziellus* sp. nov.

(Text-figs. 22 & 23)

? *H. angustifrons* (part) Boulenger, 1914, in *Wiss. Ergebn. Deuts. Zentral-Afrika Exped., 1907-1908, Zool. 3*: 256-257 (1 of the paralectotypes in the Berlin Museum [no. 19778], a female 86 mm standard length from Lake Edward; see also under synonymy of *H. angustifrons* on p. 178).

**HOLOTYPE.** A female, 76.0 mm standard length, BMNH reg. no. 1972.6.2 : 351.

The trivial name (a diminutive) is given because, in the field, specimens of this species are often confused with small specimens of *H. schubotzi*.

**DESCRIPTION.** Based on 28 specimens (including the holotype) 45.0-79.0 mm standard length, all from Lake George. The syntype of *H. angustifrons* is not included because its identification as *H. schubotziellus* is tentative, and it comes from Lake Edward.

Depth of body 33.3-38.0 ( $M = 35.7$ ) per cent of standard length, length of head 32.7-37.3 ( $M = 35.1$ ) per cent. Dorsal head profile straight or gently curved, sloping at an angle of *ca* 35°-40° with the horizontal.



Preorbital depth 12.5–18.5 ( $M = 15.6$ ) per cent of head, showing slight positive allometry with standard length; least interorbital width 17.9–20.8 ( $M = 19.5$ ) per cent, length of snout 25.0–33.3 ( $M = 29.2$ ) per cent, 0.8–0.9 times its breadth. Eye diameter 28.8–34.7 ( $M = 31.8$ ) per cent of head, cheek depth 17.6–24.1 ( $M = 22.0$ ) per cent, showing very slight positive allometry.

Caudal peduncle 13.3–18.5 ( $M = 16.5$ ) per cent of standard length, 1.1–1.6 (modal range 1.3–1.4) times as long as deep.

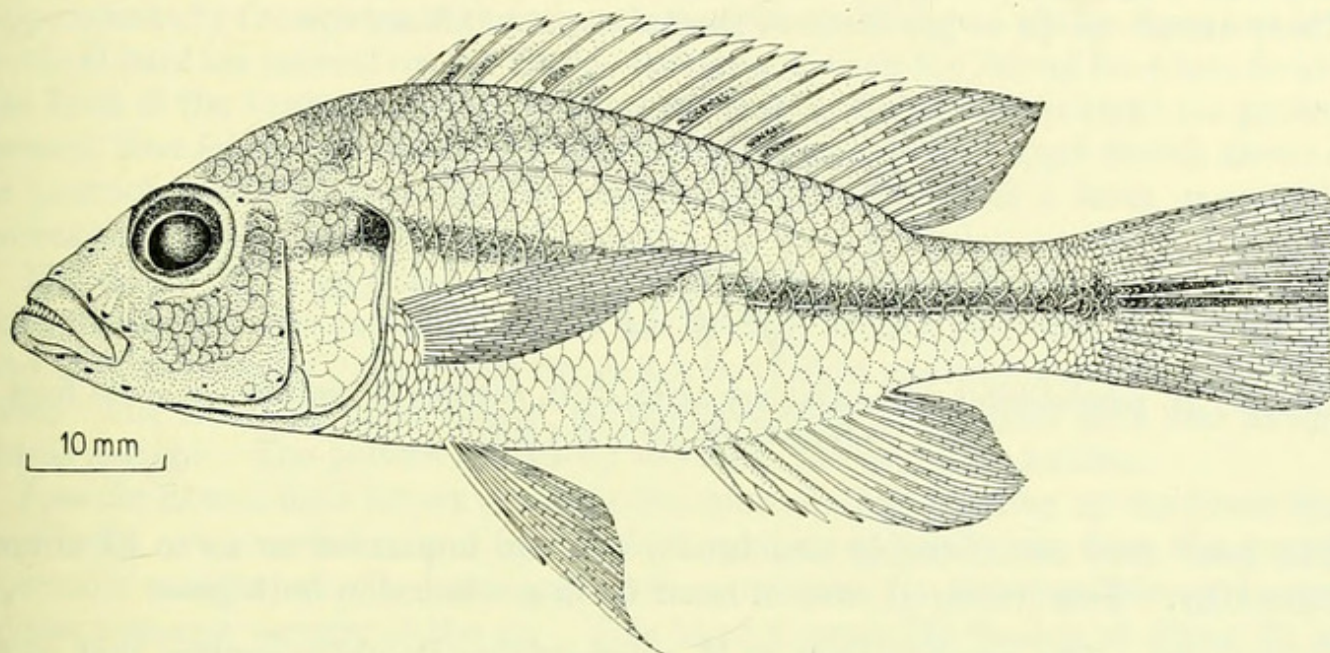


FIG. 22. *Haplochromis schubotziellus*. Holotype.

Mouth horizontal, lips very slightly thickened. Length of upper jaw, showing slight positive allometry with standard length, 28.2–37.0 ( $M = 34.2$ ) per cent of head, length of lower jaw 36.7–45.0 ( $M = 41.6$ ) per cent, 1.4–2.3 (modal range 1.7–1.9) times as long as broad. Posterior tip of the maxilla reaching a vertical through the anterior part of the orbit or a little further posteriorly.

*Gill rakers.* The tissue immediately anterior to the first gill arch is but slightly thickened, and is thrown into low, rather ill-defined folds (thus contrasting with *H. schubotzi* where this area is distinctly papillose and markedly pachydermatous). The first raker, and sometimes the 1 or 2 succeeding it, is reduced; the other rakers are short and relatively stout, with 7–9 (mode 8) on the lower part of the first arch. Pseudorakers are present but are small and sometimes ill defined.

*Scales.* Ctenoid; lateral line with 30 (f.1), 31 (f.9), 32 (f.15) or 33 (f.1) scales, cheek with 3 (rarely 2 or 4), rows, the scales not deeply embedded. Five to 6 (no distinct mode) scales between the upper lateral line and dorsal origin, 6 (mode) or 7, rarely 5 between the pectoral and pelvic fin bases, the scales not deeply embedded.

*Fins.* Dorsal with 14 (f.1), 15 (f.17) or 16 (f.10) spinous and 8 (f.1), 9 (f.18) or 10 (f.9) branched rays. Anal with 3 spines and 8 (f.17) or 9 (f.11) branched rays. Caudal weakly emarginate, scaled on its basal half. Pectoral fin 27.7–34.1 ( $M = 31.1$ )



per cent of standard length, 78.0–94.5 ( $M = 88.9$ ) per cent of head. First ray of pelvic fin produced, especially so in adult males.

*Teeth.* The predominant tooth type of the *outer row* in both jaws is a slender, very unequally bicuspid, with the major cusp produced, isoscelene to subequilateral in outline, and fairly strongly incurved (text-fig. 23). Slender unicuspid, and tricuspid, also occur in the outer row, and some fishes have all three types of teeth. A nearly constant feature is the presence of at least 1, usually 3, unicuspids at the posterior end of the premaxillary tooth row. Tooth form is less variable in larger fishes, where slender, strongly incurved unicuspids predominate.

There are 40–56 ( $M = 50$ ) teeth in the outer premaxillary row.

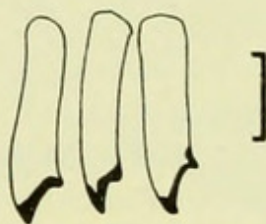


FIG. 23. *H. schubotziellus*. Premaxillary teeth (left), anterior in position. Viewed from anterior. Scale = 0.5 mm.

The *inner teeth* are tricuspid and broad, and are implanted so as to lie almost horizontally. Two (rarely 3) rows of inner teeth are found in both jaws.

**OSTEOLOGY.** The *neurocranium* of *H. schubotziellus* closely resembles that of *H. schubotzi*, but the dorsal preotic profile (especially anterior to the midpoint of the orbit) is somewhat more decurved in *H. schubotziellus*.

The *lower pharyngeal bone* is moderately stout and has an equilateral dentigerous area. The teeth are relatively fine, compressed and cuspidate, and are arranged in ca 20–24 rows. Teeth in the two median rows (especially those in the posterior third of the rows) are a little coarser than the others.

*Vertebral counts* in the 8 specimens radiographed are : 28 (f.2), 29 (f.4) or 30 (f.2), comprising 13 (f.5) or 14 (f.3) abdominal and 15 (f.3) or 16 (f.5) caudal centra.

**COLORATION IN LIFE.** *Adult males* : the ground coloration is greyish-silver with a faint iridescent blue-green sheen, particularly on the midflank region. The belly and ventral body surfaces are whitish. A fairly distinct, deep blue-black stripe extends midlaterally from the caudal fin base to the posterior opercular margin.

The dorsal fin is faintly sooty, with short black blotches along its base ; the lappets are black, the margin of the soft part is red and there are deep red spots between the branched rays. The caudal fin has similar red streaks on its proximal half and a pinkish-red flush distally. The anal is faintly dusky, with a slight pink flush ; the ocelli are orange-yellow. The pelvic fins are black.

*Females* are silver. A prominent black stripe runs midlaterally along the body and onto the caudal fin where it extends nearly to the midpoint. The band is of almost constant depth along the body but tapers somewhat on the fin. The dorsal



fin, proximal half of the caudal and the distal part of the anal are hyaline with a suffusion of pale yellow.

**PRESERVED COLORATION.** *Adult males*: the ground colour is brownish above the midlateral line, greyish to sooty below; the thoracic region is greyish to tarnished silver. The lower jaw is yellowish-brown, the branchiostegal membrane black.

Body markings are variable, but there is usually a complete dark midlateral band from the opercular margin to the caudal origin or else a band from about the middle of the body to the caudal base (sometimes this band is restricted to the posterior third of the body). Occasionally, a second longitudinal band is present, and follows approximately the course of the upper lateral line. Five to 7 rather faint but broad vertical bars are present on the flanks, and extend from the dorsal fin origin to about the level of the ventral margin of the pectoral fin. Cephalic markings are generally present (but faint) and comprise a lachrymal bar or blotch, a small blotch above and in contact with the posterodorsal margin of the orbit, and 2 faint, narrow bars across the nape.

The dorsal fin is greyish to dusky, the soft part generally maculate, the lappets dark or black. The caudal fin varies but usually is dark grey with lighter posterior and ventral margins; otherwise the entire fin is light except for a central grey basal area. The anal is grey to dusky, particularly over the spinous part and along its distal margin. The pelvics are dusky to black, the pectorals hyaline.

*Females* have a light brown ground coloration shading to silver on the lower flanks and belly. A prominent and broad, dark midlateral band runs from the posterior opercular margin onto the basal part of the caudal fin; in some specimens it extends to the posterior margin of the fin. This band is generally broken at about its midpoint, or at least is much thinner in that region. A second, but far less definite band runs a little above and parallel to the upper lateral line. The dorsal fin is greyish, often with dark lappets and sometimes with several concentrations of dark pigment along its base; each blotch extends for a short distance upwards onto the fin membrane. The caudal fin is greyish (and has a continuation of the midlateral body stripe). All other fins are hyaline.

**ECOLOGY.** *Habitat.* The species is widely distributed in Lake George and occurs in most habitats. It is particularly common in muddy bays and near papyrus-fringed shorelines, but is rarely encountered in the open waters of the midlake region.

*Food.* Very little information is available on the food or feeding habits of *H. schubotziellus*. The presence in the gut of plant and other organic debris, together with dipteran larvae, suggests bottom feeding, possibly insectivorous habits.

*Breeding.* Almost no data are available on breeding habits. The size range of individuals available for analysis is such that one cannot tell precisely at what length sexual maturity is attained. The three smallest fishes examined (45–48 mm standard length) are immature; the next smallest fish (66 mm standard length) and all others are adult and sexually active.

Of the 6 adult females studied, 4 have the right ovary much larger than the left and 2 have the gonads equally developed.

*Distribution.* Lake George and the Kazinga Channel (and probably Lake Edward as well).



DIAGNOSIS AND AFFINITIES. The close resemblance between *H. schubotziellus* and *H. schubotzi* has been noted already (p. 187). However, the species are immediately distinguishable on their coloration, even when preserved. The prominent midlateral band (especially in females) is diagnostic, and also serves to distinguish *H. schubotziellus* from all other species in Lake George (and probably Lake Edward as well). Compared with *H. schubotzi*, *H. schubotziellus* has a shallower preorbital (12.5–18.4,  $M = 15.6$  per cent head, cf. 16.4–20.9,  $M = 19.0$  per cent) a shorter snout (25.0–33.3,  $M = 29.2$  per cent head, cf. 30.4–39.6,  $M = 33.4$  per cent) a longer upper jaw (28.2–37.0,  $M = 34.2$  per cent head, cf. 27.0–33.3,  $M = 30.5$  per cent) and a longer pectoral fin (78.0–94.5,  $M = 88.9$  per cent head, cf. 73.0–87.0,  $M = 79.4$  per cent). There are also slight differences in the shape of the outer teeth, and in the relative stoutness of the lower pharyngeal bone (*H. schubotziellus* having a coarser bone with, usually, some teeth in the median rows noticeably coarser than the others).

This overall resemblance between the species means that *H. schubotziellus* also resembles the same Lake Victoria species as does *H. schubotzi* (see above p. 187). Indeed, the stouter lower pharyngeal bone and somewhat coarser median teeth in *H. schubotziellus* enhance its resemblance to *H. riponianus*, although in the latter species the lower pharyngeal dentition is rather more specialized (see Greenwood 1960). In many respects *H. schubotziellus* bears the same phenetic relationships to *H. schubotzi* as does *H. riponianus* to *H. saxicola* (Greenwood, *op. cit.*).

The relationship between *H. schubotzi* and *H. schubotziellus* could well be a truly phyletic one.

#### STUDY MATERIAL

Register number BMNH	Locality : Lake George
1972.6.2 : 351 (Holotype)	Kankurunga Island
1972.6.2 : 352 (Paratype)	Tufmac Bay
1972.6.2 : 353–355 (Paratypes)	Kankurunga Island
1972.6.2 : 356–358 (Paratypes)	Kankurunga Island
1972.6.2 : 359–366 (Paratypes)	Kankurunga Island
1972.6.2 : 367–372 (Paratypes)	Kankurunga Island
1972.6.2 : 373 (Paratype)	Kankurunga Island
1972.6.2 : 376–377 (Paratypes)	I.B.P. Jetty
1972.6.2 : 378 (Paratype)	I.B.P. Jetty
1972.6.2 : 374–375	Papyrus fringe of shore

#### *Haplochromis taurinus* Trewavas, 1933

(Text-figs. 24 & 25)

*Haplochromis taurinus* Trewavas, 1933, *J. Linn. Soc. (Zool.)*, **38** : 336 (description based on Lake Edward fishes only).

HOLOTYPE. A female, 135.0 mm standard length, BMNH reg. no. 1933.2.23 : 406 from Lake Edward.

DESCRIPTION. Based on 12 specimens, 72.0–140.0 mm standard length, all from Lake George.



Depth of body 30.4–38.5 ( $M = 36.2$ ) per cent of standard length, length of head 27.9–32.0 ( $M = 30.6$ ) per cent. Dorsal head profile variable but usually concave, sloping at an angle of *ca* 40°–45° with the horizontal.

Preorbital depth 13.6–18.2 ( $M = 15.2$ ) per cent of head, least interorbital width 22.2–29.6 ( $M = 25.4$ ) per cent, length of snout 27.4–33.3 ( $M = 30.6$ ) per cent, 0.7–0.9 of its breadth. Eye diameter 27.8–33.3 ( $M = 30.6$ ) per cent of head, depth of cheek 23.7–30.0 ( $M = 27.1$ ) per cent.

Caudal peduncle 15.7–19.0 ( $M = 17.0$ ) per cent of standard length, 1.2–1.5 (modal range, 1.2–1.3) times as long as deep.

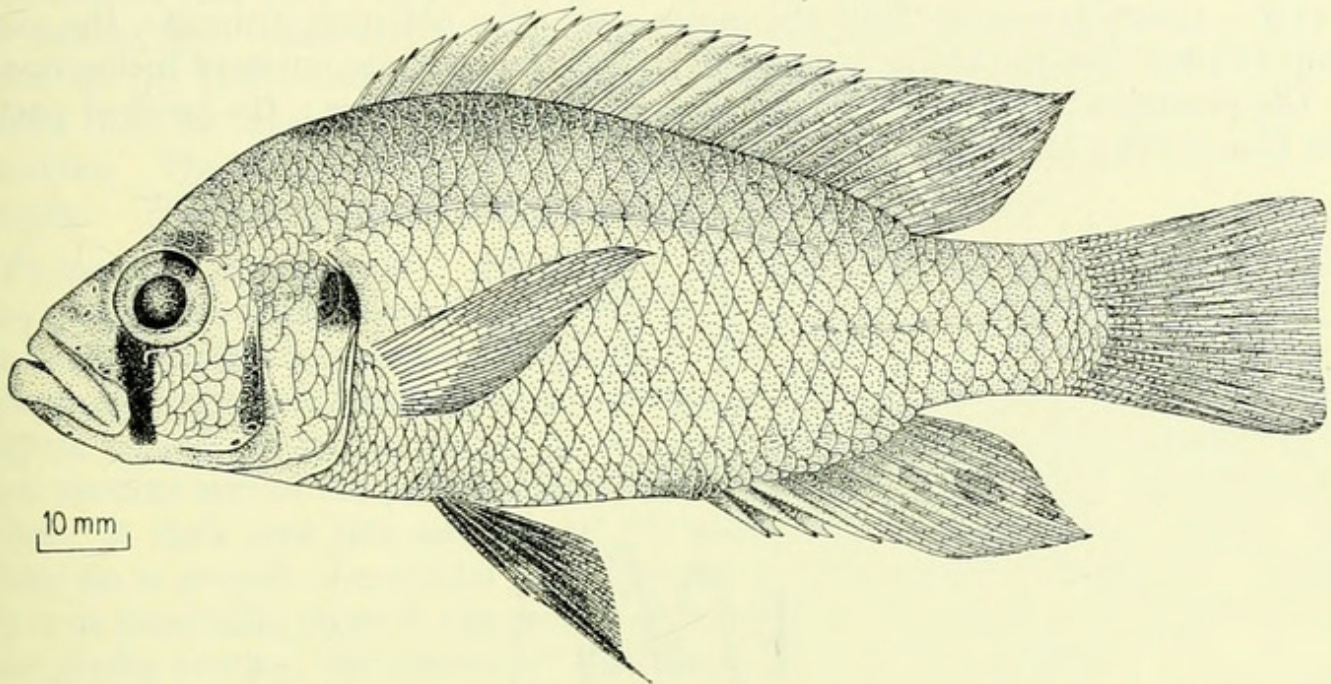


FIG. 24. *Haplochromis taurinus*. Lake George specimen; an adult male.

Mouth somewhat oblique, lips thickened; jaws equal anteriorly or the lower projecting a little. Upper jaw 38.0–42.3 ( $M = 41.0$ ) per cent of head, lower jaw 43.3–56.0 ( $M = 46.8$ ) per cent, 1.4–2.0 (modal range 1.6–1.8) times longer than broad. Posterior tip of the maxilla mostly exposed, reaching a vertical through the anterior part of the eye or one through the anterior margin of the pupil.

*Gill rakers* of variable form, from short and relatively stout to moderately long and slender; the lower 1 or 2 rakers are reduced, the upper 2 or 3 often flattened and anvil-shaped. There are 8–11 (mode 9) rakers on the lower part of the first gill arch. No clearly defined pseudorakers are present on this arch, but the tissue between the inner and outer rows of gill rakers is raised into a distinct ridge with slight but circumscribed thickenings in the position usually occupied by pseudorakers.

*Scales*. Ctenoid; lateral line with 31 (f.6) or 32 (f.6) scales, cheek with 3 (mode) or 4 rows. Five to 7 (mode 6) scales between the upper lateral line and the dorsal fin origin, 6 or 7 (rarely 8) between the pectoral and pelvic fin bases.

*Fins*. Dorsal with 15 (f.8) or 16 (f.4) spinous and 9 (f.7) or 10 (f.5) branched rays; anal with 3 spines and 8 (f.4) or 9 (f.8) branched rays. Caudal subtruncate,



scaled on its basal half or a little more. Pectoral fin 23.0–29.8 ( $M = 27.4$ ) per cent of standard length, 81.5–100.0 ( $M = 89.3$ ) per cent of head. Pelvics with the first ray noticeably prolonged.

*Teeth.* The *outer teeth* in *H. taurinus* show the form (text-fig. 25) which, in Lake Victoria *Haplochromis* species, is associated with paedophagus habits (Greenwood 1959b). Also, as in those species, the teeth of *H. taurinus* are deeply embedded in the mucosa of the jaws. In both jaws the basic tooth form is similar, namely a cylindrical neck and lower crown, but with a markedly compressed, chisel-like bicuspid upper crown. Upper jaw teeth have a crown in which the minor cusp is distinct and the major cusp is obliquely truncate; the entire crown is curved inwards. Lower jaw teeth have the major cusp very obliquely truncate, the minor cusp distinct and the entire crown has a slight but definite outward inclination.

The posterior third to half of the premaxilla is edentulous; the toothed part of the bone carries 32–48 ( $M = 36$ ) teeth.

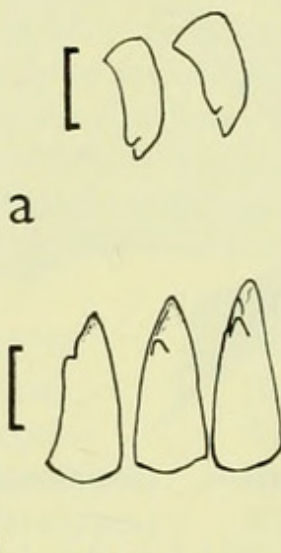


FIG. 25. *H. taurinus*. Teeth. (a) Premaxillary teeth (right), anterior in position. Viewed laterally. (b) Dentary teeth (right), anterolateral in position. Viewed from a point slightly anterior of lateral. Scale = 0.5 mm.

The *inner teeth* in both jaws are small and tricuspid, and are arranged in 1 or 2 rows. Like the outer teeth, those of the inner rows are deeply embedded in the mucosa.

**OSTEOLOGY.** The *neurocranium* of *H. taurinus* is of the generalized *Haplochromis* type. The premaxilla and dentary are also basically of a generalized type, the premaxilla not therefore showing the relative elongation of its ascending process (as occurs in some Lake Victoria paedophages, e.g. *H. parvidens*). Thus, in all syncranial features *H. taurinus* is comparable with the less specialized embryo and larval fish-eating species of Lake Victoria, viz. *H. maxillaris* and *H. obesus*.

The *lower pharyngeal bone* is relatively fine, its dentigerous area a little broader than long (*ca* 1.1 times). The teeth are slender, compressed and cuspidate, with those in the two median rows coarser than the others; there are *ca* 20–22 rows of teeth.



*Vertebral counts* in the 7 specimens radiographed are 28 (f.1), 29 (f.5) or 30 (f.1), comprising 13 abdominal and 15 (f.1), 16 (f.5) or 17 (f.1) caudal centra.

**COLORATION IN LIFE.** *Males*: the live colours of sexually active males are unknown. A *juvenile male* had similar coloration to that of a female (*see below*) except that there were faint traces of a rosy flush on the operculum and anterior parts of the flanks (especially intense above the pectoral fin insertion). Other differences noted were that the lower limb of the preoperculum, the cheek and the lower lip were a pale iridescent blue. The dorsal fin had red streaks between the rays, as had the caudal fin where the colour was most intense on the middle of the fin. Two well-defined yolk-yellow ocelli were present on the otherwise hyaline anal fin.

*Females*, both adult and juvenile, have a silvery-grey ground colour shading to white on the belly, and a faint, yellowish overlay on the flanks (more intense in adults than in juveniles). The dorsal fin is hyaline but faintly yellow along its insertion. The caudal fin is yellowish-green over its basal half, pale yellow-green distally. The anal is faintly yellow, and the pelvics are hyaline.

**PRESERVED COLORATION.** *Adult males* are brownish above, shading to silvery grey (with faint dusky overtones) on the flanks and belly; the chest is dusky silver, the branchiostegal membrane dusky grey. The head has a well-defined and intense lachrymal stripe continued through the eye and terminating as a blotch above and slightly behind the dorsal margin of the orbit. Other cephalic markings include a dark vertical arm of the preoperculum, and 2 rather faint transverse bars across the snout. A dark area just anterior to the dorsal fin origin is faintly visible. The dorsal fin is greyish, the caudal yellow-brown with traces of dark pigment between the rays (especially those in the middle of the fin). The anal fin is yellowish with a faint dusky overlay, the pelvics are black and the pectorals hyaline.

*Females* are light brownish-yellow above, shading to silvery yellow ventrally. The snout is grey-brown and there is an ill-defined and faint lachrymal stripe which does not extend through the eye to the dorsum. The dorsal and caudal fins are greyish (the former slightly the darker); all other fins are hyaline.

**BIOLOGY.** So few specimens of *H. taurinus* have been caught that it is impossible to generalize on the biology of the species. Apparently it is confined to inshore regions of the lake, where it has been taken off the papyrus fringe and also over sandy beaches in sheltered areas.

Judging from the dentition (*see above* p. 194) and the widely distensible mouth, *H. taurinus*, like similarly adapted species in Lake Victoria, feeds on the embryos and larvae of other cichlid fishes (*see Greenwood 1959b*). This supposition is borne out by the only two guts that yielded food remains. In these there were fragments of larval cichlids, bones of small fishes (of a size compatible with their being from larval fishes) and a fatty, yellow fluid closely resembling yolk.

Little information has been collected on the breeding habits of *H. taurinus*. The two available fishes less than 80 mm standard length are both immature; all specimens of 83 mm standard length and longer are sexually active. Only 2 of the adult females examined have ovaries in an advanced stage of oogenesis; in both fishes the right ovary is slightly larger than the left one.



*Distribution.* Lakes Edward and George and the Kazinga Channel.

DIAGNOSIS AND AFFINITIES. Among the *Haplochromis* species of Lakes George and Edward, *H. taurinus* is immediately recognizable by its dentition (*see above* p. 194) and by its broad and laterally distensible mouth.

Outside these lakes, *H. taurinus* bears a close resemblance in both general morphology and in its dentition to *H. maxillaris* Trewavas of Lake Victoria (*see Greenwood 1959b*). Morphometric differences between the species are slight, with the jaws of *H. maxillaris* being somewhat larger and thus the gape in this species being a little greater than in *H. taurinus*. As far as can be told from the colours of juvenile male *H. taurinus* (compared with both adult and juvenile *H. maxillaris*) there is also a difference in this character. Taking all anatomical characters into consideration, *H. maxillaris* is the more specialized species of the two.

#### STUDY MATERIAL

Register number BMNH	Locality: Lake George
1972.6.2 : 29	Sandy shoal
1972.6.2 : 30	Kankurunga Island
1972.6.2 : 31-34	Papyrus fringe opposite I.B.P. Laboratory
1972.6.2 : 35	Locality unknown
1972.6.2 : 36-37	Locality unknown
1972.6.2 : 38-42	Locality unknown
1972.6.2 : 806	
(figured specimen)	Kankurunga Island

#### *Haplochromis labiatus* Trewavas, 1933

(Text-figs. 26 & 27)

*Haplochromis labiatus* Trewavas, 1933, *J. Linn. Soc. (Zool.)*, **38**: 335 (holotype and only specimen; from Lake Edward).

*Haplochromis labiatus* was described from the holotype alone, although two smaller fishes were also mentioned (Trewavas 1933); all 3 specimens are from Lake Edward.

Only 1 specimen identifiable as *H. labiatus* has been caught in Lake George (from a locality close to the northern shore of Akika Island, in shallow water *ca* 1-1½ m deep, over mud, and near sparse stands of the reed *Phragmites*).

The Lake George fish is 87.0 mm standard length and is of indeterminable sex.

Depth of body 41.4 per cent of standard length, length of head 32.2 per cent. Dorsal head profile concave above the orbit, sloping steeply at *ca* 45° to the horizontal.

Preorbital depth 16.1 per cent of head, least interorbital width 24.3 per cent, length of snout 0.8 its breadth and 28.6 per cent of head length. Eye diameter 28.6 per cent of head, depth of cheek 25.0 per cent.

Caudal peduncle 14.1 per cent of standard length, 1.1 times its depth.

Mouth horizontal, lips noticeably thickened (but not produced into lobes medially) posterior tip of the maxilla reaching a vertical through the anterior part of the eye. Upper jaw 32.2 per cent of head, lower jaw 35.7 per cent, 1.4 times longer than broad.



*Gill rakers.* On the lower part of the first gill arch there are 8 rakers of which the lowermost is reduced, the following 2 are stout and the remaining 5 are relatively slender. Pseudorakers are present but weakly developed.

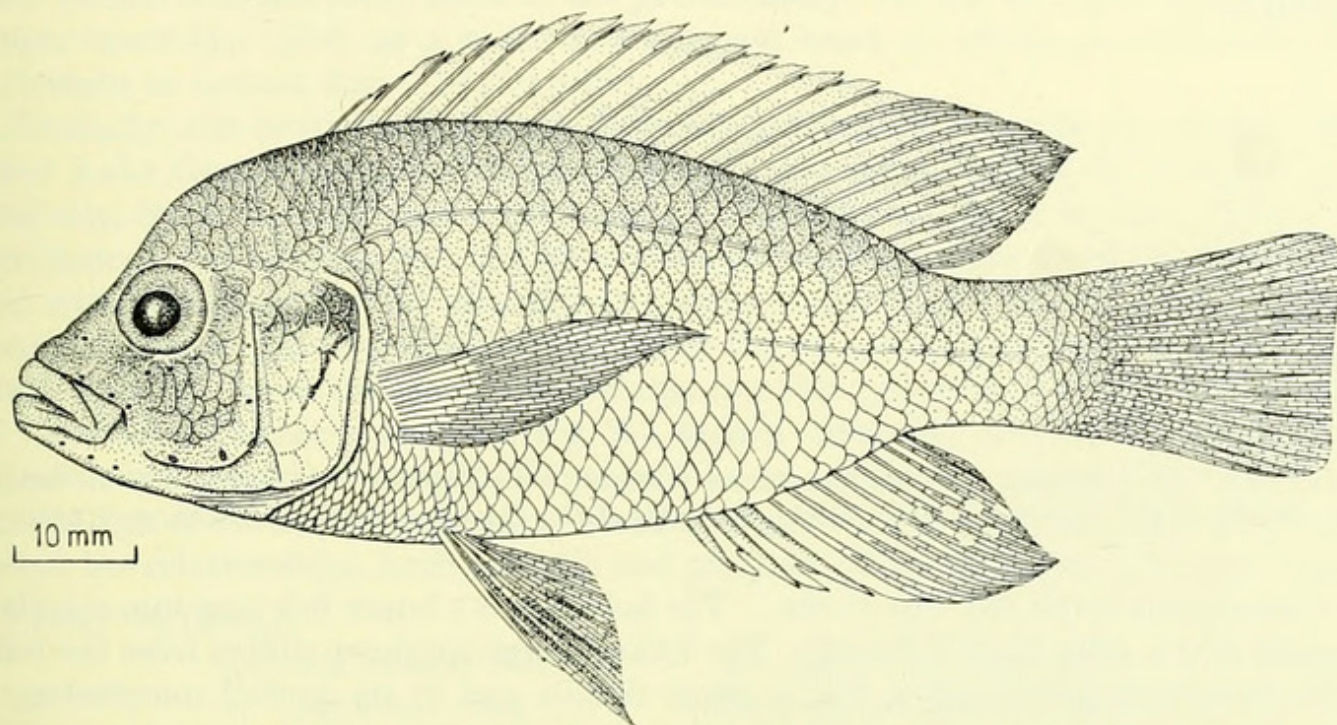


FIG. 26. *Haplochromis labiatus*. Lake George specimen.

*Scales.* Ctenoid, lateral line with 30 scales, cheek with 3 rows. There are  $5\frac{1}{2}$  scales between the upper lateral line and the dorsal fin origin, 7 between the pectoral and the pelvic fin bases. Scales on the thoracic region are small.

*Fins.* Dorsal with 15 spines and 10 branched rays, anal with 3 spines and 9 branched rays. Pectoral 31.0 per cent of standard length, 96.5 per cent of the head. Caudal scaled on its basal half; the distal margin is frayed but was apparently truncate when intact. Pelvics with the first ray barely produced.

*Teeth* of the *outer row* in both jaws are stout and somewhat compressed (text-fig. 27). In the upper jaw the two posterior teeth on each side are unicuspid, but the remainder are unequally bicuspid, with the crown vertically orientated. There are 32 teeth in this row.

All teeth in the lower jaw are bicuspid, but those located posteriorly are smaller than the more anterior teeth. Anteriorly, the lower jaw teeth are slightly procumbent, each tooth lying forward at an angle of about  $80^\circ$  to the horizontal.

The *inner teeth* in both jaws are small and tricuspid, and are arranged in 3 rows in the upper jaw and 2 in the lower.

The *lower pharyngeal bone* is moderately stout and its dentigerous area is slightly broader than long (1.1 times). The teeth are compressed and cuspidate, with the posterior teeth of the median rows coarser than the others.

The *vertebral count* is 13 abdominal + 16 caudal centra. (The type has 13 + 17 centra.)

Only *preserved coloration* is known. The body is brownish above and shades to silvery on the ventral flanks, chest and belly; the entire head is brownish. All



fins, except the pelvics, are hyaline-greyish, the soft dorsal is maculate posteriorly. The pelvics are dusky on the anterior half but hyaline posteriorly.

*Distribution.* Lakes Edward and George; not yet recorded from the Kazinga Channel.

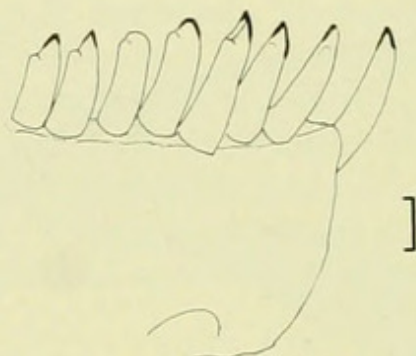


FIG. 27. *H. labiatus*. Dentary (anterior portion) with anterior and anterolateral teeth *in situ* (right side, viewed laterally); from the Lake George specimen. Scale = 0.5 mm.

COMPARISON WITH THE HOLOTYPE. The holotype is a larger fish (109 mm standard length) and is from Lake Edward. The Lake George specimen differs from the holotype in several minor ways, but in most details and in its overall morphology it resembles that specimen more closely than it does specimens of any other species.

The principal morphometric difference is in the longer jaws of the Lake George fish (35.7 and 32.2 per cent of head, *cf.* 32.3 and 28.0 per cent for the upper and lower jaws respectively); such a difference, however, is well within the range of variation for these characters in other *Haplochromis* species.

The lips of the holotype are clearly much better developed than are those of the Lake George specimen, and its teeth are predominantly unicuspid, not bicuspid as in the Lake George fish. However, some teeth in the holotype do show indications of a very small lateral cusp remnant. Both these differences could be attributable to the larger size of the holotype. Certainly the difference in lip development is well within the range of variation encountered in other species with hypertrophied lips and is not necessarily size-correlated. A further dental difference lies in the more clearly procumbent anterior teeth of the holotype. I am unable to comment on the significance of this character.

DIAGNOSIS AND AFFINITIES. As only two specimens are available (and those from different lakes) it is difficult to provide a precise diagnosis.

With so few specimens studied doubts might well be raised as to the validity of the species. However, if various dental and morphometric characters are combined, it seems most likely that *H. labiatus* is a valid species.

The teeth, thick lips and short lower jaw (*ca* 35 per cent of head) in *H. labiatus* together with its strongly concave profile distinguish the species from *H. limax* (teeth with obliquely cuspidate major cusps, compressed and relatively slender; lower jaw 36.0–40.9, mean 38.5 per cent).

The concave profile of *H. labiatus* is an immediately obvious difference when a comparison is made with *H. elegans*; the species also differ in that *H. elegans* has



a shallower cheek (18.2–24.5, mean 20.8 per cent head, *cf.* 23.5 per cent), and has obviously bicuspid teeth, even in large specimens.

Dental differences like these noted above distinguish *H. labiatus* from *H. aeneocolor* (which also has more teeth in the premaxillary, viz. 40–56, mean 48, *cf.* 32), a longer lower jaw (38.0–44.0, mean 41.0 per cent head, *cf.* about 35.0 per cent) and a straight or convex dorsal head profile.

Similarly, the dentition and gross morphology serve to separate *H. labiatus* from other Lake George species. Within this lake the appearance of *H. labiatus* (and, basically, its dentition) is most like that of *H. elegans* and *H. aeneocolor*, but the resemblances are less close than are those with *H. beadlei* Trewavas of Lake Nabugabo, and with species of the *H. crassilabris* species complex in Lake Victoria. Unfortunately I have still to resolve satisfactorily the *H. crassilabris* problem (see Greenwood 1965b). Nevertheless, species of this complex can each be distinguished from *H. labiatus*. Characters separating *H. beadlei* from *H. labiatus* holotype were detailed in Greenwood (1965b). These will be found less trenchant when the Lake George fish is taken into account. More specimens of *H. labiatus* must be studied before the relationships, both phyletic and phenetic, of the two species can be settled.

#### STUDY MATERIAL

Register number BMNH  
1972.6.2 : 809

Locality : Lake George  
East side of Akika Island

### ***Haplochromis pappenheimi*** (Blgr.), 1914 (Text-figs. 28–30)

*Tilapia pappenheimi* (part) Boulenger, 1914, in *Wiss. Ergebn. Deuts. Zentral-Afrika Exped.*, 1907–1908, *Zool.* **3** : 254–255 (10 of the 32 syntypes, all from Lake Edward, see note below).

*T. pappenheimi* (part) Boulenger, 1915, *Cat. Afr. Fishes*, **3** : 232–233 (4 of the 6 specimens listed, all from Lake Edward; the figured specimen is not in the B.M. (N.H.) collections but is in Berlin [see below]. The skeleton listed cannot be identified with certainty, but probably it is not this species).

*Haplochromis pappenheimi* : Regan, 1921, *Ann. Mag. nat. Hist.* (9), **8** : 634–635 (all Lake Edward fishes).

*Haplochromis pappenheimi* : Trewavas, 1933, *J. Linn. Soc. (Zool.)*, **38** : 334 (all Lake Edward fishes).

NOTE ON THE TYPE SERIES. Six of the syntypes were deposited in the British Museum (Natural History); the other 26 specimens were retained by the Berlin Museum.

Regan (1921) reviewed the B.M. (N.H.) material and referred 2 specimens to the new species *H. nigripinnis* and *H. eduardii* described in that paper. Regan did not examine the Berlin syntypes, and no lectotype was chosen. The 4 remaining syntypes were considered conspecific by Regan, a conclusion with which I concur.

Through the kindness and cooperation of Dr Deckert, I have been able to study the 26 syntypes (including the figured specimen) from the Berlin Museum collections. This series proved to be polyspecific and cannot be fully evaluated until the Lake Edward *Haplochromis* species are revised. For the moment, however, it should be noted that 12 syntypical specimens are conspecific and are considered to be *H.*



*pappenheimi* (see below). The other specimens, in part, are probably referable to *H. nigripinnis* (8 specimens Z.M. Berlin, nos. 22693 and 22698), *H. eduardii* (2 specimens, Z.M. Berlin, no. 22692) and 2 specimens to species as yet undescribed (Z.M., nos. 22695 and 22696).

Boulenger's (1914) original description of *H. pappenheimi* is quite inadequate by current standards, and thus it is impossible to determine from it the morphological limits of his species. The reason for my deciding that certain specimens are '*H. pappenheimi*' is essentially an attempt to avoid unnecessary nomenclatural change. There is certainly a biologically and morphologically valid taxon, occurring in both Lakes Edward and George, whose characteristics are recognizable in 16 of the *H. pappenheimi* syntypes (4 specimens from the B.M. [N.H.] and 12 from the Berlin Museum (Z.M.B. lot nos. 22689 and 22697). The four B.M. [N.H.] fishes are those on which Regan [1921] based his redescription of the species).

It is to these 16 specimens that I have decided the name '*pappenheimi*' should be restricted and from which the lectotype should be chosen. If any of the other syntypes was chosen as lectotype, then the name '*pappenheimi*' would either fall into synonymy or would replace the name of an already established taxon. Either way, a new name would have to be found for the taxon here considered to be *Haplochromis pappenheimi*.

Regrettably, the specimen illustrated in Boulenger (1914, 1915) cannot be referred to the taxon *H. pappenheimi* as recognized by Regan (*op. cit.*) or myself. It is a fish of 66.0 mm standard length, probably a female, ZMB no. 22692. As far as I can determine this fish is a specimen of *H. eduardii* Regan.

To avoid the nomenclatural changes that would follow the choice of this fish as lectotype, I have selected for that purpose a specimen from the 16 syntypes showing the diagnostic features of *H. pappenheimi*, *sensu* Regan (1921). This fish, a female 73.0 mm standard length (ZMB no. 19110) has a characteristically elongate and slender body, and also clearly shows the dental and gill raker characters of the species (text-fig. 28).

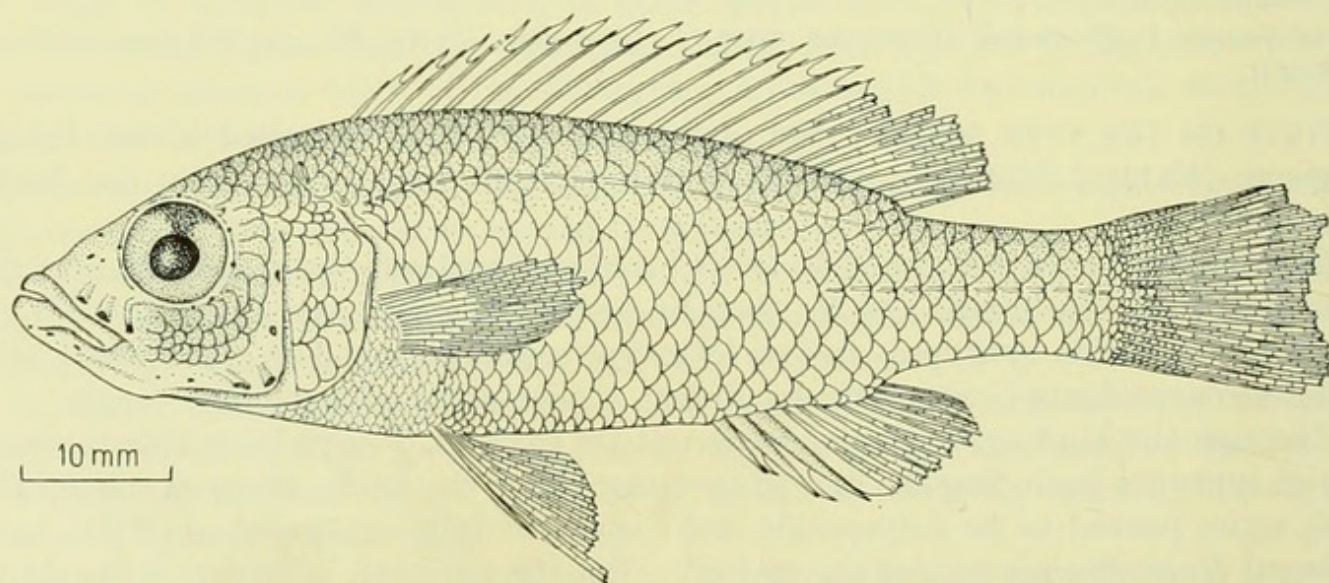


FIG. 28. *Haplochromis pappenheimi*. Lectotype; a Lake Edward specimen.



**DESCRIPTION.** Based on 20 specimens, 38.5–61.0 mm standard length, all from Lake George.

Depth of body 26.6–30.4 ( $M = 29.9$ ) per cent of standard length, length of head 30.5–34.4 ( $M = 32.3$ ) per cent.

Dorsal head profile straight, sloping gently at an angle of *ca* 20°–25° with the horizontal.

Preorbital depth 12.5–16.8 ( $M = 14.8$ ) per cent of head, least interorbital width 23.3–29.2 ( $M = 26.4$ ) per cent, length of snout 1.0–1.1 times its breadth, and 24.0–30.8 ( $M = 28.1$ ) per cent of head. Eye diameter 31.5–37.0 ( $M = 33.9$ ) per cent (not showing any allometry in this size range), depth of cheek 13.4–19.5 ( $M = 17.0$ ) per cent.

Caudal peduncle 19.5–24.5 ( $M = 22.2$ ) per cent of standard length, 1.5–2.0 (modal range 1.7–1.8) times as long as deep.

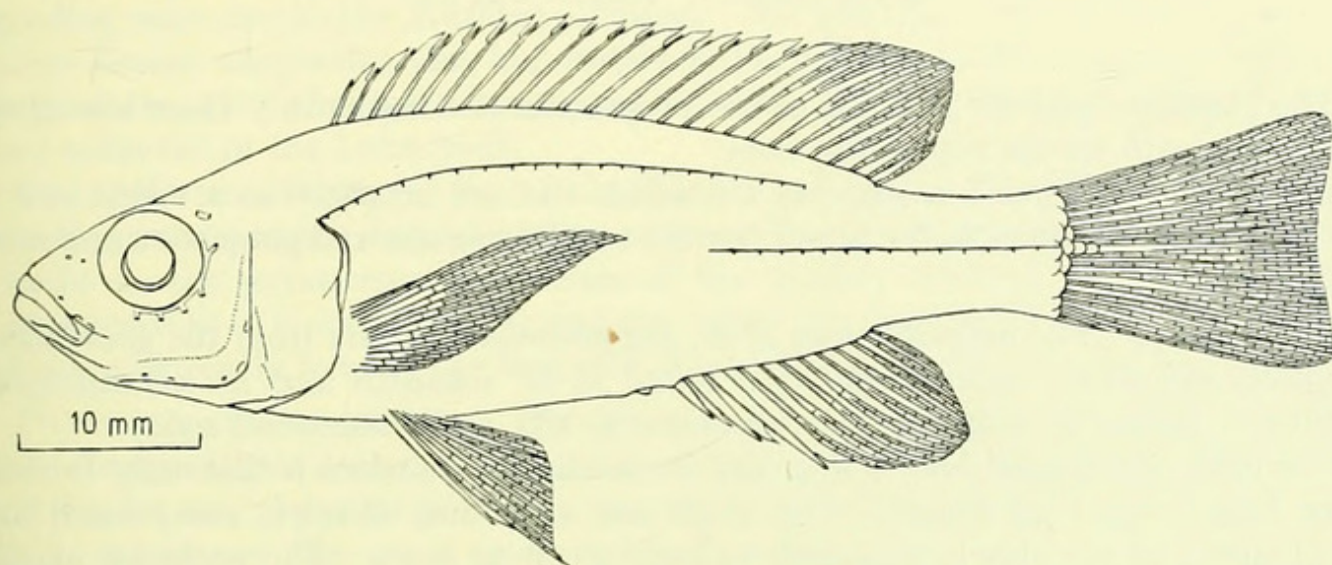


FIG. 29. *H. pappenheimi*. Outline drawing of a Lake George fish.

Mouth slightly oblique, jaws equal anteriorly. Posterior tip of the maxilla reaching a vertical slightly anterior to the orbital margin. Upper jaw 25.0–29.2 ( $M = 27.5$ ) per cent of head, lower jaw 35.7–41.5 ( $M = 39.0$ ) per cent, 1.7–2.5 (modal range 2.3–2.5) times longer than broad.

**Gill rakers.** The lower 1 or 2 rakers (rarely the first 4) are reduced, the others are long and relatively slender. Occasionally some of the uppermost rakers are flattened, or flattened and bifid. There are 10(rare)–13, mode 11, rakers on the lower part of the first gill arch. No pseudorakers are present.

**Scales.** Ctenoid; lateral line with 33 (f.7) or 34 (f.12) scales, cheek with 2 or 3 rows. Five (rarely) to 7 (mode 6) scales between the upper lateral line and the dorsal fin origin, 5–7 (mode 6) between the pectoral and pelvic fin bases.

**Fins.** Dorsal with 14 (f.1), 15 (f.10) or 16 (f.9) spinous and 8 (f.4), 9 (f.11) or 10 (f.5) branched rays. Anal with 3 spines and 7 (f.2), 8 (f.7) or 9 (f.11) branched rays. Caudal slightly emarginate, scaled on its basal half or slightly more. Pectoral fin 22.0–27.5 ( $M = 25.0$ ) per cent of standard length, 71.0–84.5 ( $M = 77.1$ ) per cent of head. Pelvics with the first ray slightly produced.



*Teeth.* The *outer teeth* in both jaws are unequally bicuspid, with the major cusp obliquely truncate in most fishes, but especially so in larger individuals (text-fig. 30); both the crown and the neck of the tooth are compressed. Occasionally, the teeth situated posteriorly and posterolaterally in the premaxilla are tricuspid or unicuspid; this difference may be size correlated, with unicuspid commoner in larger fishes (i.e.  $> 55$  mm standard length).

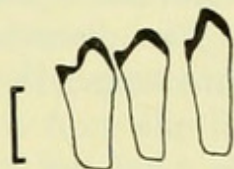


FIG. 30. *H. pappenheimi*. Dentary teeth (right), lateral and anterolateral in position. Viewed laterally. Scale = 0.25 mm.

The posterior quarter to third of the premaxilla is edentulous; there are 28–38 ( $M = 34$ ) teeth on the rest of the bone.

*Inner teeth* are small, invariably tricuspid, and are arranged in a single row in both jaws. Sometimes in the upper jaw the row is irregular and gives the impression of being double.

**OSTEOLOGY.** The *neurocranium* of *H. pappenheimi* departs from the generalized *Haplochromis* type, approaching that found in *H. schubotzi* and *H. schubotziellus*, and in *H. guiarti* of Lake Victoria (see above p. 186, and Greenwood 1962).

The *lower pharyngeal bone* is fine, and its dentigerous surface is distinctly broader than long (1.25–1.30 times). The teeth are very fine, slender, compressed and cuspidate, and are closely arranged in from 30 to 34 rows. The posterior margin of the bone is noticeably concave in outline when viewed from above, having the shape of a shallow V.

*Vertebral counts* in the 8 specimens examined are 30 (f.3), 31 (f.4) or 32 (f.1), comprising 14 (f.6) or 15 (f.2) abdominal and 16 (f.4) or 17 (f.4) caudal centra.

**COLORATION IN LIFE.** There appears to be no marked sexual dimorphism in coloration, although the possibility of this occurring cannot be overruled because no sexually active males have yet been examined. However, large and adult males were caught in the Kazinga Channel and these did not differ from females, except in being slightly darker.

The ground colour in both sexes is silver, shot with green iridescence above the midlateral line, and whitish on the belly. All fins are hyaline, but in males the lappets of the dorsal fin are black, as are the pelvic fins. The anal fin of males carries from 1 to 3 yolk-yellow ocelli.

**PRESERVED COLORATION.** Ground coloration is greyish-silver, darker (i.e. greyer) on the dorsum and flanks to about the midlateral line. All fins are hyaline to greyish, the lappets of the spinous dorsal black in males, as are the pelvic fins.

*Distribution.* Lakes Edward and George and the Kazinga Channel.



**ECOLOGY.** *Habitat.* The slender body form and pelagic habits of this species have resulted in relatively few specimens being caught in the nets used by the I.B.P. team. Thus, not a great deal is known about the habitat preferences of *H. pappenheimi*. The species is apparently confined to upper water levels in offshore regions of the lake (both in bays and in the open lake). An intensive study of the species is now in progress. The use of purse-seine nets and small-mesh trawls should result in many more samples being taken.

*Food.* The few guts examined contained only zooplankton, particularly copepods and cladocerans.

*Breeding.* Most of the specimens on which this description is based are sexually immature, but 2 fishes (females, 60 and 61 mm standard length) show signs of ovarian activity. Obviously, adults of *H. pappenheimi* in Lake George must reach a larger size (as they do in Lake Edward and the Kazinga Channel). There is, of course, the possibility that adult individuals move out of Lake George, and that the breeding sites are in the Kazinga Channel. To date the only evidence (and that rather flimsy) supporting this hypothesis is the capture, in May 1972, of numerous large adults in the channel, when, using the same gear (a purse seine), only juveniles were collected in the Lake itself.

One of the paralectotypes from Lake Edward, a female (72 mm standard length) is brooding young in the buccal cavity, as are 2 females (72.0 and 69.0 mm standard length) in the paralectotypical series of the British Museum (Natural History). Unfortunately it is impossible to sex the other paralectotypes with any certainty. All are apparently female, the largest a fish 92.5 mm standard length.

**DIAGNOSIS AND AFFINITIES.** The species is immediately distinguishable from other Lake George *Haplochromis* species by its slender body form, head shape, by its long and slender caudal peduncle, and by the shape and distribution of its outer jaw teeth. In life the silvery blue-green coloration is also diagnostic.

There is an overall similarity between *H. pappenheimi* and *H. guiarti*, a species endemic to Lake Victoria but which was once thought to occur in Lake Edward (Trewavas 1933; but see below p. 232).

*Haplochromis pappenheimi* differs from *H. guiarti* in several characters; for example, the dentition (obliquely cuspidate teeth, contrasted with the usual unicuspid and unequally but acutely bicuspid teeth of *H. guiarti*; the fewer teeth in *H. pappenheimi*, and the fully toothed premaxilla of *H. guiarti* compared with the posteriorly edentulous bone of *H. pappenheimi*), a shallower preorbital (12.5–16.8,  $M = 14.8$  per cent head, cf. 16.3–21.5,  $M = 18.3$  per cent in *H. guiarti*), shorter snout (24.0–30.8,  $M = 28.1$  per cent head, cf. 31.7–37.5,  $M = 34.4$  per cent), larger eye (31.5–37.0,  $M = 33.4$  per cent head, cf. 23.6–29.8,  $M = 26.5$  per cent in *H. guiarti* of the same size), and a longer caudal peduncle (19.8–24.5,  $M = 22.2$  per cent standard length, cf. 16.2–20.8,  $M = 18.9$  per cent).

Among the Lake Victoria *Haplochromis* species there is only one other, *H. fusiformis* Greenwood & Gee, that resembles *H. pappenheimi*. *Haplochromis fusiformis* is confined to the deeper waters (90–100 ft) of the lake and is benthic in habits. Like *H. pappenheimi* it has a partly edentulous premaxilla and is slender bodied. Interspecific differences, however, are well marked and include a shallower body,



deeper preorbital, smaller eye and longer lower jaw in *H. fusiformis*, as well as the retention of typical bicuspid teeth in that species.

#### STUDY MATERIAL

Register number BMNH	Locality : Lake George
1972.6.2 : 297-298	Kankurunga Island
1972.6.2 : 317-320	Small island north of Kankurunga Island
1972.6.2 : 328-332	Small island north of Kankurunga Island
1972.6.2 : 333-336	Small island north of Kankurunga Island
1972.6.2 : 337-342	Tufmac Bay

### *Haplochromis squamipinnis* Regan, 1921

(Text-fig. 31)

*Haplochromis squamipinnis* Regan, 1921, *Ann. Mag. nat. Hist.* (9), **8** : 636 (a single specimen, the holotype, BMNH reg. no. 1914.4.8 : 32, from Lake Edward).

*Haplochromis squamipinnis* : Trewavas, 1933, *J. Linn. Soc. (Zool.)*, **38** : 338-339 (mostly Lake Edward fishes, but 1 from Lake George).

NOTE ON *H. mentatus* Regan 1925, A PUTATIVE SYNONYM OF *H. squamipinnis*. Trewavas (1933) noted that the holotype and only specimen of *H. mentatus* (a Lake Edward species) closely resembled *H. squamipinnis*. She was unable to examine the holotype and thus did not see fit to formally synonymize the species with *H. squamipinnis*.

During a recent visit to the Museum of Comparative Zoology, Harvard University, I was able to examine *H. mentatus* holotype (MCZ no. 31523), a small fish 94.0 mm standard length, of indeterminable sex. In all morphometric characters and in most anatomical features this specimen is, as Trewavas suggested, like a young *H. squamipinnis*. However, I could not find any trace of the minute scales which are closely adherent to the bases of the anal and dorsal fin rays of *H. squamipinnis*, irrespective of the individual's size (see below p. 206).

These scales, which extend for a short distance onto the fins, are delicate and easily dislodged. Furthermore, there is considerable individual variability with regard to the number and position of the fin rays with which the scale rows are associated. Despite this variation, however, I have yet to examine a specimen of *H. squamipinnis* in which there is absolutely no trace of fin scales.

Thus, it is difficult to assess the significance of their total absence in *H. mentatus* holotype, especially since in all other trenchant characters the specimen agrees with comparable-sized *H. squamipinnis*.

Personally, I would be inclined to consider it either a young *H. squamipinnis* in which all traces of fin scales rows are lost, or an aberrant member of the species in which these scales failed to develop.

DESCRIPTION OF *H. squamipinnis*. Based on 34 specimens 34.0-202.0 mm standard length, from Lake George (including the specimens collected by Worthington in 1931). Because most characters show some allometry with standard length, the sample has been divided into two groups, viz. : (a) fishes < 120 mm standard



length and (b) fishes  $> 129$  mm standard length. Ranges and means for the various morphometric characters are given accordingly.

Depth of body (a) 32.1–37.0 ( $M = 34.7$ ), (b) 34.7–41.0 ( $M = 37.4$ ) per cent of standard length, length of head (a) 33.5–37.6 ( $M = 35.4$ ), (b) 33.9–36.2 ( $M = 35.0$ ) per cent.

Dorsal head profile straight but broken by the prominent premaxillary pedicels, sloping at an angle of *ca*  $40^\circ$  with the horizontal.

Preorbital depth (a) 15.0–19.0 ( $M = 17.0$ ), (b) 17.8–20.4 ( $M = 21.9$ ) per cent of head, least interorbital width (a) 19.2–23.0 ( $M = 21.9$ ), (b) 21.3–25.4 ( $M = 23.0$ ) per cent; length of snout equal to or slightly greater than its breadth in fishes of both size groups, but in (a) 30.8–33.8 ( $M = 32.3$ ) per cent of head and in (b) 31.5–37.1 ( $M = 34.9$ ) per cent.

Eye diameter (a) 23.0–33.0 ( $M = 27.5$ ), (b) 21.2–25.5 ( $M = 23.0$ ) per cent of head; depth of cheek (a) 18.3–27.6 ( $M = 24.5$ ), (b) 27.8–31.7 ( $M = 29.3$ ) per cent. For the cheek depth and eye diameter the lowest and highest values respectively relate to the smallest specimen examined.

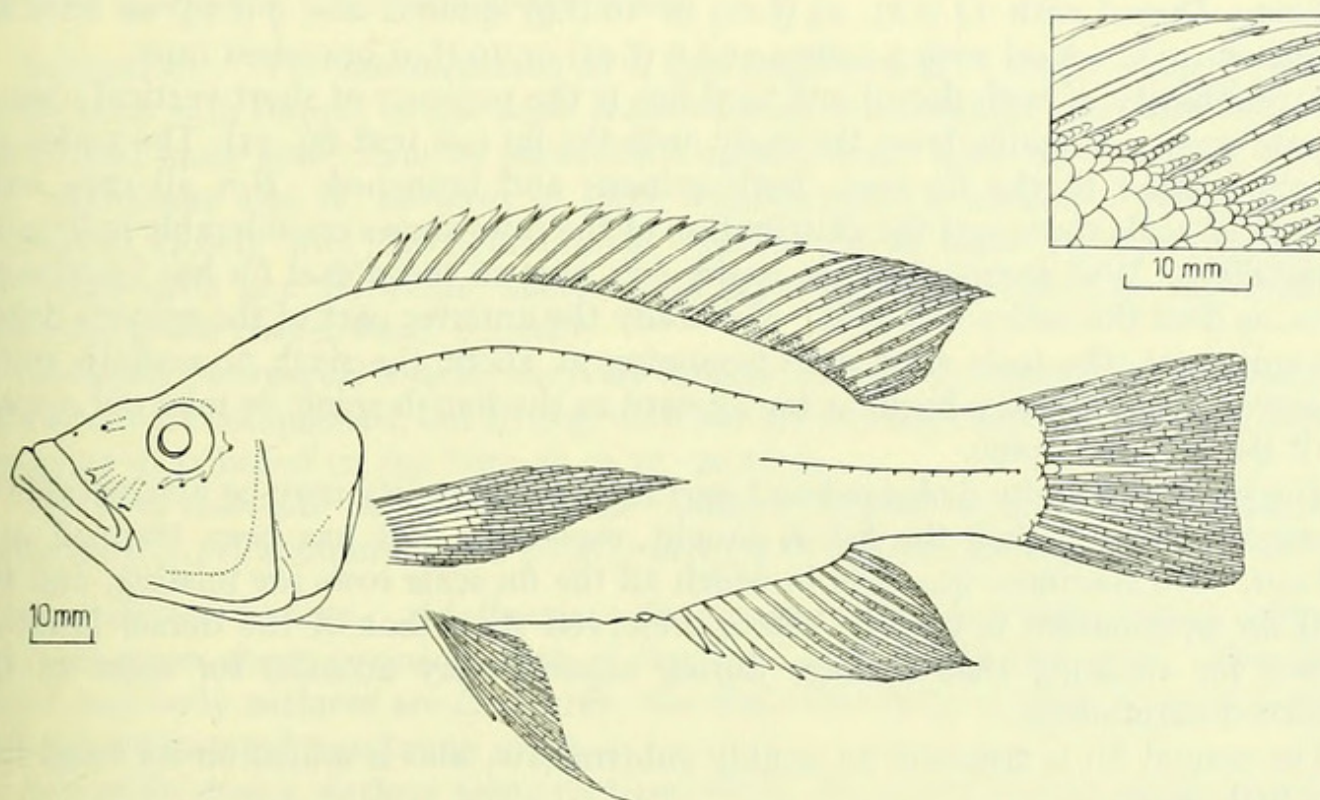


FIG. 31. *Haplochromis squamipinnis*. Lake George specimen. Inset shows squamation on dorsal fin.

Caudal peduncle not showing allometric growth, its length 14.7–20.6 ( $M = 16.8$ ) per cent of standard length, 1.1–1.5 (modal range, 1.2–1.4) times as long as deep.

Mouth distinctly oblique, sloping upwards at an angle of *ca* 35–45 degrees to the horizontal. Jaws equal anteriorly or the lower projecting slightly (the usual condition). Length of lower jaw in (a) 41.8–53.8 ( $M = 47.5$ ), (b) 47.3–56.6 ( $M = 51.3$ ) per cent of head, length of upper jaw in (a) 33.3–40.0 ( $M = 37.0$ ), in (b) 39.3–45.5



( $M = 42.4$ ) per cent, 1.1–1.5 (modal range 1.2–1.4) times longer than broad in both size groups. The smallest specimen examined (34.0 mm standard length) has, proportionately, the shortest jaws.

Posterior tip of the maxilla reaching a vertical through the orbital margin in most fishes, not quite reaching this level in a few, and extending beyond it to below the eye in others; this variation does not seem to be size correlated.

*Gill rakers.* The lower 1–3 rakers are reduced, the remainder are relatively slender. In some specimens the uppermost 1 or 2 rakers may be flat and anvil-shaped, and in some individuals all the rakers are short and relatively stout. There are 8–11 (rare), usually 9, rakers on the lower part of the first gill arch.

Pseudorakers are poorly developed: the tissue lying between the inner and outer gill raker rows is thickened and slightly produced into ill-defined, low projections.

*Scales.* Ctenoid; lateral line with 31 (f.1), 32 (f.17) or 33 (f.12) scales, cheek with 3, 4 (mode) or 5 rows. Five and a half to 7 (rare), usually 6, scales between the upper lateral line and the dorsal fin origin, 5–7 (mode 6) between the pectoral and pelvic fin bases.

*Fins.* Dorsal with 14 (f.1), 15 (f.21) or 16 (f.9) spinous and 9 (f.19) or 10 (f.12) branched rays. Anal with 3 spines and 9 (f.22) or 10 (f.9) branched rays.

A peculiarity of both dorsal and anal fins is the presence of short vertical rows of minute scales extending from the body onto the fin (*see* text-fig. 31). The scales are closely applied to the fin rays, both spinous and branched. Not all rays have associated scale rows, and the distribution of the rows shows considerable individual variability. Most frequently, the entire soft part of the dorsal fin has basal scale rows, as does the entire soft anal. Generally the anterior part of the spinous dorsal is asquamous, the scale rows only beginning at about the sixth or seventh spine. However, the rows may begin as far forward as the fourth spine, or may not appear until the eleventh spine.

The scales are easily dislodged and part of this variability may be attributable to damage sustained when the fish is caught, especially if it has been trapped in a gill-net. No specimen was seen in which all the fin scale rows are missing, and the anal fin squamation is usually better preserved than that of the dorsal (another reason for thinking that damage during capture may account for some of the observed variability).

The caudal fin is truncate to weakly subtruncate, and is scaled on its basal half or a little more.

Pectoral fin length shows no marked allometry with standard length; however, the relatively shortest fin is found in the smallest fish (34.0 mm standard length). Length of pectoral 23.5–30.0 ( $M = 28.1$ ) per cent of standard length, 66.6–87.0 ( $M = 79.9$ ) per cent of head.

Pelvic fins have the first ray produced and relatively more elongate in adult males than in females.

*Teeth.* Except for the smallest specimen (34.0 mm standard length), the predominant tooth form in the *outer row* of either jaw in fishes of 49.0–202.0 mm standard length is a slender but strong unicuspid with a slightly to strongly incurved



crown. Some fishes in the size range 75–85 mm standard length have a few weakly and unequally bicuspid teeth interspersed among the unicuspid teeth anteriorly and anterolaterally in both jaws; in one fish, most outer teeth in the lower jaw are bicuspid, although some typical unicuspid teeth occur anteriorly. In fish of all sizes the posterior premaxillary teeth are unicuspid.

The 34 mm standard length fish has typically unicuspid teeth posteriorly and posterolaterally in the upper jaw, but unequally bicuspid teeth (the major cusp long and slender) anteriorly; all the lower jaw teeth in this fish are unicuspid and typical.

The number of outer premaxillary teeth is positively correlated with standard length; in fishes < 118 mm standard length there are 34 (in the smallest specimen) to 70 ( $M = 48$ ) teeth, and in fishes > 130 mm standard length, 46–80 ( $M = 60$ ) teeth.

Fishes > 90 mm standard length have the *inner tooth rows* composed of slender unicuspid teeth, although in fishes as long as 100 mm some weakly tricuspid teeth may also occur. At lengths between 70 and 90 mm, there is usually an admixture of tri- and unicuspid teeth, but in some fishes only tri- and weakly tricuspid teeth are found. In smaller specimens, tricuspid teeth predominate.

**OSTEOLOGY.** The *neurocranium* in *H. squamipinnis* is of a relatively specialized type, both with respect to the basic *Haplochromis* neurocranial type, and also to the presumed basic skull form in piscivorous species (such as is shown by *H. guiarthi*, *H. victorianus* and *H. serranus* of Lake Victoria, see Greenwood 1962, 1967). It compares closely with the neurocranial type found in Lake Victoria species like *H. longirostris* and *H. mento*, species that have deviated from the near basic *H. serranus* grade (Greenwood, *op. cit.*).

The *lower pharyngeal bone* is relatively fine and has an equilateral dentigerous area. The teeth are compressed, but strong, with weakly developed cusps and are somewhat sparsely distributed on the bone in ca 18–20 rows.

*Vertebral counts* in the 11 specimens radiographed are 29 (f.3) and 30 (f.8), comprising 13 (f.11) abdominal and 16 (f.3) or 17 (f.8) caudal elements.

**COLORATION IN LIFE.** *Adult males*: the ground colour is greyish with a turquoise to blue-green sheen covering most of the flank and caudal peduncle. The dorsal head and body surfaces are dark grey, the chest and belly greyish to greyish-sooty, the branchiostegal membrane sooty.

Dorsal fin dusky, darkest along its basal third, the upper margin of this dark area with a gently undulating outline; the lappets are black but there is a narrow, pinkish margin to the soft part of the fin. Deep orange-red spots occur between the posterior rays of the soft dorsal. Caudal fin dark hyaline, with deep red spots and a light red (almost pink) flush over the ventral half of the fin and at its upper and lower distal angles. Anal fin almost completely pink, but with a hyaline area around the yolk-yellow ocelli. The pelvic fins are black.

*Females and immature males* are golden-silver dorsally, shading to yellowish-green on the flanks, and to white on the belly and ventral flanks. Dorsal fin yellowish-green, becoming hyaline dorsally. The caudal is similarly coloured, but



has dark spots over its proximal two-thirds. Anal fin dark hyaline basally, yellow-green distally; females often have yellow spots in the position of the ocelli in males, but young males may lack any indications of such markings. The pelvics are hyaline or yellowish, becoming dusky in near-adult males.

**PRESERVED COLORATION.** *Adult males*: the ground colour is brownish-grey above, shading to silvery grey or dusky silver on the lower flanks and belly; the chest is silvery or dusky silver. Upper surface of the snout and the lips (at least anteriorly) are dark grey, the lower jaw and branchiostegal membrane dusky grey. The only cephalic marking is an ill-defined lachrymal stripe.

The dorsal fin is grey, the lappets black. Basally there is a darker band (in places almost black) which widens over the soft part of the fin so that the basal third to half of the fin is black or very dark grey in colour. The distal part of the soft dorsal is densely and darkly maculate. The caudal is dark grey, most intensely so over its proximal third to half. The anal is grey to dusky grey, with the basal third noticeably darker. The pelvic fins are black.

*Females and juvenile males* are light brown above, shading to silvery yellow on the flanks and belly. The lips, snout and lower jaw are coloured as in adult males, but are slightly paler in some individuals. The lachrymal blotch is poorly defined but is generally visible. The coloration of the dorsal, caudal and anal fins is like that of adult males, but is more variable in its intensity. The pelvics are hyaline or a little dusky (more so in juvenile males) over the distal part of the first 3 rays.

**ECOLOGY.** *Habitat.* At least when adult, individuals of *H. squamipinnis* are found in all habitats, but are especially common in the offshore open-water areas of the lake. Juveniles may have a more restricted distribution to areas nearer the shoreline.

*Food.* Fishes predominate in the diet of *H. squamipinnis* at all the growth stages investigated (70–200 mm standard length), and appear to be the sole food source of fishes more than 150 mm standard length. In small fishes insects contribute substantially to the diet.

As far as could be determined, the principal prey species are other *Haplochromis*, but the macerated nature of the gut contents in *H. squamipinnis* generally precludes accurate identification.

*Breeding.* *Haplochromis squamipinnis* is a female mouth brooder. All examined individuals less than 120 mm standard length are immature; the first indications of sexual activity are found in fishes (of both sexes) in the size range 125–130 mm standard length.

Because all specimens larger than 155 mm standard length are females, there may be sexual dimorphism in the maximum adult size attained.

Of the 13 sexually active females examined, 5 have the right ovary larger than the left one, 2 have the right ovary slightly larger and 6 have the ovaries equally developed.

*Distribution.* Lakes Edward and George and the Kazinga Channel.

**DIAGNOSIS AND AFFINITIES.** The overall appearance of *H. squamipinnis* with its long and obliquely sloping jaws, its unicuspid teeth, and the peculiar scale rows



on the median fins, immediately distinguishes this species from all known *Haplochromis* species in Lake George. The same criteria would distinguish it from all known *Haplochromis* species in Lake Edward, but a rather similar species is now known to occur in that lake (Greenwood, unpublished information).

*Haplochromis squamipinnis* resembles a number of piscivorous *Haplochromis* species in Lake Victoria, but none of these has scale rows on the fins.

Taken in concert, the cranial and dental characters of *H. squamipinnis* place it near *H. victorianus* and *H. serranus* (i.e. the 'serranus' group of Greenwood 1967). However, in certain characters, especially skull form, *H. squamipinnis* approaches the rather more specialized structural grade seen in *H. mento* and *H. longirostris* (i.e. of the 'prognathus' group as defined by Greenwood, *op. cit.*).

Despite the general and often particular resemblances between *H. squamipinnis* and these various Lake Victoria species, it can be distinguished from them by various combinations of morphometric characters. It may be significant, in phylogenetic terms, that the male coloration of *H. squamipinnis* is not markedly different from that of *H. victorianus* (see Greenwood 1962, p. 157), and that several Lake Victoria species of the 'serranus' group show basically similar male breeding coloration.

*Haplochromis squamipinnis* also resembles *H. venator* Greenwood, the sole piscivorous *Haplochromis* species of Lake Nabugabo (Greenwood 1965b). Skull morphology in *H. venator* is rather more like that of *H. mento* than of *H. squamipinnis*, and there are some differences in gross body form as well as some specific morphometric ones (especially the deeper body and wider interorbital of *H. squamipinnis*). *Haplochromis venator*, of course, lacks the scale rows on its dorsal and anal fins. Certainly the similarities between this species and *H. squamipinnis* are no closer than those between *H. squamipinnis* and the Lake Victoria species considered above.

#### STUDY MATERIAL

Register number BMNH	Locality : Lake George
1972.6.2 : 379	I.B.P. Jetty
1972.6.2 : 380	I.B.P. Jetty
1972.6.2 : 381-386	Kashaka Bay
1972.6.2 : 387-395	Various localities
1933.2.23 : 449	Collected by Worthington
1933.2.23 : 439-443	Collected by Worthington
1933.2.23 : 450-451	Collected by Worthington
1933.2.23 : 452-455	Collected by Worthington
1933.2.23 : 444-448	Collected by Worthington

#### *Haplochromis petronius* sp. nov.

(Text-figs. 32-34)

**HOLOTYPE.** A male 85.5 mm standard length, BMNH reg. no. 1972.6.2 : 1, from Kashaka Crater, Lake George.

The trivial name, from the Latin, meaning 'of, or pertaining to rocks', refers to the usual habitat of this species in Lake George.



DESCRIPTION. Based on 25 specimens, 67.0–88.0 mm standard length (including the holotype), all from Lake George.

Depth of body 33.2–38.3 ( $M = 35.8$ ) per cent of standard length, length of head 31.8–35.8 ( $M = 33.8$ ) per cent.

Dorsal head profile straight, sloping steeply at an angle of *ca* 50°–55° with the horizontal.

Preorbital depth 14.5–19.3 ( $M = 17.6$ ) per cent of head, least interorbital width 19.2–25.0 ( $M = 22.1$ ) per cent. Snout length 0.7–0.9 (mode 0.8) of its breadth, 28.0–34.6 ( $M = 31.2$ ) per cent of head, diameter of eye 25.0–30.8 ( $M = 28.0$ ), depth of cheek 24.5–30.2 ( $M = 27.2$ ) per cent.

Caudal peduncle 12.6–16.8 ( $M = 15.7$ ) per cent of standard length, 1.1–1.4 (modal range 1.2–1.4) times as long as deep.

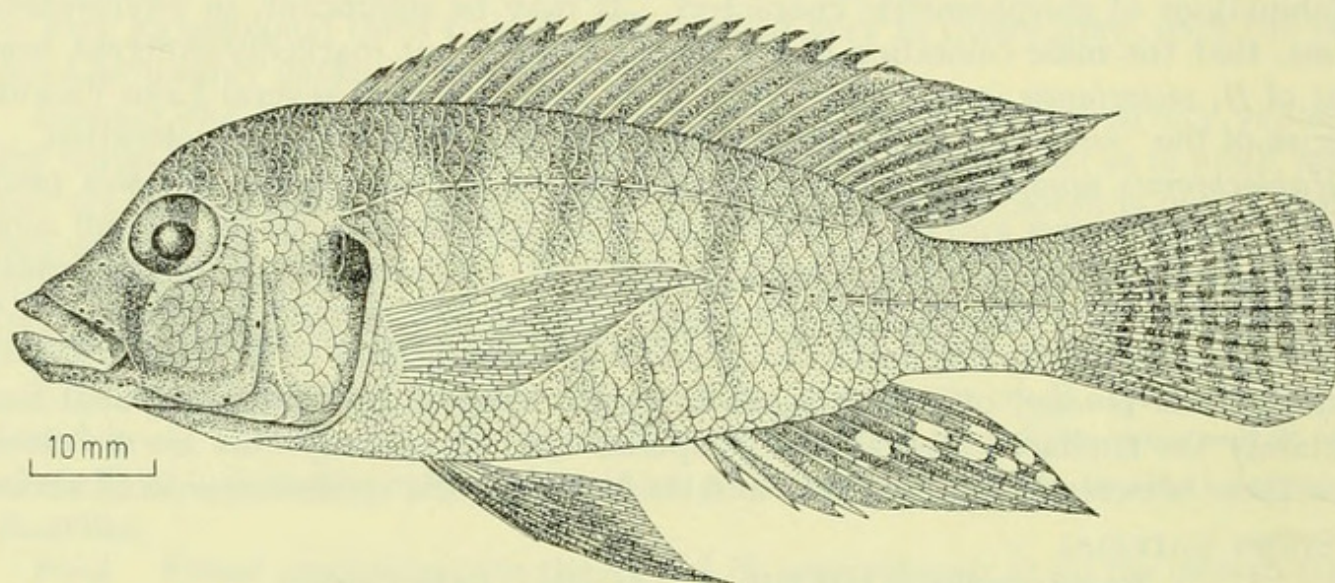


FIG. 32. *Haplochromis petronius*. Holotype.

Jaws equal anteriorly, mouth horizontal, the lips thickened. Posterior tip of the maxilla reaching a vertical through the anterior margin of the pupil, rarely not reaching so far posteriorly. Length of upper jaw 34.2–41.6 ( $M = 36.8$ ) per cent of head, length of lower jaw 34.8–41.5 ( $M = 37.8$ ) per cent, 1.3–1.7 (modal range 1.3–1.5) times its breadth.

*Gill rakers.* The lower 1–3 rakers of the first gill arch are reduced, the others are usually short and stout, but rather slender in some fishes. There are 7 or 8 (mode) rarely 9, rakers in the outer row on this arch.

The pseudorakers are very well developed and are transversely aligned so as to link the inner and outer rows of true gill rakers on the first arch.

*Scales.* Ctenoid; lateral line with 30 (f.3), 31 (f.4), 32 (f.15) or 33 (f.2) scales, cheek with 3 or 4 rows. Scales on the nape and chest are small, the latter rather deeply embedded. The transition between the larger ventral belly scales and the much smaller thoracic scales is abrupt, and occurs at about the level of the pectoral fin insertion. This abrupt type of size transition is unusual in *Haplochromis* (see Greenwood 1971). Another unusual character of the squamation in *H. petronius*



is the presence of a small naked area (equivalent to about 4 or 5 scales) immediately anterior to the insertion of the first dorsal fin spine.

There are 5-7 (mode 6) scales between the upper lateral line and the dorsal fin origin, and 7-10 (modal range 8-9) between the pectoral and pelvic fin bases.

*Fins.* Dorsal with 15 (f.3), 16 (f.21) or 17 (f.1) spinous and 8 (f.1), 9 (f.21) or 10 (f.3) branched rays. Caudal strongly subtruncate, almost rounded; scaled on its basal third to half.

Pectoral fin 26.5-32.4 ( $M = 28.1$ ) per cent of standard length, 75.0-97.8 ( $M = 82.0$ ) per cent of head length. Pelvics with the first ray somewhat produced in both sexes.

*Teeth.* In the *outer row*, the teeth posteriorly in the premaxilla are unicuspid and caniniform; anteriorly in this jaw and throughout the lower jaw the teeth are stout, unequally bicuspid (often weakly so), and have the crown incurved (text-fig. 33). These teeth are cylindrical in cross-section, with the upper part of the crown compressed. Occasionally, a few unicuspids occur anteriorly in the upper jaw, interspersed among the usual bicuspids. Also, in a few fishes the posterior premaxillary teeth are slender and bicuspid, not unicuspid as is usual for teeth in that position.

There are 36-50 ( $M = 42$ ) teeth in the outer premaxillary row.

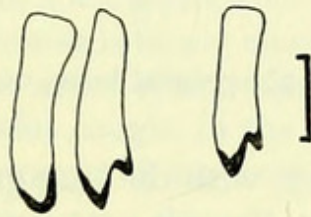


FIG. 33. *H. petronius*. Premaxillary teeth (left), anterolateral in position. Viewed laterally. Scale = 0.5 mm.

*Inner teeth* are usually tricuspids in fishes < 75 mm standard length (and in a few larger individuals) but most fishes > 75 mm long have an admixture of tricuspid, weakly tricuspid and unicuspid teeth. There are 2 or 3 rows of inner teeth in the upper jaw, and 2 (less frequently 3) in the lower jaw.

**OSTEOLOGY.** The *neurocranium* is of the generalized *Haplochromis* type (see p. 147) with a moderately decurved preorbital profile.

The *lower pharyngeal bone* is relatively stout, its dentigerous surface equilateral. The teeth are cuspidate and compressed, with those of the median rows noticeably coarser (text-fig. 34). In a few specimens some or all of the median teeth are submolariform. There are *ca* 20-24 rows of teeth.

*Vertebral counts* in the 12 specimens radiographed are 29 (f.10) and 30 (f.2), comprising 12 (f.1), 13 (f.10) or 14 (f.1) abdominal and 15 (f.1), 16 (f.8) or 17 (f.3) caudal centra.

**COLORATION IN LIFE.** *Males, adult but not sexually active*: the flanks are greenish-yellow, tinged with blue, the blue concentrated along the scale margins; dorsally



the colour changes to greenish-violet. The belly and chest are white, the branchiostegal membrane light grey. The lips are turquoise, and there are strong tinges of turquoise on the basically grey snout and cheeks.

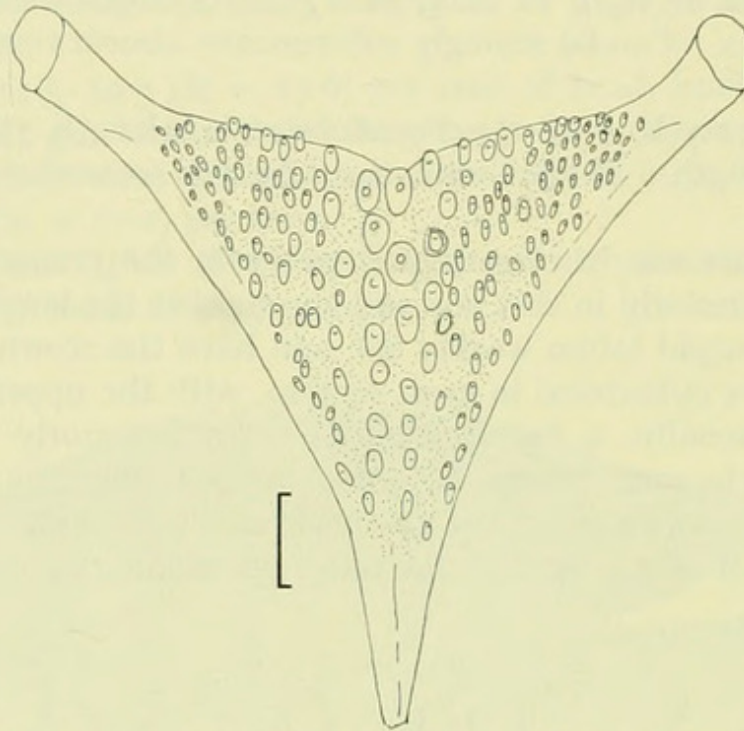


FIG. 34. *H. petronius*. Lower pharyngeal bone, occlusal view. Scale = 1.0 mm.

The dorsal fin is light sooty-grey, with the base greenish-blue, and the lappets red (as is the margin of the soft part); the soft part also has a scattering of well-marked, elongate, deep red streaks and spots. The anal fin is also sooty-grey (sometimes flushed with pink or red, perhaps a correlate of sexual activity) with a light-blue area along its base and a narrow scarlet outline to its margins; there are as many as eight bright orange ocelli on the posterior part of this fin. The caudal is dark grey, outlined in red, this marginal band expanding at the posterodorsal and ventral angles of the fin; deep maroon streaks occur between the rays. The pelvic fins are black or sooty, the spine and first ray are, however, bluish-white.

*Females*: no live females have been observed.

**PRESERVED COLORATION.** Only males are available, all are adult. The ground colour is uniformly light grey-brown; in some specimens there are traces of up to 7 dark but faint vertical bars across the flanks and caudal peduncle, those on the flanks extending from the dorsal body outline almost to the ventral body margin. The snout is dark grey to dusky, the lower jaw dusky-grey and the lips pale. The ventral aspects of the cheek and operculum are of variable duskiness, almost black in some fishes but only a dark brown in others. The branchiostegal membrane is greyish-sooty. Cephalic markings comprise a usually distinct and intense lachrymal stripe, and 2 transverse bars, of variable intensity, across the snout.

The dorsal fin is dark grey to sooty, the membrane between the last few branched rays maculate. The caudal is grey, maculate distally and dark grey, almost black



basally. The anal fin is greyish to sooty, the pelvics variable, from dusky to black but with the spine and first ray much lighter.

**ECOLOGY. Habitat.** *Haplochromis petronius* is the only Lake George *Haplochromis* species that appears to have a clearly circumscribed habitat. With a few exceptions (*see below*) the species has been found only in a rocky bay situated immediately behind the village of Kashaka. This bay is an old volcanic crater, one wall of which has collapsed and thus connected the crater with the lake. The bay is roughly ovoid in outline, its greatest and least axes being about 1.3 and 0.8 km. At its centre the water is some 6 m deep, but around the margins it is between 1 and 3 m. This marginal area has a rough substrate composed of rocks and stones derived from the crater walls. Some plant debris (including dead trees) lies among the rocks which, in places, are also covered lightly by a thin slick of organic mud. The bay is sheltered from all directions and has a relatively narrow entrance.

*Haplochromis petronius* is found only over the marginal rocky area of Kashaka Bay; nets set in the deeper central area, either at the bottom or floating at the surface, caught no *H. petronius*, although other fishes (both cichlid and non-cichlid), including species found inshore, were caught.

The species is common in catches from its habitat; other *Haplochromis* species inhabiting the same region include *H. angustifrons*, *H. elegans*, *H. aeneocolor* and *H. schubotziellus*, but none occurs in such abundance as does *H. petronius*.

Outside Kashaka bay, *H. petronius* is rarely encountered; it is probably significant in this connection that no other areas of the lake have a similar rock-boulder substrate. The very few *H. petronius* caught in the main lake are either from near the papyrus fringe over a mud-bottom or from over a sandy substrate on an exposed shore facing the lake centre.

**Food.** Insects, both larval and emergent, seem to be the commonest food organisms in the diet of *H. petronius*, but the sample I examined was small (20 specimens).

**Breeding.** The specimens I have examined are all males, and indeed I have been unable to catch any females, despite intensive fishing in the area. Thus, it would seem that there is a definite segregation of the sexes, and probably at all times of the year, itself an unusual phenomenon amongst *Haplochromis* species.

The smallest fish examined (67 mm standard length) is a ripening male, although another specimen 69 mm standard length is probably immature.

**Distribution.** Known only from Lake George.

**DIAGNOSIS AND AFFINITIES.** Taken in its totality, the appearance of *H. petronius* is highly characteristic, and readily distinguishes this species from other *Haplochromis* in Lake George. The small chest and nape scales, the abrupt size transition between the thoracic and ventral body squamation, and the small scaleless area before the first dorsal fin spine are trenchant diagnostic features.

However, these particular characters are also found in a species known from Lake Edward, viz. *H. pharyngalis* Poll (*see also* p. 177). The overall morphology of *H. pharyngalis* is also very like that of *H. petronius*, especially the steep head profile, the horizontal mouth with its thickened lips and the near-rounded caudal fin outline.



The principal interspecific differences are twofold. First, in *H. pharyngalis* the lower pharyngeal bone is greatly enlarged (massive in 1 of the 3 known specimens), and there are several rows of enlarged molariform or near-molariform teeth (see Poll 1939a, p. 46, fig. 26). Second, the nuchal and thoracic scales (particularly the former) are relatively smaller in *H. pharyngalis*. In addition, there are fewer (i.e. 6) gill rakers in *H. pharyngalis*, and there is a naked area, about 1 scale row deep, on the ventral margin of the cheek.

With only 3 specimens of *H. pharyngalis* available for comparison and with no information on their live colours, it is difficult to assess the precise relationship between the species. Certainly the differences in pharyngeal bone development (and correlated dental differences) and in the size and shape of the apophysis for the upper pharyngeal bones seem well marked. But, these are of similar nature to those distinguishing the George-Edward populations of *Astatoreochromis alluaudi* from those of Lake Victoria (see Greenwood 1959a, and especially 1965a). That *H. pharyngalis* shows a range of pharyngeal bone enlargement (even in only 3 specimens), and that *H. petronius* exhibits incipient molarization of the pharyngeal teeth, adds to the impression of close relationship between the species. The question can only be pursued when larger samples of *H. pharyngalis* are available.

An even closer resemblance exists between *H. petronius* and *H. wingatii* (Blgr.), a species of the Nile and Lake Albert (see Greenwood 1971 for a revision of this often misidentified species). Again, comparisons are hampered by the small number of specimens available. Only 2 well-preserved and 1 poorly preserved specimen of *H. wingatii* are known, all much smaller than the smallest *H. petronius* available, and there are no data on their live colours.

Morphometrically, *H. wingatii* and *H. petronius* are indistinguishable except for the longer pectoral fin in *H. petronius* (75.0–97.8,  $M = 86.4$  per cent head length, cf. 65.0–66.5 per cent for *H. wingatii*) and a higher vertebral count (29 or 30, cf. 28). Two slight interspecific differences are the absence of a naked predorsal area in *H. wingatii* and the existence of a naked strip below the cheek scales in that species. There is also a difference in the dentition. In the holotype of *H. wingatii* (53 mm standard length) the majority of the outer teeth in both jaws are slender, strongly recurved unicuspid. The outer teeth in *H. petronius* are relatively coarser and, except in the largest fishes, are all bicuspid. Even in large individuals the predominant tooth form is the bicuspid. The two other *H. wingatii* specimens are smaller and do have bicuspid teeth (as is usual for small individuals of species with a unicuspid definitive dentition). The bicuspid teeth in these specimens are slender (like the few bicuspid teeth of the holotype) and thus are unlike the bicuspid teeth of *H. petronius*.

Resemblances between *H. wingatii*, *H. petronius* and *H. pharyngalis* are striking, particularly since they involve, principally, details of squamation not found in other species of Lakes Edward, George or Victoria, or even in the fluviatile *Haplochromis* species of east Africa. Reduced pectoral and nuchal squamation is known from other *Haplochromis* and *Haplochromis*-like species, but in all these fishes it is associated with rheophilic habits (Greenwood 1954; Thys van den Audenaerde 1963). The habitats of the 3 species under consideration are far removed from the torrential,



and thus it is difficult to attribute the resemblances in squamation to environmentally induced parallelism. If, therefore, the similarities are a reflection of phyletic affinity, then *H. wingatii*, *H. petronius* and *H. pharyngalis* would appear to be of a lineage distinct from all other *Haplochromis* in Lakes Victoria, Edward and George. The implications of this conclusion will be considered later (p. 235).

## STUDY MATERIAL

Register number BMNH	Locality : Lake George
1972.6.2 : 1 (Holotype)	Kashaka Crater Bay
1972.6.2 : 2-10 (Paratypes)	Kashaka Crater Bay
1972.6.2 : 11-21 (Paratypes)	Kashaka Crater Bay
1972.6.2 : 22 (Paratype)	North end of Kankurunga Island
1972.6.2 : 23 (Paratype)	Caught over sandy shallows
1972.6.2 : 788 (Paratype)	Kashaka Crater Bay
1972.6.2 : 811 (Paratype)	Kashaka Crater Bay
1972.6.2 : 293	Sandy shoal

***Haplochromis eduardianus* (Blgr.), 1914**

(Text-figs. 35-37)

*Schubotzia eduardiana* Boulenger, 1914, in *Wiss. Ergebn. Deuts. Zentral-Afrika Exped., 1907-1908, Zool.* **3** : 258-259 (Lake Edward).

*Schubotzia eduardiana* : Regan, 1921, *Ann. Mag. nat. Hist.* (9), **8** : 639.

*Schubotzia eduardiana* : Trewavas, 1933, *J. Linn. Soc. (Zool.)*, **38** : 340.

All these references are to specimens from Lake Edward ; the species was not discovered in Lake George until recently.

NOTE ON THE ALTERED GENERIC STATUS OF THE SPECIES. Boulenger (1914) defined the monotypic genus *Schubotzia* solely on the basis of its dental morphology.

The outer jaw teeth are unusual (text-fig. 36). The crown is somewhat expanded relative to the cylindrical neck, has the tip distinctly rounded and strongly incurved so as to lie almost horizontally. In outline (i.e. as a flattened object) the tooth is paddle-shaped.

The inner teeth, by contrast, are typical tricuspid but are restricted to 1 or 2 rows in each jaw.

In other characters, *Schubotzia* does not differ from *Haplochromis*. The lower jaw, especially the dentary, is deep and stout, and the premaxilla is rather inflated. However, both these characteristics can be seen in other *Haplochromis* species (e.g. *H. nigricans* and *H. obesus* of Lake Victoria), although the condition could not be described as a common one ; it is usually associated with a specialized dentition. The lower jaw of *Schubotzia* is slightly overhung by the upper jaw, again an unusual condition but one found in some *Haplochromis* species (e.g. *H. xenognathus* of Lake Victoria, a species with an unusual dentition, albeit one quite unlike that of *Schubotzia eduardiana* ; see Greenwood 1957).

The teeth of *Schubotzia* are outstandingly different when compared with those of other Lakes Edward and George cichlids (text-fig. 36) and especially with those of the



*Haplochromis* species known to Boulenger in 1914. But, when the *Schubotzia* tooth type is seen against the wide range of tooth morphology found within the genus *Haplochromis* as a whole (or just a segment like the species of Lake Victoria), then it does not seem to be so unusual.

In my opinion, the morphological differences separating *Schubotzia* from *Haplochromis* are relatively slight, and certainly less than those distinguishing *Haplochromis* from the Lake Victoria monotypic genera *Hoplotilapia* and *Platytaeniodus* (or those genera from one another).

To retain *Schubotzia eduardiana* in a separate and monotypic genus serves only to hide its close phyletic relationship with *Haplochromis*. Thus, I would favour classifying this taxon with its closest relatives, that is in the genus *Haplochromis*.

Rosen and Bailey (1963, p. 6) have succinctly stated the pragmatic and theoretical difficulties associated with the generic concept. Particularly they stress the often phyletically misleading results of undue emphasis placed on one or two outstanding morphological differences as generic criteria. I am fully in agreement with these authors' support for a wider use of the subgenus to indicate morphological divergence without losing sight of phyletic relationships. Reducing the genus *Schubotzia* to subgeneric status could well meet the requirements of this particular case. However, there is a great need for new and careful consideration of the generic and infrageneric classification of the 'genus' *Haplochromis* as currently defined. Such a study must be based on phyletic principles and must test the phyletic integrity of what might well be a polyphyletic taxon.

It is my intention to undertake just such a study; for the moment, I prefer not to establish *Schubotzia* formally as a subgenus of *Haplochromis*.

**LECTOTYPE.** A specimen 71.0 mm standard length, BMNH reg. no. 1914.4.8 : 35, from Lake Edward. This specimen is eviscerated and its sex cannot be determined; the absence of dark pigment on the body suggests that it is a female (*see below* p. 220).

Three paralectotypes are in the collections of the Berlin Museum; all are from Lake Edward.

**DESCRIPTION.** Based on 20 specimens, 50.5–79.0 mm standard length, from Lake George. A smaller fish, 35 mm standard length is not included in the morphometric section, since it is distorted, but certain features of its dentition are considered on p. 218.

Depth of body 30.5–36.7 ( $M = 33.5$ ) per cent of standard length, length of head 31.5–34.3 ( $M = 33.1$ ) per cent.

Dorsal head profile gently decurved, but sometimes straight, sloping at an angle of 30°–35° with the horizontal.

Preorbital depth 11.2–15.4 ( $M = 13.3$ ) per cent of head, least interorbital width 23.0–28.3 ( $M = 25.9$ ) per cent. Length of snout 0.8–0.9 of its width, 23.0–28.3 ( $M = 25.9$ ) per cent of head, eye diameter 29.6–36.0 ( $M = 32.8$ ) per cent, depth of cheek 16.7–22.2 ( $M = 20.0$ ) per cent.

Caudal peduncle 14.7–19.5 ( $M = 16.9$ ) per cent of standard length, 1.2–1.7 (modal range 1.3–1.5) times longer than deep.



Mouth horizontal, lips slightly thickened ; lower jaw shorter than the upper when the mouth is closed. Length of upper jaw 30.8–36.0 ( $M = 32.8$ ) per cent of head, length of lower jaw 29.2–35.1 ( $M = 33.1$ ) per cent, 1.0–1.4 (mode 1.1) times longer than broad. Posterior tip of the maxilla reaching a vertical through the anterior margin of the eye, rarely not quite reaching that level.

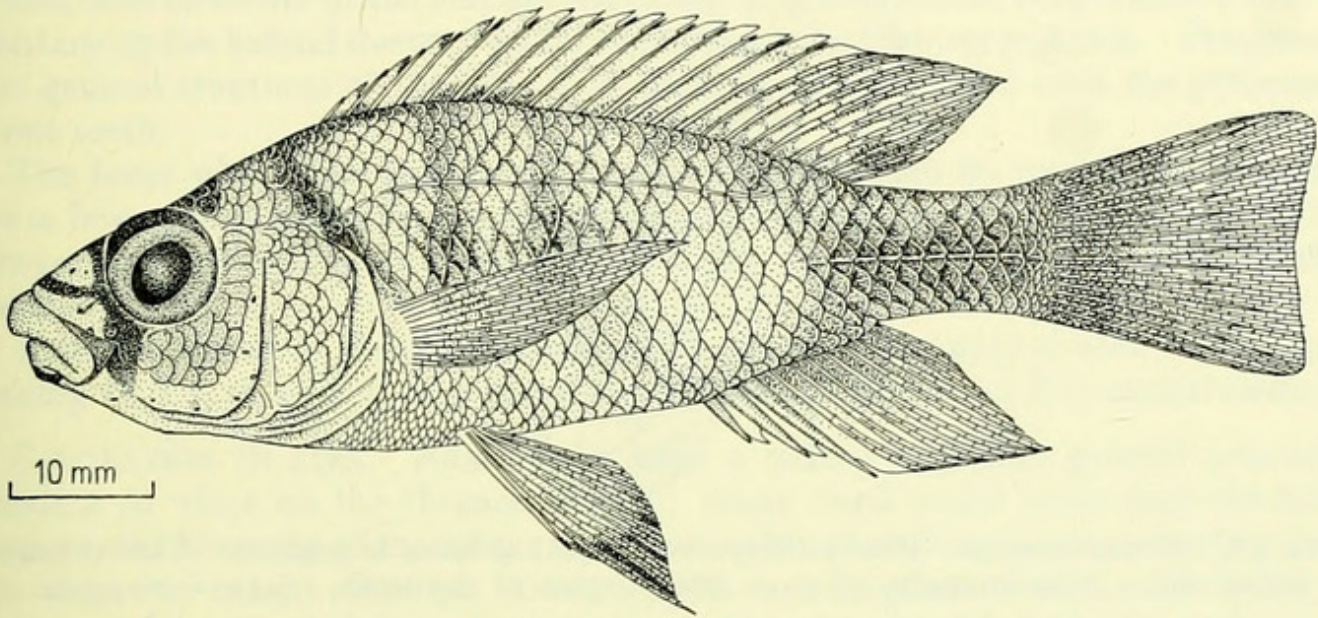


FIG. 35. *Haplochromis eduardianus*. Lake George specimen ; a male.

*Gill rakers.* The lowermost 1 or 2 rakers are reduced, the others are relatively slender although as many as 3 of the lower rakers may be relatively stout. The pseudorakers are well developed and prominent, but are short and stout.

There are 8 or 9 (rarely 10) gill rakers in the outer series on the lower part of the first gill arch.

*Scales.* Ctenoid ; lateral line with 31 (f.8), 32 (f.11) or 33 (f.1) scales, cheek with 2 or 3 (mode), rarely 4 rows. Five to 7 (modes at 5 and  $5\frac{1}{2}$ ) scales between the upper lateral line and the dorsal fin origin, 6–8 (mode 7) between the pectoral and pelvic fin bases.

*Fins.* Dorsal with 14 (f.1), 15 (f.11) or 16 (f.8) spinous and 8 (f.6), 9 (f.13) or 10 (f.1) branched rays. Anal with 3 spines and 7 (f.2), 8 (f.16) or 9 (f.2) branched rays. Pectoral fin 26.5–32.4 ( $M = 28.1$ ) per cent of standard length, 80.5–98.0 ( $M = 82.0$ ) per cent of head. Caudal subtruncate, scaled on its basal half. Pelvics with the first ray slightly elongate.

*Teeth.* With one exception in the material studied, the shape of the *outer teeth* in both jaws is remarkably uniform. Each tooth is unicuspid, with a flattened crown that is almost half the total length of the tooth. The whole crown is strongly incurved (especially in teeth situated anteriorly and anterolaterally), and its tip is broadly rounded (text-figs. 36 & 37). The neck of the tooth is cylindrical and, compared with that of a typical bicuspid tooth, much stouter. If a tooth were straightened out so that the crown and neck are in one plane, then it would have the outline of a paddle.



The exceptional specimen mentioned earlier (a fish 50.5 mm standard length) differs from the others only in having a few small tricuspid teeth intercalated among the typical teeth posterolaterally in the upper jaw.



FIG. 36. *H. eduardianus*. Premaxillary teeth (right) anterior in position. Viewed from below and a little laterally, to show labial aspect of the teeth. Scale = 0.25 mm.

In the smallest available specimen (35 mm standard length), most teeth are like those of larger fishes, but in both jaws there are a few teeth with traces of a small lateral cusp. This minor cusp is not separated from the major one by a distinct gap, as in typical bicuspid. Instead, the demarcation between cusps is more in the nature of a narrow, V-shaped groove. Because a minor cusp is present, the outline of these teeth is not rounded but is rather bluntly oblique. Posteriorly in the lower jaw of this small fish there are a few tricuspid teeth.

There are 40-52 ( $M = 48$ ) teeth in the outer row of the upper jaw; the number not showing any correlation with the fish's size.

*Inner teeth* (text-fig. 37) in both jaws are tricuspid, with the crown compressed and strongly incurved; arranged in 2 or rarely 3 rows in the upper jaw and a single (rarely double) row in the lower jaw. Virtually no interspace exists between the outer tooth row and the first row of inner teeth.

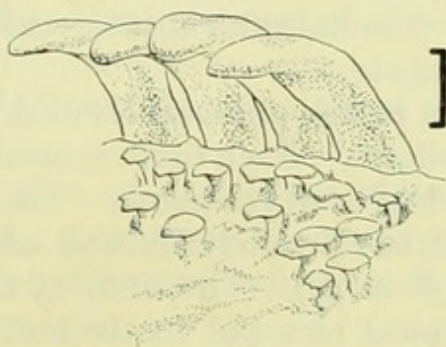


FIG. 37. *H. eduardianus*. Dentary teeth (left), anterolateral in position. Viewed from medial aspect to show lingual face of teeth. Scale = 0.25 mm.



**OSTEOLOGY.** The *neurocranium* is of the generalized *Haplochromis* type with a moderately decurved preorbital profile ; that is, a skull of the type found in *H. limax* and *H. petronius* rather than of the type in *H. macropsoides* and *H. elegans*. The premaxilla is a stout and inflated bone (especially the dentigerous arm) and resembles a more extreme form of the premaxilla found in *H. limax*. Stoutness and compactness also characterize the lower jaw. Both dentary and articular are stout, deep bones, and elements of the suspensorium are so arranged and proportioned that the dentary tip lies behind the vertical through the premaxillary symphysis. Presumably the general stoutness of the jaws is at least partly correlated with the presence of stout teeth.

The *lower pharyngeal bone* is relatively stout, although its teeth are fine (except for a few coarser posterior teeth in the middle tooth rows of larger fishes). There are *ca* 24–26 rows of teeth arranged over a dentigerous area about 1.3 times broader than it is long.

*Vertebral counts* in the 10 specimens radiographed are 29 (f.7) and 30 (f.3), comprising 13 (f.7) or 14 (f.3) abdominal and 15 (f.2), 16 (f.6) or 17 (f.2) caudal elements.

**COLORATION IN LIFE.** *Adult males* have a silvery blue-grey ground coloration, shading to white on the thoracic region ; many flank scales have deep red-brown centres, the intensity of the colour and the number of reddened scales correlated with the degree of sexual activity. Dark cephalic markings are always well developed. A thin stripe crosses the snout at the level of the lower orbital margin, and a much broader band runs between the upper orbital margins. Often this upper band is interrupted medially. A broad lachrymal stripe is continued above the eye as a wide blotch, the blotches from each side usually meeting medially. Behind this mark is another, this time in the form of a broad band crossing the nape from an origin at about the level of the upper opercular margin's midpoint.

The dorsal fin is hyaline with bright scarlet lappets and a diffuse scarlet flush between the spines ; this flush becomes concentrated into discrete blotches and spots between the branched rays. The anal is dusky on its proximal half, pinkish to scarlet distally ; the almost round ocelli (1 or 2) are very large and are yolk-yellow in colour. The caudal is entirely suffused with bright scarlet, although its ground colour is greyish-green. The pelvic fins are dusky but have scarlet streaks between the rays posteriorly on the proximal half of the fin.

*Females (at all stages of sexual activity)* : the ground colour is dark silver-grey shading to white on the belly and chest. Cephalic markings are usually absent, but if visible are a faint replica of those in the male (*see above*). The dorsal fin is hyaline, with a narrow scarlet marginal band on the soft part, and thin red streaks on the lappets of the spinous part ; in some individuals red streaks are present between the spines and rays. The caudal is hyaline with an overall pink flush, sometimes intensified to scarlet streaks between the rays and along the posterior margin of the fin. The anal is very pale yellow, with 2 deeper yellow spots (not ocelli) in the position of ocelli in males. The pelvics are whitish-hyaline.

**PRESERVED COLORATION.** *Adult males* : the ground colour is silver-grey, the flanks crossed by up to 10 vertical bars of variable intensity and definition ; the



first 2 bars lie immediately behind the opercular margin, the last on the caudal peduncle. Dorsally, the bars extend to the body outline and at least anteriorly may extend onto the dorsal fin membrane; ventrally the bars do not reach much below the level of the pelvic fin insertion.

Cephalic markings are very intense. Across the snout are 2 parallel bars, the upper generally twice the width of the lower. A broad lachrymal stripe is present, and there is a well-defined bar or triangular blotch extending towards the midline immediately behind the orbit. Posterior to this mark is another, but strap-shaped one which lies anterior to the dorsal fin origin. This bar appears to be a medial extension of the first vertical bar on the flank.

All fins, except the pectorals and pelvics, are yellowish, the basal region of the caudal often dusky. The pectorals are hyaline, and the pelvics black on the outer third, otherwise dusky.

*Females* are silvery grey or yellowish, with all fins yellow or hyaline. No cephalic markings are visible except, in some specimens, for a faint darkening below the eye, that is, in the position of a lachrymal stripe.

**ECOLOGY. Habitat.** The species is found in most inshore areas of the lake, over sand and mud bottoms, and in both exposed and sheltered localities. It has also been caught in the near-shore areas of the open lake but not further than about 100 m from the nearest land (in this case a small, reed-fringed island). No specimens have been collected in midlake or other distinctly offshore regions.

*Food.* The diet of *H. eduardianus* is still unknown. Most specimens examined had nothing recognizable except for a few sand grains and a few macrophyte fragments in any part of the gut.

The highly specialized dentition would suggest equally specialized feeding habits. By analogy with the similarly shaped teeth of *Plecodus* spp., one might suspect a similar diet of fish scales (Marlier & Leloup 1954).

Since the intestine of *H. eduardianus* is short (about half the length of the body) a vegetarian diet is almost certainly ruled out.

As so many (ca 90 per cent) of the specimens examined have nothing in the guts it seems probable that, whatever the food, it is rapidly digested.

*Breeding.* *Haplochromis eduardianus* is a female mouth brooder. Sexual maturity is reached at a standard length of ca 55 mm, and both sexes attain the same maximum length.

All of the 9 sexually active females examined have the right ovary much larger than the left one, and in some individuals only the right ovary is developed.

*Distribution.* Lakes Edward and George and the Kazinga Channel.

**DIAGNOSIS AND AFFINITIES.** *Haplochromis eduardianus* is distinguished from all other *Haplochromis* species in Lakes George and Edward by the morphology of its teeth. This peculiar tooth form led Boulenger (1914) to place the species in a distinct and monotypic genus. Reasons for not accepting Boulenger's classification are discussed above (p. 215). In essence, I argue that to place *H. eduardianus* in a monotypic genus (i.e. *Schubotzia*) is to obscure its phyletic relationships. That the dentition (both oral and pharyngeal) of *Haplochromis* group cichlids is, in an evolutionary sense, easily modified can be seen readily amongst the component species



of the Lake Victoria *Haplochromis* species flock (see Greenwood 1965c for summary and further references). Indeed, in at least one instance the morphological sequence leading from generalized to highly specialized dentitions is still preserved among the extant species of that lake (Greenwood 1957). There are also examples where intraspecific variability is such that if only the extreme condition was known, and the criteria for generic status were based solely on morphological 'gaps', then the species would have to be accorded generic status (see Greenwood, *op. cit.*, p. 96, with reference to *H. xenognathus*).

The reality of a morphological gap like that between the *H. eduardianus* tooth form and the shape of the teeth in any other *Haplochromis* species cannot be denied; the difficulty lies in attempting to interpret the significance of the gap. The existence within a single species flock of such examples as *H. xenognathus* (and others where different species bridge a morphological gap) warns against hasty action that could obscure the essence of a phyletic classification; that is, the demonstration of relationships as well as divergence. Is there any reason to suppose that, phylogenetically, the current evolutionary end-point seen in '*Schubotzia*' *eduardiana* and *Platytaeniodus degeni* or *Hoplotilapia retrodens* (both Lake Victoria monotypic genera; see Greenwood 1956a) is any different from that represented by *H. xenognathus*? Certainly all three monotypic genera have as their nearest relatives a species of *Haplochromis*. That such a species can be found for *H. xenognathus* (Greenwood 1957) but not for *Schubotzia*, *Platytaeniodus* or *Hoplotilapia* may be more a reflection of a past epigenetic situation than of phyletic history.

#### STUDY MATERIAL

Register number BMNH	Locality: Lake George
1972.6.5 : 1-3	Tufmac Bay
1972.6.5 : 4	Kashaka Crater
1972.6.5 : 5-7	Small island north of Kankurunga Island
1972.6.5 : 8-13	Various localities
1972.6.5 : 14-20	Various localities

#### NON ENDEMIC *HAPLOCHROMIS* AND *HAPLOCHROMIS*-GROUP SPECIES IN LAKE GEORGE

##### *Haplochromis nubilus* (Blgr.), 1906 (Text-fig. 38)

*Haplochromis nubilus* (part) : Trewavas, 1933, *J. Linn. Soc. (Zool.)*, **38** : 329.

Most of the Lake George specimens referred to *H. nubilus* by Trewavas (1933) were misidentified, but two specimens (BMNH reg. nos. 1933.2.23 : 285-286) from Worthington's (1932) station 618 appear to be of this species. They are not included in the description given below.

Four specimens collected by the I.B.P. team can be identified with certainty since all are sexually active males and their live colours were recorded. These fishes came from a catch made close inshore, near reeds, in a bay of Akika Island.



A summary of morphometric characters is given below. It is based on 3 specimens only because the fourth is distorted and damaged. The latter specimen is, however, used in the description of the teeth and for fin ray and scale counts.

S.L.	Depth †	Head †	PO %	IO %	Snt %	Eye %	Cheek %	Lj %	Uj %	CP †
67.0	37.3	34.3	17.4	21.7	28.3	30.3	21.8	34.8	34.8	16.4
70.5	39.3	34.1	16.7	27.0	31.3	29.2	22.9	37.5	37.5	16.5
74.5	37.5	34.2	15.6	24.7	28.4	27.4	23.5	39.1	35.3	16.1

† = per cent of standard length.

% = per cent of head.

Lj = lower jaw, Uj = upper jaw.

Caudal peduncle 1.3–1.4 times longer than deep.

Dorsal head profile sloping steeply at *ca* 40°–45° with the horizontal, its outline straight except for a marked concavity above the orbital region. Upper margin of the orbit distinctly below the level of the dorsal profile.

Mouth horizontal, lips somewhat thickened; posterior tip of the maxilla reaching a vertical through the anterior margin of the orbit. Jaws equal anteriorly, the lower *ca* 1.3 times longer than broad. Snout slightly broader than long.

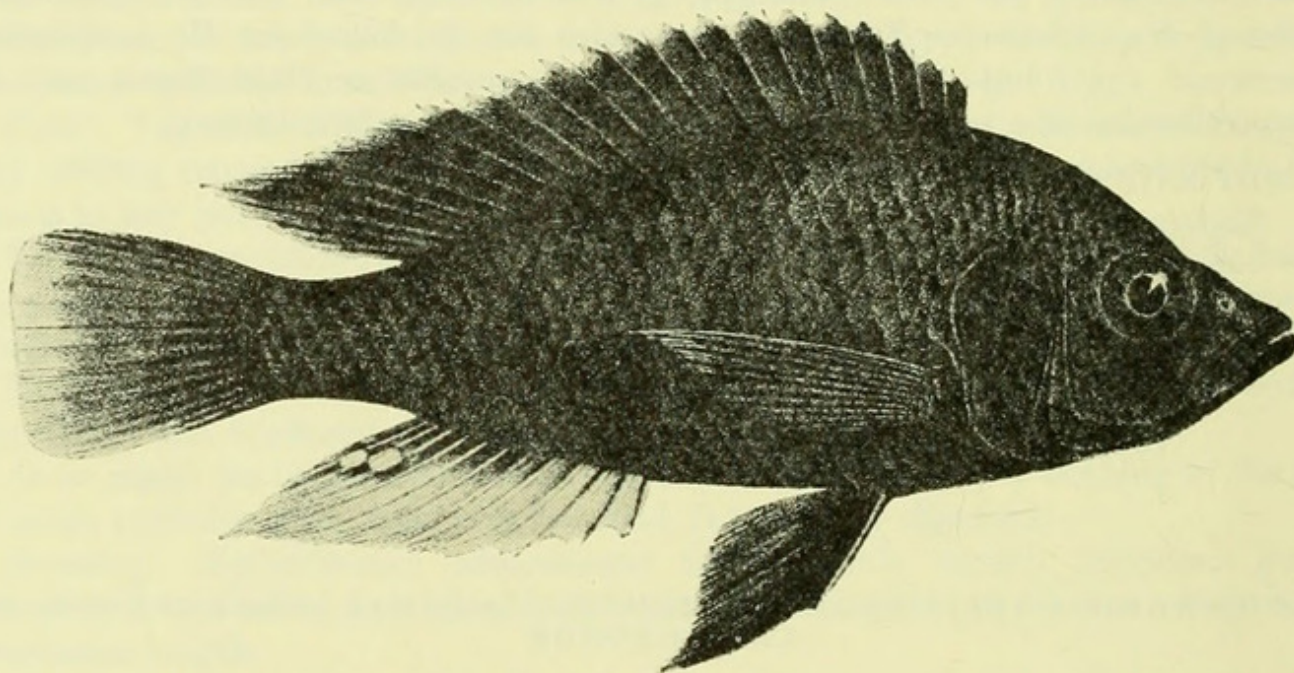


FIG. 38. *Haplochromis nubilus*. A Lake Victoria specimen. From Boulenger, *Fishes of the Nile*.

*Gill rakers*. Eight or 9 on the lower part of the first arch; the lower 2 rakers are reduced, the remainder are relatively stout. Pseudorakers are present and discrete, but are rather low and small.

*Scales*. Ctenoid; lateral line with 31 (f.2) or 32 (f.2) scales, cheek with 3 or 4 rows. Five or 5½ scales between the upper lateral line and the dorsal fin origin, 6 between the pectoral and pelvic fin bases.

*Fins*. Dorsal with 15 (f.4) spinous and 9 (f.2) or 10 (f.2) branched rays, anal with 3 spines and 8 (f.2) or 9 (f.2) branched rays. Pectoral 26.2–28.2 per cent of standard



length, 76.5–83.3 per cent of head. Pelvics with the first ray variably produced, markedly elongate in one fish. Caudal distinctly subtruncate, almost rounded; scaled on its basal third to half.

*Teeth.* Posteriorly in the upper jaw the *outer teeth* are large and unicuspid. Elsewhere in this jaw, and throughout the lower jaw, the teeth are unequally bicuspid and moderately stout, or are an admixture of such teeth with slender unicuspid. Bicuspid teeth have the major cusps equilateral in outline and barely incurved; some teeth have faint indications of a flange on one aspect of the cusp (see p. 151).

There are 40–44 teeth in the outer premaxillary row.

*Inner teeth* in both jaws are small and tricuspid, are arranged in 2 or 3 rows in the upper jaw, and in 1 or 2 rows in the lower.

*OSTEOLOGY.* The *syncranium* of *H. nubilus* is typically that of a generalized *Haplochromis* species.

The *lower pharyngeal bone* is relatively slender, its teeth compressed and bicuspid, with those of the median rows slightly coarser (especially posteriorly). There are *ca* 24–28 rows of teeth arranged on a dentigerous area that is *ca* 1.2–1.3 times broader than long.

*Vertebral count* is 29 (comprising 13 abdominal and 16 caudal centra) in the 4 fishes radiographed.

*COLORATION IN LIFE.* *Adult males* have a highly characteristic velvety-black coloration that is virtually uniform over the whole body. The dorsal fin also is black except for a narrow scarlet margin along its entire length, and some scarlet spots and streaks on the soft part. A scarlet flush covers most of the anal fin, although the spinous part may be a little dusky; the ocelli are yolk-yellow. Proximally the caudal fin is black, and this dark colour may extend along the centre of the fin almost to its margin. The margin is bright scarlet, the colour expanding at the posteroventral margin of the fin. The pelvics are jet black.

The live colours of *females* from Lake George are unknown; in Lake Victoria the body is deep olive-green and all the fins are greyish-green.

*Preserved males* are either uniformly black on the body or the dorsum (above the midlateral line) may be lighter (i.e. a deep brown) and crossed by 4 or 5 rather faint vertical bars. The dorsal fin is black except for a pale (yellowish-orange) margin. Almost the entire anal is pale yellow, although there is a faint and narrow dark band basally. The caudal is dark proximally and between the middle rays, but otherwise it is yellowish. The pelvics are black.

*ECOLOGY.* Little can be said about *H. nubilus* in Lake George. The specimens I examined came from a shallow inshore area close to emergent vegetation. A similar habitat seems to be the preferred one for *H. nubilus* in Lakes Victoria and Nabugabo (Greenwood 1965b).

No data are available on the feeding and breeding habits of the species in Lake George. Lake Victoria populations are female mouth brooders, and have a rather omnivorous diet in which laral insects and small Crustacea predominate.



*Distribution.* Lakes Victoria, Kyoga, Nabugabo, Edward and George, and in many rivers and streams connected with these lakes. To date no specimens have been caught in the Kazinga Channel.

**DIAGNOSIS.** Morphologically, *H. nubilus* closely resembles *H. aeneocolor* (see p. 154) in nearly all characters, especially morphometric ones. Pseudorakers are present in *H. nubilus* but not in *H. aeneocolor*, and the caudal fin is virtually rounded in *H. nubilus* (but truncate in *H. aeneocolor*).

There are some dental differences between the species but these are not particularly trenchant. However, in *H. nubilus* flange development on the major cusp is certainly less common than in *H. aeneocolor*, and the flange, when developed, is less prominent. Also, judging from Lake Victoria *H. nubilus*, it seems probable that unicuspid outer teeth occur more frequently in this species than in *H. aeneocolor*.

In life, male breeding coloration is certainly diagnostic.

### ***ASTATOREOCHROMIS* Pellegrin, 1903**

This genus is readily distinguished from *Haplochromis* by the higher number of anal fin spines: 4 or more, usually 5.

For a full diagnosis of the genus see Greenwood 1959a and 1965a, b.

### ***Astatoreochromis alluaudi* Pellegrin, 1903**

(Text-fig. 39)

*Astatoreochromis alluaudi*: Trewavas, 1933, *J. Linn. Soc. (Zool.)*, **38**: 321 (1 specimen from Lake George).

*Astatoreochromis alluaudi occidentalis* Greenwood, 1959, *Bull. Br. Mus. nat. Hist. (Zool.)*, **5**: 174-175.

Very few specimens of *A. alluaudi* have been collected from Lake George by the I.B.P. team, despite an intensive fishing effort. Four specimens (45-104 mm standard length) are available for study.

Because *A. alluaudi* is easily recognized by its having 4 or more anal spines and greatly enlarged pharyngeal bones, and because the Lake George fishes do not differ greatly from those described elsewhere (Greenwood 1959a) no full description is necessary.

The live colour of Lake George fishes (previously unknown) is identical with that described for the Lake Victoria populations (see Greenwood, *op. cit.*, p. 172).

The lower pharyngeal bone and dentition of *A. alluaudi* from Lakes Edward and George are much less massive than those from comparable-sized fishes in Lake Victoria. This led me to describe a subspecies, *A. a. occidentalis*, for these western lakes (Greenwood 1959a). Subsequent research, however, strongly suggests that the degree of pharyngeal bone development (and of tooth molarization) is probably under direct environmental control (Greenwood 1965a). In other words, the differences between Lake Victoria and Lake Edward-George fishes is not genetically determined. Thus it seems inadvisable to continue recognizing two subspecies.

Lower pharyngeal bones and teeth in the 4 Lake George fishes fit broadly into the reductional pattern described for fishes from lakes other than Victoria and Kyoga



(Greenwood 1959a). However, the Lake George fishes seem to have rather more massive bones (and greater molarization of the teeth) than do fishes from Lake Nakavali. In the two smallest Lake George specimens (45 and 46 mm standard length) the bone is only a little less developed than in a comparable-sized specimen from Lake Victoria, and there is equal molarization of the teeth (see fig. 3 top right, in Greenwood 1959a). The 80 mm standard length Lake George fish has a bone comparable with that of the 123 mm standard length Lake Nakavali specimen figured (*op. cit.*), but the 104 mm standard length fish has a relatively less massive bone which is comparable with the same specimen from Lake Nakavali.

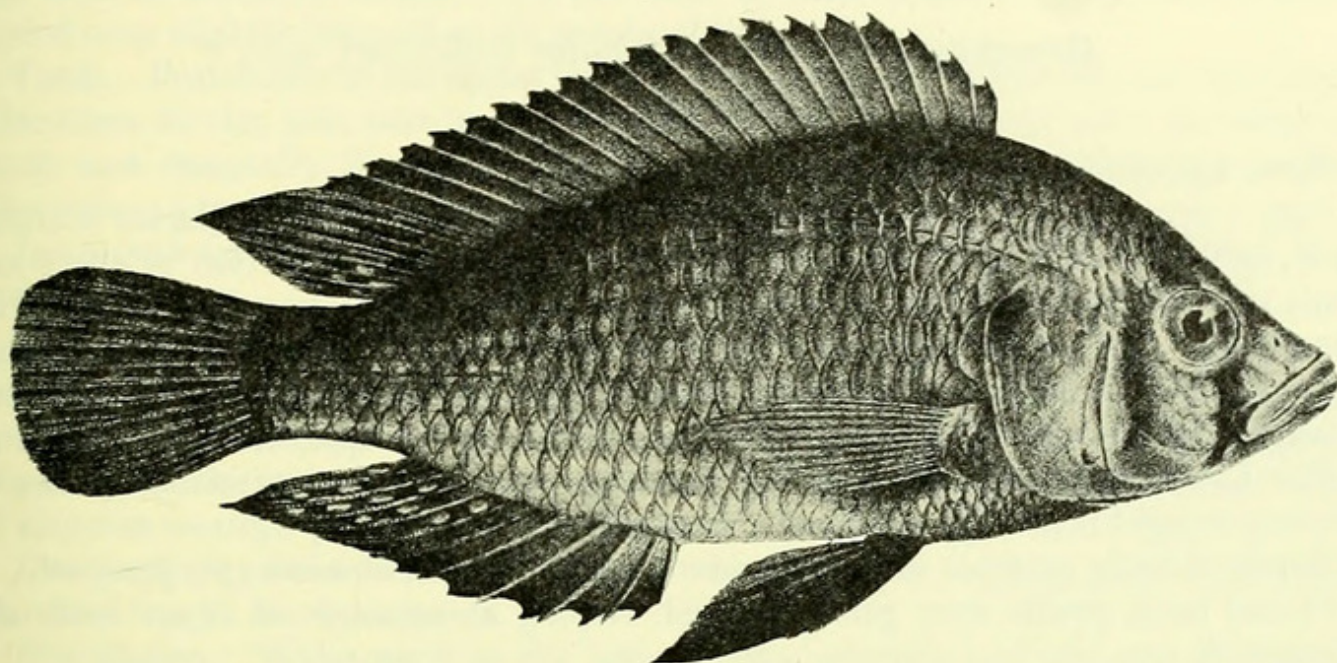


FIG. 39. *Astatoreochromis alluaudi*. A Lake Victoria specimen. From Boulenger, *Fishes of the Nile*.

The ratio of head length to pharyngeal bone width (measured from tip to tip of the upper arms) is in the range 2.9–3.0 (see Greenwood, *op. cit.*).

*Vertebral counts* for the 4 specimens are 13 + 16 (f.2), 13 + 15 (f.1) and 14 + 15 (f.1).

**ECOLOGY.** Little more can be added to our knowledge of this species in Lake George. The 4 specimens came from different areas of the lake, but a common feature for each locality is its proximity to the shore and the presence of rooted aquatic vegetation in the area.

Only fragments of gastropod shells were found in the intestines of the larger fishes (80 and 104 mm standard length); the 2 smaller individuals (45 and 46 mm standard length) yielded fragmentary remains of chironomid larvae.

### ***HEMIHAPLOCHROMIS* Wickler, 1963**

The primary generic distinction of this superficially *Haplochromis*-like taxon is its reproductive biology (see Wickler 1963).

The two morphological characters that separate it from *Haplochromis* (at least those species occurring in Uganda) are :



(i) The typical elongate and raised cover to the lateral line canal opening in each pore scale on the body is absent from many of these scales in *Hemihaplochromis*. Instead there is either a simple pore or seemingly no opening at all; scales in the posterior part of the upper lateral line series and those of the entire lower line are those most often missing a cover.

(ii) In males, instead of there being well-developed ocelli on the anal fin, there is a bright orange spot at the posteroventral angle (or tip) of the fin. This character is, of course, associated with the different reproductive behaviour of species in this genus (Wickler, *op. cit.*).

*Hemihaplochromis multicolor* (Schoeller), 1903

(Text-fig. 40)

For a full synonymy of this species, see Greenwood 1965b.

Only 1 specimen has been collected by the I.B.P. team. This apparent scarcity of *H. multicolor* in collections from the lake is probably a reflection of the small adult size attained and the habitats occupied, rather than a true indication of its abundance. Trewavas (1933) does not record *H. multicolor* from either Lake George or Lake Edward, and the only record from the Kazinga Channel is a few specimens I caught (by dip-netting amongst reeds) near Katungura (unpublished information).

The Lake George fish (BMNH reg. no. 1972.6.5 : 21) is 32 mm standard length and was caught near Busatu Island; its sex is indeterminable.

Depth of body 35.9 per cent of standard length, length of head 35.9 per cent.

Dorsal head profile very gently curved, sloping at an angle of *ca* 40° with the horizontal.

Preorbital depth 17.4 per cent of head, least interorbital width 30.3 per cent, snout length 0.8 of its breadth and 26.0 per cent of head; eye diameter 30.3 per cent of head, cheek depth 26.0 per cent.

Caudal peduncle as long as deep, 15.6 per cent of standard length.

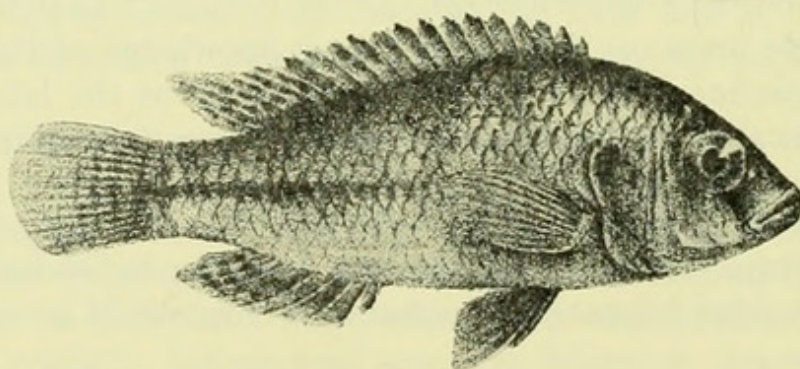


FIG. 40. *Hemihaplochromis multicolor*. A Lake Victoria specimen. From Boulenger, *Fishes of the Nile*.

Mouth slightly oblique, lips not thickened. Upper jaw 30.3 per cent of head, lower jaw 34.8 per cent. Posterior tip of the maxilla not quite reaching a vertical through the anterior orbital margin.



*Gill rakers* all short and stout, the lower 3 a little shorter than the others ; 7 rakers on the lower part of the first gill arch.

*Scales.* Ctenoid ; 29 in the lateral line series. Many of these scales (particularly in the lower series and posteriorly in the upper series) lack the longitudinal, arched cover to the pore opening, which is represented by a simple pit ; other scales are without any visible opening at all.

Cheek with 2 rows of scales ; 5 scales between the upper lateral line and the dorsal fin origin, 3 between the pectoral and pelvic fin bases.

*Fins.* Dorsal with 14 spines and 10 rays, anal with 3 and 9. Pectoral 23.4 per cent of standard length, 65.2 per cent of head length. Caudal fin rounded, scaled over slightly more than its proximal third.

*Teeth.* Posteriorly in the upper jaw, the *outer teeth* are very slender and unicuspid. Elsewhere in this jaw, and in the entire outer row of the lower jaw, the teeth are stout and unequally bicuspid. The major cusp is somewhat oblique in outline. There are 34 teeth in the upper jaw outer series.

*Inner teeth* are slender, slightly curved and unicuspid, and are arranged in a single row in each jaw.

*Vertebral count.* Thirteen abdominal and 16 caudal vertebrae.

**ECOLOGY.** Nothing is known about the bionomics of this species in Lake George. It seems probable (by analogy with its behaviour elsewhere) that in Lake George *H. multicolor* lives among submerged plants and in open-water areas within the margin of papyrus swamps (see Greenwood 1965b).

*Hemihaplochromis multicolor* is a female mouth brooder ; adults more than 55 mm standard length are uncommon.

*Distribution.* Widespread in the lakes, rivers, swamps and streams of Uganda, and probably in other regions of eastern Africa as well. The species also occurs in the Nile.

## DISCUSSION

### Biology of the Lake George *Haplochromis* species flock

Detailed biological studies of the fishes are being carried out by members of the International Biological Programme team. Some of their results will be available shortly and it is thus appropriate now merely to make some general observations.

Unlike the Lake Victoria *Haplochromis* species, those of Lake George are less closely associated with a particular habitat or substrate type. Nevertheless, any one kind of habitat, for example, offshore open water, the papyrus fringe, protected bays or an exposed sandy shore, has a definable assemblage of species in which a few are numerically dominant.

Open offshore waters have the fewest species, and of these only a few are found also in other habitats, and then never as the dominant elements.

Species with clearly restricted habitat preferences are : the mollusc-eating *H. mylodon*, the supposed larval and embryo cichlid-eating *H. taurinus* and the grazer on epiphytic and epilithic algae, *H. limax*. Species caught infrequently



(despite widespread sampling in many habitats) like *H. schubotzi*, *H. labiatus*, *H. nubilus*, *Hemihaplochromis multicolor* and *Astatoreochromis alluaudi*, may be presumed to have limited habitat preferences.

Only *Haplochromis petronius* can be said to have a truly restricted habitat since it is virtually confined to a rocky crater bay (the only one of its kind in the lake). Even in this example, however, there are exceptions since three specimens of *H. petronius* have been collected in the main lake (over sand and close inshore).

As with the *Haplochromis* species of Lake Victoria, the most readily observed adaptations seen in the Lake George fishes are those associated with feeding habits. Differences in tooth form and number, pharyngeal bone shape and dentition, and in jaw size and arrangement are the more obvious characters involved in this adaptive radiation. The overall impression gained is of a small-scale Victoria flock. In other words, one in which the major trophic adaptations are developed but to a slightly lower degree of specialization, and with fewer species occupying one trophic niche or showing the same level of specialization.

Lakes George and Edward harbour one trophic specialization not found among the *Haplochromis* of Lake Victoria, namely a species (*H. pappenheimi*) feeding, as an adult, almost exclusively on pelagic zooplankton. Possibly the absence of an *Engraulicypris* species from Lakes Edward and George has enabled a *Haplochromis* to fill this niche.

Two *Haplochromis* species in Lake Edward (*H. mylodon* and *H. pharyngalis*) have the enlarged pharyngeal bones and teeth associated with a diet of molluscs. Only *H. mylodon* occurs in Lake George, but, as in Lake Edward, another mollusc crushing cichlid, *Astatoreochromis alluaudi*, is present.

Specialized mollusc shellers (as opposed to crushers) have not evolved in the Edward-George flock. This specialization is well-represented in the *H. sauvagei*-*Macropyleurodus bicolor* series of Lake Victoria (Greenwood 1957, 1965c). Possibly snails are a less abundant food source in Lakes Edward and George than in Lake Victoria; qualitative sampling in all three lakes certainly suggests that this is so (personal observations).

Another sharp contrast between the flocks of Lake Victoria and George is the presence in Lake George of only one truly piscivorous species (*H. squamipinnis*). Among the inshore species of *Haplochromis* from Lake Victoria, about 30 per cent are piscivores. The situation in Lake Edward is different again because there are at least three piscivorous species among the known but yet undescribed species from that lake. However, the proportion of piscivores to non-piscivores in Edward is still much lower than in Victoria, probably about one in ten species.

A discrepancy is also noticed in the absolute number of larval and embryo fish-eating species. Only one paedophagus species, *H. taurinus*, is known from Lake George (and Edward) whereas at least seven species occur in Victoria. The relative proportion of paedophages to all other species (from all habitats and trophic groups) is, however, less disparate, being *ca* 6 per cent in Lake George and *ca* 4 per cent in Lake Victoria.

Although there is only one epiphytic and epilithic algal grazer in Lake George (*H. limax*) as compared with at least four such species in Lake Victoria (Greenwood



1956b), the total for Lakes Edward and George together is three, proportionately a much higher number than in Lake Victoria.

It is difficult to generalize about the insectivores and detritus feeders, except to say that in both flocks species belonging to these trophic groups are numerous (Greenwood 1965c).

At least one species in Lake Victoria (*H. erythrocephalus*) and one in Lakes Edward and George (*H. nigripinnis*) is a specialized feeder on suspended phytoplankton.

In Lake George there is a very rapid extinction of incident light so that over much of the lake the photic zone extends merely to a depth of about 60 cm. Most *Haplochromis* species live below this zone or at least spend a great deal of the day in very poorly lit waters. This raises several interesting questions regarding the fishes' adaptations and behavioural responses to such photic conditions. In particular there are problems associated with breeding behaviour; there would seem to be insufficient light for potential mates to recognize one another visually. Another difficulty associated with breeding is the nature of the substrate in Lake George. Over much of the lake the bottom is composed of soft, near liquid, organic ooze. This would appear to provide a most unsuitable substrate on which to spawn in the typical *Haplochromis* fashion. There are, of course, places in the lake where the bottom is hard and where there is reasonably good light penetration. But, no evidence has been collected to suggest that these areas are the only ones used as spawning sites. Brooding females have been found in all habitats, although this does not necessarily imply that the spawning site was near by. It does, however, indicate that for the species involved there are no definite 'nursery' zones.

Field conditions in Lake George virtually preclude direct observations on the fishes' spawning behaviour, and what information we may get in the future must therefore be indirect, i.e. from aquarium studies. A comparative study of the Lake George species with those from the deep, near-aphotic waters of Lake Victoria would be particularly valuable, especially since the latter species are also faced with a generally soft substrate.

Whether or not vision plays an important part in courtship and species recognition, the Lake George *Haplochromis* species, like those from other and clearer lakes, show distinctive and species-specific male coloration. The Lake George species do, however, differ in one respect. Many females have large, pigmented spots in the same position and of the same colour as the ocelli (or egg dummies, see Wickler 1962) in males. These pigment spots lack the clear border that, in males, makes the spot an ocellus. Unfortunately I do not know if female 'egg spots' are so well developed, or if they are present at all, in Lake Edward populations of the same species.

As a footnote to these remarks on coloration it may be noted that no Lake George (or, as so far recorded, no Lake Edward) *Haplochromis* species exhibits a colour polymorphism like that found in several Lake Victoria species. In these fishes a certain percentage of females has an outstanding coloration in the form of piebald black on silver or black on yellow, or a peppered black, red and orange on a yellowish background. Sex-limited polychromatism is now recorded in at least eight species from Lake Victoria, but none has been found in any Lake George species from among the thousands of *Haplochromis* specimens examined by the I.B.P. team.



This absence of polychromatism in the Edward-George flock is rather surprising, not only in view of the flock's obvious relationship to that of Victoria, but because polychromatism is found in species of *Haplochromis* from Lake Kivu (see Poll 1939b). (The Kivu *Haplochromis* are related to those of Lake George in probably much the same way as are those of Lake Victoria.) No explanation is immediately apparent.

Species living in such poorly lit waters as those of Lake George might be expected to show certain compensatory hyperdevelopment of various sensory organs, especially the eyes and acustico-lateralis systems. Only the gross morphology of these organs has been investigated so far, and the conclusions reached are equivocal. The cephalic lateral line canals and their openings are not noticeably enlarged. In general, the eye (as measured by its diameter relative to head length) of Lake George species does not seem to be greatly enlarged. A comparison was made between the mean eye diameter in Lake George *Haplochromis* and their ecological counterpart species from Lake Victoria (the comparisons confined to individuals of the same size, and from species with the same maximum adult size). In the Lake Victoria species examined, the range of mean eye diameter is from 27.0–31.0 per cent of head length, whereas in the Lake George species it is from 28.0–38.0 per cent (the modal range being 31–35 per cent). *Haplochromis squamipinnis* is excluded from these figures because individuals attain a larger adult size, and eye diameter proportions generally show a strong negative allometry with body length. When a comparison is made between *H. squamipinnis* and similar-sized individuals of Lake Victoria piscivores, no noticeable difference was noted in eye size (mean eye diameter for *H. squamipinnis* 23.0 per cent of head, cf. 20.0–26.0 per cent for the Victoria species).

These comparisons were extended to include species from the deeper waters of Lake Victoria (see Greenwood & Gee 1969), where light values are probably similar to those found below the upper 30 cm of water in Lake George. The deep-water Victoria fishes have a range of eye diameter between 25.0 and 36.0 per cent of head length, with a modal value at about 31.0 per cent. This compares with values of 27.0–38.0 per cent (modal range 31.0–35.0 per cent) for the Lake George species, a suggestive similarity.

A comparison of the cephalic lateral line canals in these two species-groups was most inconclusive, mainly because of the difficulty in quantifying the characters involved.

#### The relationships and history of the Lake George *Haplochromis* species

From both zoogeographical and historical standpoints, the fishes of Lake George should be considered in conjunction with those of Lake Edward. The two lakes are now interconnected by the Kazinga Channel, they share many otherwise endemic cichlid species, and there is no evidence to suggest that Lake George has ever been in direct connection with any other major water body.

Regrettably, it was neither possible to effect a full revision of the Lake Edward *Haplochromis* species, nor was it feasible to collect in parts of the lake never previously sampled. There is no doubt that many species remain to be discovered in the deeper (i.e. western) parts of the lake (as, for example, was the case in the deep waters



of Lake Victoria). The few recent collections made in Lake Edward (by Dr Dunn of the I.B.P. team), coupled with a brief re-examination of existing collections, show that there are definitely several undescribed species from inshore habitats.

Despite the drawback of having to exclude Lake Edward in detail, the material examined, together with that from Lake George enables one to reconsider currently held views on the origin of the Lake Edward-George *Haplochromis* species flock. Such reflection is very necessary, both in view of the more detailed geological and palaeontological knowledge now available (Greenwood 1959c; Doornkamp & Temple 1966; Bishop 1969) and because of the rather different conclusions I have reached on the interrelationships of the Lake George and Lake Victoria *Haplochromis* species (themselves extensively revised since Trewavas' [1933] pioneer work on the Edward-George species).

That the *Haplochromis* species flocks of Lakes Victoria and Edward-George have a close phyletic as well as a phenetic relationship is beyond doubt. What has still to be determined is whether the Edward-George flock was derived directly from part of the Victoria species assemblage, or whether the two flocks evolved independently, but in parallel, from common ancestral species.

Trewavas (1933) believed that Lake Edward '...received its Cichlidae, or their not very remote ancestors, from Lake Victoria,...'. This concept has been basic to thinking on the subject ever since (Brooks 1951; Greenwood 1959c; Temple 1969). Trewavas' views were influenced mainly by the overall similarity of the *Haplochromis* species in the two lakes, and by the fact that three otherwise endemic Victoria species were thought to be present in both lakes (*see below*). At the time of Trewavas' paper there was little geological evidence available to suggest either the nature or the duration of the route through which the faunal exchange might have taken place. The Rivers Katonga and Ruizi (now with a drainage via swamp divides into both the Victoria and Edward-George basins) suggested a possible passage way, particularly if, in earlier times, the swampy areas were readily passable. Later, Wayland's (1934) geological and palaeoclimatic hypotheses seemed to support the idea of an aquatic connection between the lake basins (Greenwood 1951, 1959c).

The ichthyological evidence once used in support of a Victoria-Edward (and George) interconnection will be reviewed first.

On Trewavas' reckoning there were six cichlid species shared between the lakes, viz. *Hemihaplochromis multicolor*, *Astatoreochromis alluaudi*, *Haplochromis nubilus*, *H. guiarti*, *H. macrops* and *H. ishmaeli*. Furthermore, every endemic *Haplochromis* species from Lake Edward-George was, in her opinion, closely related to a species from Lake Victoria (the endemic Edwardian monotypic genus *Schubotzia eduardianus* providing the only clear-cut exception [*but see above* p. 215]).

As noted earlier, the idea of a close overall relationship between the Victoria and Edward-George *Haplochromis* is still valid (and in many instances is reinforced by new information). I would find it difficult, however, to establish a direct phyletic relationship of an ancestor-descendant kind between each Edward-George species and its Victoria counterpart (the supposed *H. guiarti* of Lake Edward and *H. mylodon* excepted).



It is my opinion that *H. ishmaeli*, *H. guiarti* and *H. macrops* are not present in Lake Edward or Lake George. The fishes once identified as *H. ishmaeli* are now placed in a new taxon (*H. mylodon*, see p. 172) and the specimens thought to be *H. macrops* do not conform with the revised definition of that species (Greenwood 1960), nor are they conspecific with any other endemic Victoria species (see below). The status of the supposed *H. guiarti* from Lake Edward is difficult to determine without a full revision of the Lake Edward *Haplochromis*; no similar species occurs in Lake George. For the moment I can only say that *H. guiarti* might be the sole example of an otherwise endemic Victoria species occurring in Lake Edward. The importance of determining the identity of Edward '*H. guiarti*' needs no further emphasis.

Two specimens identified by Boulenger (1914) as *H. macrops* were kindly lent to me by the Berlin Museum. A detailed morphometric and morphological study shows that both specimens differ from *H. macrops* (see Greenwood 1960) in dental and certain proportional characters. One specimen (a female 70 mm standard length) can be identified as a specimen of *H. nigripinnis*. The other (64 mm standard length, probably a female) is of *H. macropsoides* (see above p. 162). A third specimen (in the British Museum [Natural History], reg. no. 1933.2.23 : 397), identified by Trewavas (1933), has outer jaw teeth with markedly oblique major cusps, quite unlike the acute cusps of *H. macrops* (see Greenwood, *op. cit.*). This specimen also differs from *H. macrops* in several morphometric characters. In all these divergent characteristics, and especially in its dentition, the B.M. (N.H.) fish agrees closely with the type (and some paratypes) of *H. vicarius* Trewavas, a Lake Edward endemic (see Appendix I, p. 238, for a discussion on the status of this species).

Thus, all three Lake Edward fishes formerly identified as *H. macrops* are now referred to endemic Edward-George species.

The identity of Edward-George specimens previously identified as *H. ishmaeli* is discussed on p. 176. All the specimens are now included in a new and endemic species from Lakes Edward and George, *H. mylodon*. Anatomically, *H. mylodon* is very like *H. ishmaeli* and *H. pharyngomylus* of Lake Victoria. The main interspecific difference lies in the coloration of the adult males. In this respect, *H. mylodon* bears the same relationship to its Victoria counterparts as do certain endemic *Haplochromis* species of Lake Nabugabo to their counterparts in Lake Victoria (see Greenwood 1965b). It could, therefore, be argued that *H. mylodon* represents an instance of direct speciation from an *H. ishmaeli* or *H. pharyngomylus*-like ancestor that invaded the Edward basin at some time past.

Material collected by Worthington from Lake Edward and subsequently identified by Trewavas as *H. guiarti* is polyspecific. In fact, only a small part of it can be confused with *H. guiarti* as currently defined (see Greenwood 1962). Of the remaining specimens, one resembles *H. squamulatus* of Lake Victoria, and the others show characters of the *H. victorianus*-*H. serranus* species complex in that lake. It must be stressed that none of these specimens is referable to its Lake Victoria counterpart. Preliminary work suggests that in Lake Edward there are, in addition to an *H. guiarti*-like species, two other piscivorous species endemic to Lake Edward.



On the basis of preserved material alone, it is difficult to separate the *H. guiarti*-like specimens from the true *H. guiarti*. When specimens are placed side by side, the Lake Edward fishes are distinguishable on the basis of their total morphology, especially head shape. The situation here is quite comparable with that existing between *H. mylodon* and *H. ishmaeli* (or *H. pharyngomylus*) but without the benefit of information on live male coloration.

Turning for the moment to the cichlid species which are definitely shared by the lakes. *Hemihaplochromis multicolor* has such a wide distribution in eastern Africa (including the Nile) that it is irrelevant to this discussion. Its absence from Lakes Edward and George would be of greater significance than its presence.

*Haplochromis nubilus* has a somewhat more restricted range and can definitely be categorized as a species of the Victoria drainage basin. *Astatoreochromis alluaudi* can also be categorized in this way. Both species, unlike other Victorian *Haplochromis* and related genera, are common in streams and rivers entering the lake, and both penetrate for some distance into papyrus swamps.

Taken in its entirety, the ichthyological evidence does not really seem to provide a strong argument in favour of a strictly Victorian derivation for the Edward-George cichlid species. In particular it does not support the idea of derivation from a developed, or partly developed *Haplochromis* species flock, an idea that I had previously espoused (Greenwood 1959c; also Temple 1969).

The degree of anatomical differentiation between most known Edward-George species and their morphological counterparts in Lake Victoria is sufficiently well marked to suggest that one is observing the results of parallel evolution and not direct speciation in Edward-George from an already specialized invader species. Since both *Astatoreochromis alluaudi* and *Haplochromis nubilus* are relatively eurytopic, their presence in both lake basins could mean that they were components of the cichlid complex inhabiting the area prior to lake formation. Possibly, but less likely on ecological grounds, the two species could have gained access to Lake Edward-George via the Katonga-Mpanga River system.

The distribution of the extant non-cichlid fishes in the area contributes little of value to this discussion (see Greenwood 1959c). Only the occurrence of *Barbus altianalis* in both Victoria and Edward-George argues strongly for some past connection between the basins (as it does for a connection with Lake Kivu; see below). Otherwise, the non-cichlid fishes of these lakes have little in common; the number of endemic Victoria fishes contrasts with the depauperate but clearly Nilo-Albertine nature of the Edward-George non-cichlid species assemblage (Greenwood, *op. cit.*).

At this point brief mention should be made of Lake Kivu and its small *Haplochromis* flock. Historically, Lake Kivu was derived from a river that once flowed northwards into what is now the Edward-George basin. This river was dammed by the formation of the Bufumbiro volcanic chain, probably during the late Pleistocene. As the embryo Kivu gradually filled, it found a new outlet, now the Ruzizi, which drained into Lake Tanganyika. Rapids in the Ruzizi seem to block the passage of fishes (at least northwards) between Lake Kivu and Lake Tanganyika, although



certain non-cichlids (e.g. *Barilius moorii* and *Barbus pellegrini*) are found in both lakes, perhaps as relicts of an earlier, unimpeded river connection.

The *Haplochromis* of Lake Kivu definitely show no relationships with those of Lake Tanganyika, but are distinctly of the Victoria-Edward type. There has been no recent revision of the Kivu *Haplochromis* species, and data on their live coloration are unavailable; furthermore, an examination of the type series of two species (personal observations) strongly hints of more species than are currently recognized (Poll 1939a, b).

Comparing the Edward-George *Haplochromis* with the Kivu species, on a purely morphological basis, suggests that the Kivu fishes are quite distinct, although showing affinity with Lake Edward-George species (or, in one case, a Lake Victoria species).

Of the Kivu species I have studied in detail, *H. astatodon* Regan resembles *H. serridens* of Lake Edward, *H. graueri* Blgr. (at least, that is, one of the types) resembles fairly closely *H. schubotzi*, and *H. paucidens* Regan has the general orodental specializations of *H. labiatus* but in many features is more like members of the *H. crassilabris* species complex in Lake Victoria (see Greenwood 1965b). *Haplochromis vittatus* (Blgr.), too, shows most phenetic affinity with a Victoria species group (especially *H. gowersi*, a member of the 'prognathus' group in that lake; see Greenwood 1967); it does not closely resemble *H. squamipinnis* of Lakes Edward and George.

The remaining Kivu *Haplochromis* species (and those still undescribed) I feel less able to comment upon. *Haplochromis wittei* Poll and *H. schoutedeni* Poll could be related to either *H. elegans* or *H. aeneocolor* of Lake Edward-George, especially the former species, while *Haplochromis adolphifrederici* (Blgr.), if it is distinct from *H. graueri*, has superficial resemblances to *H. schubotzi* and *H. schubotziellus* of Edward and George.

As noted earlier (p. 230) sex-limited female polychromatism occurs in at least two Kivu species (*H. wittei* and *H. adolphifrederici*) but has not been recorded from any of the Edward-George species.

A detailed revisionary study of Lake Kivu *Haplochromis* species may throw more light on their phylogeny. This would be of great interest because the ancestors of these fishes could have been derived from the proto-George-Edward flock (before the Bufumbiro dam was formed) or could have evolved after that time, from ancestors living in the river before it was dammed. Since this river originated in the Ruanda Highlands it might well have been populated by different species from those in the westward flowing rivers of the Kenya Highlands which populated the embryo Lakes Victoria and Edward-George.

Modern geological studies on the Pleistocene sequence in Uganda also seem to support the idea of parallel evolution in the cichlid species flocks of the Victoria and Edward basins. (See summaries in Doornkamp & Temple 1966; Bishop 1969). Older ideas and temporal sequences based on Wayland's pluvial hypothesis (1934) are no longer tenable.

The formation of Lake Victoria is currently dated at about the later mid-Pleistocene, and is thought to be consequent upon the reversal and ponding-back of rivers



that flowed across its present basin into the western Rift lake system (i.e. into a proto-Lake Edward-George and Albert). For a summary of the evidence, see particularly Doornkamp & Temple (1966).

River reversal was initiated by local uplift along a line nearer the western Rift than the developing Victoria basin. As a result of this uplift the formerly westward-flowing rivers drained both to the east and to the west, an anomalous situation still persisting. Extensive swamps developed over the watershed, and today these provide an effective barrier to fish dispersal along the rivers.

If one accepts the geological evidence, then one must conclude that a lake existed in the western Rift some time before Lake Victoria started to develop as a series of small lakes in the eastern sections of the reversed rivers. There is good palaeontological evidence for the existence of the western Rift lake or lakes from at least Kaiso Formation times (earlier Pleistocene) onwards (Greenwood 1959c). Essentially, this fossil record is one of non-cichlid fishes so it throws little direct light on the question of *Haplochromis* relationships.

Judging from the reconstructed topography of western Uganda in the earlier Pleistocene (Doornkamp & Temple, *op. cit.*) there was a steep escarpment bordering the eastern shoreline of proto-Lake Edward-George. It seems unlikely, therefore, that *Haplochromis* species could enter this western lake after the formation of Victoria. Furthermore, if the species that evolved in the developing Lake Victoria were as stenotopic (i.e. lacustrine) as are their present derivatives, it is highly improbable that they would spread along the inter-lake rivers (even assuming that such a passage was physically possible).

Thus the conclusion seems inevitable that, for all of their histories as lakes, Victoria and Edward-George have been effectively isolated from each other, and that Lake Edward-George is older than Lake Victoria. Since both basins were filled from the same river systems (the old east-west drainage) it is reasonable to assume that their initial fish colonizers were the same. In other words, their present-day *Haplochromis* species flocks were derived from common ancestral species, presumably of the generalized type now represented by *H. bloyeti* (see Greenwood 1971).

One Lake George species, *H. petronius* (see p. 209), does not fit this picture of a close phyletic relationship between the flocks of Lakes Victoria and Edward-George. Nor does it seem to be related to the *H. bloyeti* stock. As discussed in greater detail above (p. 213), *H. petronius* shows marked affinities with *H. wingatii*, a species known from the Nile and Lake Albert (Greenwood 1971). The characters relating these two species (and also *H. pharyngalis* of Lake Edward; see p. 214) are not present in any Lake Victoria *Haplochromis* species. It is unlikely, too, that these characters are products of convergent evolution.

To me, the implication is that *H. petronius* was derived from a different lineage than that of the other species. It cannot, of course, be told if that lineage occurred in the Victoria basin but failed to survive there. Certainly there is no indication of *H. wingatii*-like species in any of the streams and rivers flowing into Lake Victoria today.

That related species appear to have persisted in Lake Albert and the Nile, and also in Lake George, suggests that the ancestor of *H. petronius* entered that lake from a source other than the old westward draining rivers. The nearest living relative



of *H. wingatii* is probably *H. desfontainesi*, a species now restricted to North Africa (see Greenwood 1971). Perhaps the ancestor of *H. petronius* (and *H. pharyngalis*) was a northern rather than an east-west river species, that gained access to Lake Edward-George from the Nile before the lake was isolated from that river by the Semliki rapids (see Greenwood 1959c).

The distribution of *Haplochromis nubilus* and *Astatoreochromis alluaudi* in Lakes Victoria and Edward-George, as well as in the small lakes lying between these basins (Trewavas 1933) suggests that the species are remnants of the original species complex inhabiting the old east-west river systems. Trewavas (*op. cit.*) interpreted the presence of *H. nubilus* and *A. alluaudi* in Lakes Nakavali, Kachira and Kijanebalola as possible evidence of the route through which the postulated Victoria to Edward faunal exchange took place. It now seems more likely that the species are fluviatile relicts in those lakes. The absence of other and more typically Lake Victoria or Lake Edward species from these small lakes puzzled Trewavas (*op. cit.*, p. 311). Probably the explanation is simply that these species or their immediate ancestors were never in that area.

Elsewhere I have argued (Greenwood 1965c) that the *Haplochromis* species flock in Lake Victoria represents the amalgamation of several smaller flocks, each evolved in isolation from a common ancestor or, later in the lake's history, a few common ancestral species. The isolation I envisaged was essentially one of small lakes lying within the area of what is now the basin of a single large lake. The present fauna of Lake Edward-George could be looked upon as another of these isolates but one which, because its basin retained its physical identity, has been given the status of a separate species flock. Phyletically speaking it is perhaps wrong to do so. Rather, one should refer to it as the Edward-George subflock.

As matters stand, there is insufficient knowledge of the physical and ecological factors involved in the processes of speciation and adaptive radiation within the Edward-George subflock. Lake George has now been sufficiently well sampled for one to be almost certain that some species occurring in Lake Edward are absent from Lake George. Likewise it is clear that there are many more species in Lake Edward than are currently recorded. (Personal observations on recent collections from Lake Edward.) Collections from the Kazinga Channel show that its cichlid fauna is virtually identical with that of Lake George. That is, the Edward species not recorded from George are also absent from the Channel (see Appendix II). It seems, therefore, that the channel is at least partially a differential species filter between the lakes. The factors inhibiting occupation by certain species (and these do include some from Lake George) have not been discovered. This question is yet another whose solution will depend upon learning more about the ecology of the fishes, especially those from Lake Edward.

The unusually complete fossil record for the fishes of Lake Edward shows that throughout the Pleistocene, and well into the Holocene, the non-cichlid fishes were more diverse than at present (Greenwood 1959c). The genera *Lates* and *Synodontis*, now absent, were present until local Mesolithic times, and another present-day absentee, *Polypterus*, persisted into the early Holocene (de Heinzelin's level N.F.P.R. at Ishango is now dated at ca 8000-10 000 years B.P.).



Depauperization of this Nilo-Albertine fauna was sudden and of a relatively recent date (*see* Greenwood, *op. cit.*, p. 73). Localized vulcanicity polluting the water (especially of inflowing streams) may have been a major factor in this process. The differential adaptability of species to these altered conditions could account for the fact that some survived while others were wiped out.

If the arguments presented above on the origin of the Lake Edward-George cichlids are sound, then these fishes must have survived the environmental hiatus that exterminated several non-cichlid species. There is no evidence that the cichlids or their ancestors reinvaded the lake after the volcanic period, although the time elapsed could have been sufficient for the flock to evolve (*see* Greenwood 1965b).

Assuming that the Edward-George *Haplochromis* evolved from mid-Pleistocene fluvial colonizers implies that speciation and adaptive radiation took place in the presence of such predators as *Lates* and *Hydrocynus*. Worthington's ideas on the inhibitory effects of *Lates* and *Hydrocynus* on these processes are well known and well argued over (*see* Fryer & Iles, 1972, for a comprehensive summary of various viewpoints in this discussion). The history of the Lake Edward-George *Haplochromis* species flock now seems to provide an even stronger counter-argument to the Worthington hypothesis than the one presented in my 1959c paper. There, I had assumed that the flock was derived from an at least partly differentiated one (at the species and adaptational levels) invading from Lake Victoria.

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#### APPENDIX I

##### The status of *Haplochromis vicarius* Trewavas, 1933

Poll (1939), synonymized *H. vicarius* with *H. eduardii* Regan, 1921 on the grounds that the large collection of specimens available to him bridged the morphological gap distinguishing the species. However, Poll seems only to have considered as specifically trenchant the posterior extent of the maxilla, and does not mention the dental characteristics of either taxon. My experience with various *Haplochromis* leads me to place little importance on the maxillary character, but considerable value on the form of the teeth.

The question raised by Poll's proposed synonymy is complicated by the fact that the type series for *H. vicarius* is very probably polyspecific. One specimen is labelled 'Holotype' although no holotype was formally designated (Trewavas 1933). This fish and at least two paratypes have a distinctive cusp shape to the outer teeth of both jaws (see p. 171), a cusp type that does not occur in the teeth of *H. eduardii* holotype. Furthermore, I can find no reasons to believe that the tooth shape in *H. vicarius* holotype represents an extreme variant of the *H. eduardii* tooth-type (or vice versa).

Thus, I would suggest that *H. vicarius* is specifically distinct from *H. eduardii*. When the Lake Edward *Haplochromis* species are fully revised I suspect that other characters will be found to support this separation.

#### APPENDIX II

##### Kazinga Channel fishes

During May and June, 1972, collections were made at several places in the Kazinga Channel, particularly in the neighbourhood of Katungura (approximately the midpoint of the channel). Other regions sampled were near the Lake George end of the channel and at Mweya, near the opening into Lake Edward. Small-mesh gill nets and a purse seine were used, and sites near the shoreline and in midchannel were sampled.

A list of the species collected in the area around Katungura, with notes on the region of the channel in which they most frequently occur, and a subjective evaluation of their abundance, is given below.

*Haplochromis elegans*: common inshore, especially near reed beds; also caught offshore, but is less abundant there.



*H. aeneocolor* : inshore near reeds ; not very abundant.

*H. nigripinnis* : only in midchannel ; rare.

*H. oregosoma* : inshore ; rare.

*H. macropsoides* : inshore and midchannel ; rare.

*H. mylodon* : inshore ; very rare.

*H. angustifrons* : mostly from midchannel where it is fairly abundant ; occurs inshore but is rare.

*H. schubotzi* : inshore ; rare.

*H. schubotziellus* : rare in midchannel, even rarer inshore.

*H. taurinus* : midchannel only and then infrequently.

*H. pappenheimi* : abundant everywhere, particularly inshore. Unlike catches of this species in Lake George, those from the channel contained large (110–130 mm standard length) and sexually active individuals of both sexes.

*H. squamipinnis* : ubiquitous, but in small numbers.

*H. eduardianus* : infrequently caught, and then only by dip-netting among the reeds.

Collections made near the Mweya landing were hampered by technical difficulties ; only gill nets, set inshore and in midchannel, were used and then on but one occasion. These yielded specimens of *H. elegans*, *H. aeneocolor*, *H. angustifrons*, *H. taurinus*, *H. pappenheimi* and *H. squamipinnis*, all in small numbers.

Because of inadequacies in the sampling methods used at Mweya landing, and since only one collection was made there, this list must be incomplete.

It is surprising that the well-sampled Katungura area did not produce any specimens of *Haplochromis limax*, *H. nubilus* or *Astatoreochromis alluaudi*. All three species were found in similar habitats in Lake George. There is, of course, a noticeable water flow in the channel, but this alone could hardly be the cause of these particular species' absence. More probably, their 'absence' is a reflection of the sampling methods used (and the time available for sampling).

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A GUIDE TO THE IDENTIFICATION OF THE *HAPLOCHROMIS* SPECIES  
FROM LAKE GEORGE

A simple dichotomous key cannot be compiled for these fishes. Intraspecific variability is high and few species can be diagnosed on the basis of single characters. Thus, this 'key' should be used as a general guide rather than as a means of identifying a taxon without recourse to other discriminating characters included in the full species descriptions. It is based on adult and subadult specimens.

*Haplochromis labiatus* is not included here because only one Lake George specimen is known. A specimen of *H. labiatus* would probably key out to *H. elegans*, but its dental characters (see p. 198) should prove diagnostic.

Morphometric characters are defined on p. 145. Unless otherwise specified, 'teeth' refers to the outer row of teeth in both jaws.

The Lake George species<sup>1</sup>

- Teeth spatulate, the upper half of each tooth strongly incurved (see text-fig. 37); lower jaw shorter than the upper . . . . . ***H. eduardianus***
- Teeth bicuspid or unicuspid and caniniform, sometimes a mixture of both, and occasionally with some tricuspid intercalated; lower jaw not shorter than upper . . . . . ***A***
- A*** Scales on the chest very small and deeply embedded (difficult to detect), especially when compared with those on the belly; a small scaleless area immediately anterior to the first dorsal spine . . . . . ***H. petronius***
- Scales on chest not deeply embedded, not disproportionately smaller than those on the belly, and readily visible; no naked area at base of the first dorsal spine . . . . . ***B***
- B*** A vertical row of small scales extending onto the fin membrane along the basal part of many (if not all) dorsal and anal fin rays and spines. Lower jaw long (42–57, mode ca 50 per cent of head length, showing positive allometry) and oblique; teeth usually unicuspid. Adults reach a large size (> 150 mm) . . . . . ***H. squamipinnis***
- No small scales extending onto the dorsal and anal fins. Adults rarely more than 115 mm long, modally ca 80 mm . . . . . ***C***
- C*** Lower pharyngeal bone massive (see text-fig. 16), most of its teeth strong and molariform . . . . . ***H. mylodon***
- Lower pharyngeal bone not massive, if molariform pharyngeal teeth present, few in number, small, confined to middle row . . . . . ***D***
- D*** Teeth few in number (32–48, mean 36 in upper jaw), stout, deeply embedded in jaw tissue (difficult to see) and, although bicuspid, of characteristic shape (see text-fig. 25); gape of mouth manifestly large, lower jaw 43–56, mean 47 per cent of head; dorsal profile of head concave. Adults reach a standard length of 140 mm . . . . . ***H. taurinus***
- Teeth otherwise than above; mean lower jaw length less than 45 per cent of head usually less than 40 per cent . . . . . ***E***
- E*** Depth of body less than 35 per cent of standard length (mean = 31 per cent); modal number of gill rakers 10 or 11 (but as many as 13), the rakers slender . . . . . ***F***
- Depth of body usually more than 35 per cent of standard length; modal number of gill rakers less than 10 (usually 8 or 9) . . . . . ***G***
- F*** At least the posterior third of the premaxilla without teeth; teeth small, flat and of a characteristic shape (see text-fig. 30), 28–38 (mean = 32) in upper jaw. Body colour uniformly silver in both sexes. Body fusiform, its depth 27–31 (mean = 30) per cent of standard length . . . . . ***H. pappenheimi***

<sup>1</sup> The two other *Haplochromis*-group species are identified as follows:

More than 3 (usually 4 or 5) anal spines: *Astatoreochromis alluaudi*.

Many scales of the lateral line series without pores: *Hemihaplochromis multicolor*.



- Entire length of premaxilla toothed; teeth relatively slender (*see* text-fig. 9), 42–60 (mean = 50) in upper jaw. Males dark, females greyish-silver. Body depth 30–34 (mean = 32) per cent of standard length . . . . . *H. oregosoma*
- G Teeth in outer row of both jaws with an obliquely truncate cusp (*see* text-fig. 14), long and movably implanted; 4 or 5 (rarely 3) rows of inner teeth in the upper jaw . . . . . *H. limax*
- Teeth otherwise than above, and only 2 or 3 inner rows (often only 1 row) . . . . . H
- H Usually less than 40 teeth in the upper jaw (34–42, mean = 38); teeth bicuspid, most without a well-developed flange on the major cusp (*see* text-fig. 3, and *cf.* text-fig. 5). Upper jaw 28–34 (mean = 30) per cent of head (i.e. equal to or less than the eye diameter) . . . . . *H. elegans*
- More than 40 teeth in the upper jaw (40–60, mean = 50) . . . . . I
- I Distinct and prominent midlateral dark band running from behind operculum onto the caudal fin; snout length 31–40 (mean = 33) per cent of head . . . . . *H. schubotziellus*
- No distinct midlateral band (or, if a series of short midlateral streaks present, the last not extending onto caudal fin); snout length usually less than 30 per cent of head length . . . . . J
- J When fish is viewed laterally, the upper margin of the orbit is seen to be continuous with the dorsal profile, or the eye appears to extend above this line . . . . . K
- The upper margin of the orbit lies below the dorsal profile of the head . . . . . L
- K Dorsal head profile sloping smoothly (not obviously interrupted by prominent premaxillary pedicels). Preorbital depth 12–15 (mean = 14) per cent of head. Outline of toothed area on lower pharyngeal bone broader than long (*see* text-fig. 12). Caudal fin not distinctly maculate . . . . . *H. macropsoides*
- Slope of dorsal head profile interrupted by the prominent premaxillary pedicels. Preorbital depth 13–19 (mean = 17) per cent of head. Outline of toothed area on lower pharyngeal bone noticeably longer than broad (bone appears long and narrow, *see* text-fig. 19). Caudal fin very distinctly maculate . . . . . *H. angustifrons*
- L Thickened and papillose area of tissue preceding first gill raker of first gill arch; pseudorakers between inner and outer row of gill rakers especially well developed and prominent. Snout length 31–40 (mean = 33.4) per cent of head . . . . . *H. schubotzi*
- No manifestly thickened and papillose area preceding first gill raker (or if tissue in that region slightly thickened, definitely not papillose); pseudorakers absent or poorly developed. Snout length usually less than 30 per cent of head . . . . . M
- M Caudal fin with an almost rounded distal margin . . . . . *H. nubilus*
- Caudal fin with truncate or weakly subtruncate distal margin. Two species, viz.:
- (i) Most teeth with a well-developed flange on the major cusp (*see* text-fig. 5). Upper jaw 30–38 (mean 35) per cent of head. Eye diameter 28–35 (mean = 31.4) per cent of head. Lips slightly thickened. Nostril opening much larger than the anterior opening to the nasal lateral line canal. Intestine *ca* 1½ times total body length . . . . . *H. aeneocolor*
- (ii) Few teeth with a flange on the major cusp (*see* text-fig. 7). Eye diameter 33–40 (mean = 36) per cent of head. Lips not noticeably thickened. Opening to nostril of equal size to that of nasal lateral line canal. Intestine long (*ca* 2–2½ times total body length) and much coiled . . . . . *H. nigripinnis*







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