

THE CICHLID FISHES
OF LAKE NABUGABO, UGANDA



BY

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British Museum (Natural History)

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By P. H. GREENWOOD

CONTENTS

	<i>Page</i>
INTRODUCTION	315
<i>Tilapia</i>	318
<i>Haplochromis velifer</i>	319
<i>Haplochromis simpsoni</i> sp. nov.	325
<i>Haplochromis annectidens</i>	329
<i>Haplochromis beadlei</i>	335
<i>Haplochromis venator</i> sp. nov.	342
<i>Haplochromis nubilus</i>	346
<i>Hemihaplochromis multicolor</i>	348
<i>Astatoreochromis alluaudi</i>	349
DISCUSSION	351
KEY TO THE GENERA OF CICHLIDAE IN LAKE NABUGABO	355
KEY TO THE <i>Haplochromis</i> SPECIES	355
SUMMARY	356
ACKNOWLEDGEMENTS	356
REFERENCES	356

INTRODUCTION

LAKE NABUGABO is a small body of open water lying within an extensive swamp which fills a former bay on the western shore of Lake Victoria (see map, fig. 1.). Its shape is roughly pyriform, the main axis about five miles long and the width approximately three miles. Except for the western shore, the lake margin is swamp. The western shore is more varied, with, in some places, gently sloping sandy beaches and in other places forest reaching to the lake edge. The swamp margin begins with a zone of Hippo grass (*Vossia cuspidata*) whose rhizomes grow out into the open water. Behind the Hippo grass is a high "hedge" of the grass *Miscanthidium* forming a floating platform of matted roots and rhizomes jutting out into the lake. Away

from the margin this platform becomes more solid through the addition and incorporation of dead and decaying vegetation. In places the platform, although still afloat, is sufficiently compacted to support the growth of trees.

Along its eastern and south-eastern lakeside boundaries the *Miscanthidium* zone is replaced by a large area of *Sphagnum* swamp, an unusual feature at this altitude in east Africa and one not encountered in the swamps around Lake Victoria.

The Bladder-wort *Utricularia* is common in the open water pools found within the eastern part of the swamp. In this region the dominant plant is the grass *Loudetia phragmitoides*, its tussocky habit allowing the development of small open pools. *Utricularia* is also common in the sheltered bays and inlets around the lake margin, and along the sheltered open shores.

Two species of water-lily (*Nymphaea lotus* and *N. caerulea*) occur in the open lake, especially in sheltered bays. Some stands of *Papyrus* are found all around the lake shore but this plant is nowhere a dominant. The relative scarcity of *Papyrus* in Nabugabo contrasts strongly with other swampy areas in the surrounding countryside and, particularly, in Lake Victoria (For a more detailed account, see Beadle and Lind, 1960).

Nowhere in Lake Nabugabo is the water more than fifteen feet deep; in most places it is between five and twelve feet. Except along the western shore the bottom does not shelf and it is in that area that the few patches of exposed sandy bottom are found. Elsewhere the sand is covered by a blanket of liquid mud (Cambridge expedition's field notes).

Very little published information is available on the hydrology of the lake. During the visit of the second Cambridge expedition (June to August, 1962) the open water was well-mixed and supersaturated with oxygen, even in the upper layers of mud. The oxygen content fell sharply in the deeper mud layers and in the water at the bottom of swamp inlets; surface water in these inlets was, however, as highly oxygenated as that of the open lake.

The water of Nabugabo is more alkaline than that of Lake Victoria (pH. of open water 8.2 *cf* 7.8 for Victoria) but in the surrounding swamps it is more acid (pH. 5.35–6.00). Perhaps the most striking hydrological feature is the very low salt concentration of the lake water; its electrical conductivity is about a quarter of that for water from Lake Victoria. Unfortunately no detailed water analyses are yet available.

The main affluents to Nabugabo are the Juma river and the Lwamunda swamp; the latter is fed by small, swampy rivers. Numerous small springs discharge along the western lake shore. The outflow of the lake is into Lake Victoria (some fifty feet lower) and is effected solely by seepage through the sand-bar which forms the eastern barrier between the two water masses; there is no surface contact.

Present day lake Nabugabo represents the greatly diminished body of open water which was gradually cut off from Lake Victoria by the formation of longshore bars across the mouth of an extensive open bay. Bishop (1959) has described the probable history of this empondment: "The landward shore of the lake was an old shoreline of Lake Victoria which consisted in the south-west of a lateritic oldland with low cliffs.

The Juma River divided the oldland into two spurs which were linked again by a series of bay bars across its mouth. Further to the north, a curving longshore bar protruded to the north-east from the mainland and finally joined a former island at Kisasa."

"At some later period another complex longshore bar commenced to grow towards the north-north-east from a point six miles south of the Juma River and finally it also reached the former island of Kisasa to complete the enclosure of Lake Nabugabo. The lake is at present approximately 50 feet above Lake Victoria and is rapidly being overgrown by swamp vegetation. The open water is now separated from the parent lake to the south-east by more than a mile of swamp and two miles of complex sand and gravel ridges comprising the longshore bar."

The age of Lake Nabugabo has been estimated at approximately 4,000 years. This figure is based on the radiocarbon dating of some rolled charcoal fragments found in a former shoreline of Lake Victoria at about the same height above the present level of the lake as is the sandbar which cuts off Nabugabo (personal communication from Dr. Bishop quoted by Beadle, 1962).

The first collections of fishes from Lake Nabugabo were made in 1930 by the

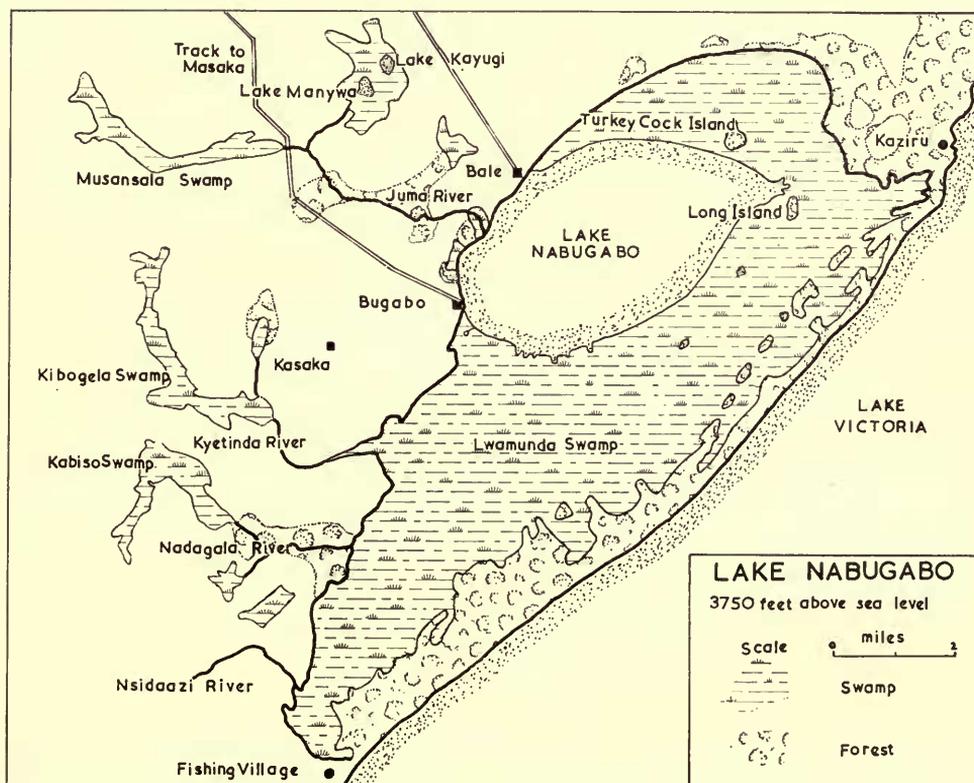


FIG. 1. Sketch map of Lake Nabugabo; after a map produced by the Cambridge Nabugabo Biological Survey.

Cambridge expedition to the East African Lakes. The Cichlidae were studied by Dr. Ethelwynn Trewavas (1933) who recognised their importance in helping to understand the evolutionary processes which had resulted in the complex *Haplochromis* species-flock of Lake Victoria. Dr. Trewavas recorded four *Haplochromis* species, of which three were described as new and endemic, and the fourth assigned to a species already known from Lake Victoria.

Since 1930 our knowledge of Lake Victoria *Haplochromis* has increased, both from the systematic and from the ecological view-points. So too has our knowledge about the geological history of the area, and there has recently been revived interest in the evolutionary problems posed by the cichlid species-flocks. Thus, it seemed desirable to revise the *Haplochromis* of Lake Nabugabo against the newly acquired information from Lake Victoria. This possibility became a reality when a group of Cambridge students offered to collect specimens from Lake Nabugabo for the British Museum (Natural History). Their collection (hereinafter referred to as the C.N.B.S. collection) has proved invaluable for several reasons. Not only did it substantially increase the number of specimens but the expedition also made detailed notes on the live colours of the fishes, and on their distribution and habitats. Observations were also made on the fishes' feeding habits and some data on breeding conditions were collected as well. With this sort of information it was possible to make a more detailed and direct comparison between the *Haplochromis* of the two lakes and thus to make a reappraisal of relationships on characters other than purely anatomical ones.

To the original four *Haplochromis* species must now be added two others and two species of *Haplochromis*-group genera, viz. *Hemihaplochromis multicolor* (Schoeller) and *Astatoreochromis alluaudi* Pellegrin. Three of the newly recorded species (*H. nubilus*, *Hh. multicolor* and *A. alluaudi*) are of fairly wide distribution in the Lake Edward-Victoria drainage basins; their occurrence in Lake Nabugabo is not surprising. Unfortunately it is not absolutely certain that one can accept their presence as natural because some introductions have been made into Lake Nabugabo since the original collections were made over thirty years ago. In 1960, the Nile Perch (*Lates*) was introduced. If the newly recorded cichlids gained access in this way it was accidental and, I would consider, unlikely if only Nile Perch were involved. *Haplochromis* are more likely to be introduced accidentally when *Tilapia* are moved from one area to another because small individuals of the two genera are easily confused.

In addition to the cichlid fishes described below, the C.N.B.S. collection contained a large number of non-cichlid species, including several new records for the lake. These fishes will be dealt with in a separate publication.

THE FISHES

I. *TILAPIA* A. Smith, 1840

Two species of *Tilapia* (*T. esculenta* Graham and *T. variabilis* Blgr.) are recorded from Lake Nabugabo; both are otherwise endemic to Lakes Victoria and Kyoga. The C.N.B.S. mentioned both species in their preliminary report but no specimens were sent to the British Museum (Nat. Hist.).

II. *HAPLOCHROMIS* Hilgendorf, 1888

Regan, C. T. 1920. The classification of the fishes of the family Cichlidae. I. The Tanganyika genera. *Ann. Mag. nat. Hist.* (9), 5 : 33-53.

Haplochromis velifer Trewavas, 1933

(Text figs. 2 and 3)

H. velifer (part) Trewavas, 1933, *J. Linn. Soc. (Zool)*, 38 : 322.

HOLOTYPE. A male 75 mm. S.L., B.M. (N.H.) Reg. No. 1933.2.23.194, collected by E. B. Worthington.

DESCRIPTION. Based on the holotype, 6 paratypes and eight additional specimens, 75-108 mm. S.L.

Depth of body 35.7-41.3 (Mean, M , = 39.1) per cent of standard length, length of head 32.3-36.0 (M = 34.7) per cent; dorsal profile of head slightly curved (but with a concavity above the orbit), sloping moderately steeply (*ca* 40°-45° to the horizontal).

Preorbital depth 13.8-18.5 (M = 16.3) per cent of head length, least interorbital width 21.8-29.0 (M = 24.1) per cent and snout length 29.1-33.4 (M = 31.3); snout slightly broader than long or as long as broad. Eye diameter shows weak negative allometry with standard length, 26.3-33.4 (M = 30.6) per cent of head; depth of cheek 21.8-26.0 (M = 23.3) per cent.

Caudal peduncle 14.5-17.5 (M = 15.9) per cent of standard length, 1.2-1.4 (mode 1.3) times as long as deep.

Mouth horizontal or very slightly oblique; jaws equal anteriorly, the lower 37.1-44.8 (M = 39.7) per cent of head, 1.4-2.0 (mode 1.5) times as long as broad. Lips often slightly thickened. Posterior tip of the maxilla reaching (the modal

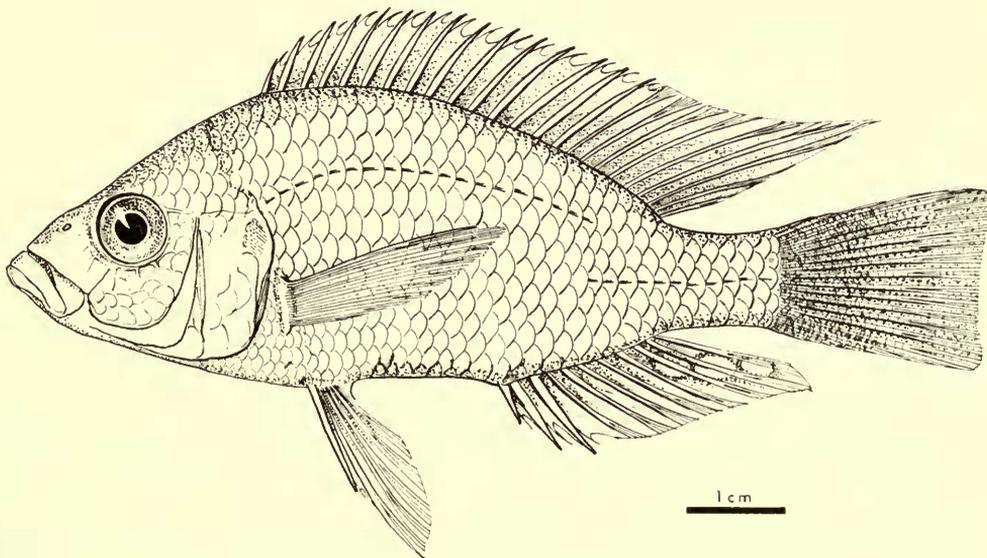


FIG. 2. *Haplochromis velifer*. Drawn by Barbara Williams.

condition) or almost reaching the vertical through the anterior orbital margin but in four specimens extending to below the anterior part of the eye.

Gillrakers short and stout, 7-9 (mode 8) on the lower limb of the first arch, the lowermost one to three rakers reduced.

Scales ctenoid; lateral line with 30 (f.4), 31 (f.7) or 32 (f.4) scales; cheek with 3 (f.14) or 4 (f.1) rows; 5-6½ (mode 6) scales between the dorsal fin origin and the upper lateral line, 5-6 (mode) between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.1), 24 (f.10) or 25 (f.3) rays comprising 15 (f.11) or 16 (f.3) spinous and 8 (f.3), 9 (f.9) or 10 (f.2) branched elements; anal with 11 (f.5) or 12 (f.9) rays comprising 3 spinous and 8 (f.5) or 9 (f.9) branched rays. Caudal fin truncate or subtruncate with slightly rounded distal corners (Trewavas, *op. cit.*, suggests that the degree of rounding is greatest in males), scaled on its basal half. First two branched pelvic rays produced in both sexes. Pectoral 25.4-29.8 ($M = 27.6$) per cent of standard length.

Teeth. The outer teeth in both jaws are slightly recurved, relatively stout and have compressed bicuspid crowns (see text-fig. 3); the postero-lateral and posterior teeth are somewhat less robust than those situated anteriorly. The acutely pointed smaller cusp is prominent and stout; the major cusp has an oblique edge which meets the nearly vertical medial aspect of the cusp at an angle of 45°-60°. There are 40-58 (mean 50) teeth in the outer row of the upper jaw.

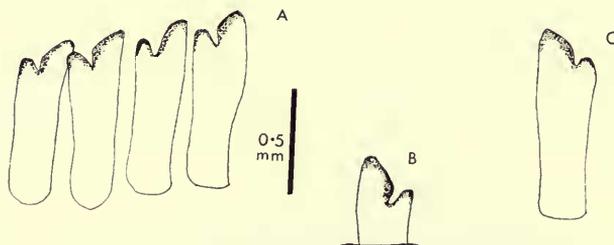


FIG. 3. *Haplochromis velifer*. Outer teeth (labial aspect) from: A, premaxilla, and C, dentary. B, newly erupted tooth (dentary).

The inner rows in both jaws are composed of small, compressed and tricuspid teeth arranged in 2-4 (mode 3) and 2 (mode) or 3 rows in the upper and lower jaws respectively. A distinct interspace separates the inner rows from the outer row.

The form of the outer teeth in *H. velifer* is one of the two generalized types found in many species of *Haplochromis*. In the other type, the major cusp is more acutely pointed.

Lower pharyngeal bone slender, the triangular dentigerous surface broader than long. The teeth are slender and cuspidate, fairly close-set and arranged in 24-28 antero-posterior rows; teeth in the two median rows are generally somewhat stouter than the others but are otherwise identical.

Vertebrae: 28 or 29, comprising 13 abdominal and 15 (f.2) or 16 (f.7) caudal elements.

Coloration in life. Males (adult but of undeterminable sexual state): ground colour dark grey-blue to olivaceous dorsally (dark indigo on head), shading on flanks to olivaceous with violet to turquoise sheen; ventral surface sooty-violet, the chest with a red flush. Males less than 65 mm. S.L. and probably juvenile have a similar coloration dorsally and laterally but the ventral surface is silvery-white and the chest lacks the red flush.

Dorsal fin dark olive (overlain with sooty in fishes > 65 mm. S.L.) basally, light blue-grey distally; dull red spots and blotches between the rays; the lappets and margin to the soft part crimson. Anal fin greenish-blue basally, buff to pink distally (olivaceous in small fishes); ocelli orange with light yellow surround on a transparent area of fin membrane. Pelvics with anterior quarter sooty except for the dead-white, elongated first and second rays; remainder of fin hyaline in fishes < 65 mm. S.L., pink to crimson in larger individuals. Caudal fin dark olivaceous to indigo proximally, light olive distally in small fishes, scarlet in larger ones.

Females: ground colour dull metallic grey with violet lights (particularly on the cheeks), shading through greyish-buff on the flanks to pinkish-white on the ventral surface.

Dorsal fin pale buff with a narrow basal band of crimson on that part of the fin posterior to the fifth spine. Anal with a crimson basal band followed by a broader buff band and, along the distal margin, a narrow sooty band; in some specimens there are dull orange spots in about the position of the ocelli in males. Pelvics faintly sooty.

Coloration in preserved specimens. Adult males. Body dark brown, black on belly and chest, in ripe individuals this dark coloration extending along the entire ventral surface and on the flanks as far dorsally as the upper lateral line; in some specimens there is a pearly sheen visible on the dark areas. A well-developed lachrymal stripe of varying width, two parallel transverse bars on the snout and two transverse nuchal bands are also present. The anterior nuchal band is a continuation of the lachrymal stripe; the posterior band originates at the anterior, upper angle of the operculum and also extends ventrally along the preopercular-opercular junction. On the flanks there are traces of six, moderately broad bands which reach the origin of the dorsal fin and fuse ventrally with the dark belly; these bands are much fainter than the nuchal and snout bars.

The dorsal fin in sexually quiescent fishes is hyaline but in active individuals it has dusky lappets and a solid, parabolic dusky area originating at the base of the third to sixth spinous ray from where it rises fairly steeply so that the area of membrane between the 10th and last spine is completely black; thereafter it falls rather gently so that the distal third to half of the membrane between the branched rays is hyaline but the base is black. Caudal fin is hyaline in quiescent fishes but the proximal two-thirds is black in active individuals; in some specimens darker spots are visible through the sooty ground colour. The anal has the entire interspinous membrane black; in active fishes the basal third to half of the soft part is black, the remainder hyaline (as is the entire fin in quiescent individuals); two or three, dead-white, round to oval ocelli are present in both sexes.

Certain variant patterns are fairly common; the most frequently seen being variation in the intensity and area of the dark parabola of the dorsal fin and a tendency for the posterior nuchal bar to be expanded medially into a large triangular black patch with its apex at the base of the first dorsal spine.

Females are greyish-silver, darkest dorsally; there is a fairly distinct lachrymal stripe running from the angle of the jaw through the anterior rim of the orbit. All fins are hyaline, with the soft dorsal and caudal maculate, and dark lappets to the dorsal in some specimens. Traces of six narrow vertical bars may be visible on the flanks; these do not extend to the belly and they become extremely faint near the base of the dorsal fin.

Ecology. Habitat. *Haplochromis velifer* has a wide distribution within the lake, being found both close inshore and at some distance out, over muddy and sandy bottoms in bays, and over the clear sandy beaches of the western shore. It does not appear to live in the isolated swamp pools, nor does it extend far up those arms of the lake which penetrate into the swamps.

Food. The C.N.B.S. notes, supplemented by a personal examination of eight additional specimens, indicate that *H. velifer* is an omnivorous bottom feeder with insect larvae (especially those of chironomids and trichopterans) providing the main source of nourishment. A considerable amount of plant material was found in the gut but it showed few signs of digestion. Since the bottom in many habitats is covered by a layer of plant matter (both algal and phanerogamic) the plant remains should probably be considered as being incidentally ingested during the search for insect larvae and other invertebrate animals. Sand grains were also recorded and in some instances these could be identified as coming from the cases of larval Trichoptera.

Breeding. No data are available. The largest specimen (108 mm. S.L.) is a female, but both sexes are found in the next largest size group, 75–85 mm. S.L.

Distribution. Known only from Lake Nabugabo.

Affinities and diagnosis. Anatomically and trophically *H. velifer* belongs to the group of generalized *Haplochromis* which are found both in the rivers and in the species-flocks of the major lakes. Comparison will be made first with the widely distributed species *H. nubilus* and *H. wingatii*, the former occurring in Lakes Nabugabo, Victoria and Edward, the latter in Lakes Edward and Albert and in the Nile.

From *H. velifer*, *H. nubilus* is immediately distinguished by the velvety black and uniform body colour of adult males, as well as by its stouter and more acutely cuspidate teeth, more obviously rounded caudal fin and its smaller eye. *Haplochromis wingatii* differs in having fewer teeth in the outer row of the upper jaw (30–40 in specimens of a size comparable with the *H. velifer* sample examined), larger and more numerous unicuspid teeth posterolaterally in this row, markedly smaller scales on the chest region, in having some blunt pharyngeal teeth and in the coloration of adult males.

Amongst the Lake Victoria endemics, *H. velifer* is perhaps nearest to *H. cinereus*, *H. macrops*, *H. lacrimosus* and *H. pallidus*. It differs from all these species in various combinations of characters (see Greenwood, 1960). In all cases the nature of the

preserved coloration serves to separate males of the various species; the live coloration of male *H. macrops* (the only species of the four in which this is known) also differs markedly from that of *H. velifer*. The most obvious anatomical characters distinguishing *H. velifer* from the Victoria species are: from *H. cinereus* the dentition (in *H. cinereus* slender unicuspid or weakly bicuspid outer teeth, uni- and bicuspid, obliquely implanted inner teeth); from *H. macrops*, the absence of tricuspid teeth posterolaterally in the upper, outer tooth row of fishes <85 mm. S.L., smaller eye (26.3–33.4, M = 30.6% of head in *H. velifer*, cf. 28.6–35.4, M = 33.0 in *H. macrops*) and deeper cheek (21.8–26.0, M = 23.3% of head cf. 17.4–24.2, M = 21.1 in *H. macrops*); from *H. lacrimosus*, the more robust less curved outer teeth with their expanded major crowns, the shorter pectoral fin (M = 81% of head in *H. velifer*, 88.5% in *H. lacrimosus*) and slightly deeper cheek (21.8–26.0, M = 23.3% of head, cf. 17.6–23.5, M = 20.5% in *H. lacrimosus*); from *H. pallidus* (which species *H. velifer* closely resembles in its oral dentition) the larger chest and nape scales, the fewer teeth in the median tooth row of the lower pharyngeal bone, and a lower modal number of gillrakers (8 cf. 9 for *H. pallidus*; the range of gillraker numbers (7–9) is identical).

In her original description of *H. velifer*, Trewavas (1933) compared the species with *H. gestri* (now a synonym of *H. obesus* (Blgr), see Greenwood 1959b). The two species are but distantly related, *H. obesus* belonging to the group of specialized larval-fish eating species which is characterized by a reduced dentition and an expansible mouth.

Amongst the Lake Edward endemics *H. velifer* shows the greatest superficial resemblance to *H. schubotzi*. It differs from this species in the following characters: its dentition, a shallower preorbital, and a shorter caudal peduncle. Small specimens of *H. schubotzi* (i.e. in the range comparable with that known for *H. velifer*) have relatively slender teeth with the minor cusp reduced and the major cusp acutely pointed; in larger specimens the teeth are, relatively, even more slender and may have the minor cusp reduced almost to vanishing point. In specimens at all sizes the inner teeth of *H. schubotzi* are tricuspid, but in specimens over 120 mm. S.L. the cuspidation is feebly manifested. Trewavas (1933), believed that the lower jaw of *H. schubotzi* is longer than in *H. velifer* but I am unable to confirm this; the lower jaw has the same relative length in both species.

The other Lake Edward species showing a superficial resemblance to *H. velifer* are *H. nigripinnis*, *H. eduardii* (including *H. vicarius* acc. Poll, 1939), *H. elegans* and *H. engystoma*.

Both *H. nigripinnis* and *H. engystoma* are distinguished from *H. velifer* by their shorter snouts, larger eyes (eye diameter about equalling snout length in *H. velifer*, much longer than snout in the two Edward species), more decurved dorsal head profile and, in *H. nigripinnis*, by the more slender and numerous gill rakers (10 or 11); also, *H. engystoma* has fewer teeth (36 in the upper, outer row of the unique holotype) with more strongly recurved cusps.

From *H. eduardii*, *H. velifer* is distinguished by its coarser teeth (and the absence of unicuspid teeth in larger specimens), shorter, coarser and fewer gill rakers (7–9, cf.

9-12 in. *H. eduardii*), straighter dorsal head profile and shorter pectoral fin (always clearly shorter than the head in *H. velifer*, as long as the head, or nearly so, in *H. eduardii*).

Haplochromis elegans differs least of all but is nevertheless distinguished by its shallower body, somewhat shorter snout, smaller chest scales (both ventrally and laterally) and its more strongly curved dorsal head profile.

Haplochromis velifer certainly appears to have greater affinity with the Lake Victoria species discussed here than with those of Lake Edward. *Haplochromis elegans* is the only Edward species to have about the same overall degree of affinity with *H. velifer* as have the Victoria species. However, it must be remembered that these comparisons are based on fewer Edward than Victoria specimens and that less is known about their ecology and live colours.

Within Lake Nabugabo, *H. velifer* has closest affinity with the new species, *H. simpsoni* (see p.325); indeed, five paratypes of *H. velifer* are now identified as *H. simpsoni*. The species are distinguished principally by their dentition; the outer teeth of *H. simpsoni* are more slender, have an acutely pointed major cusp (the minor cusp greatly reduced or absent) and are more numerous (50-70, mean 60, in the outer, upper series, cf. 40-58, $M = 50$, for *H. velifer*). The body form of the two species is similar although the dorsal head profile of *H. simpsoni* is straighter and lacks the interorbital concavity of *H. velifer*; also, in *H. velifer* the orbit lies distinctly below the outline of the profile, whereas in *H. simpsoni* the upper margin of the orbit is generally included in the profile. In *H. velifer* the snout is broader than it is long (or at least as broad as long) but in *H. simpsoni* the snout is longer than broad (the difference becoming more pronounced in larger fishes) so that these fishes have the appearance of being thinner faced than *H. velifer*. This is reflected in the width of the lower jaw; the mean length/width ratio for *H. velifer* is 1.5 (range 1.4-1.7) and for *H. simpsoni* 2.0 (range 1.5-2.1). A difference also exists in the modal number of gill rakers (7 for *H. simpsoni*, 8 for *H. velifer*) and the lower limit for *H. velifer* is higher (7 cf. 6 for *H. simpsoni*). Finally, there are differences in the coloration of adult males; *H. velifer* has a red flush on the chest and crimson lappets to the spinous dorsal, this colour continuing onto the margin of the soft dorsal as well. In *H. simpsoni* the chest is sooty and the dorsal lappets black. There are also inter-specific differences in the colours of the anal, caudal and pelvic fins, and the body is more definitely blue in *H. simpsoni*.

No single anatomical character can be considered diagnostic but if those mentioned above are taken in concert, the two species may be distinguished fairly readily.

STUDY MATERIAL

<i>B.M. (N.H.) reg. no.</i>	<i>Collector</i>
1933.2.23.194 (Holotype)	Worthington
1933.2.23.181-193 (Paratypes)	Worthington
1933.2.23.200-209	Worthington
1964.7.1.34-50	C.N.B.S.

Haplochromis simpsoni sp. nov.

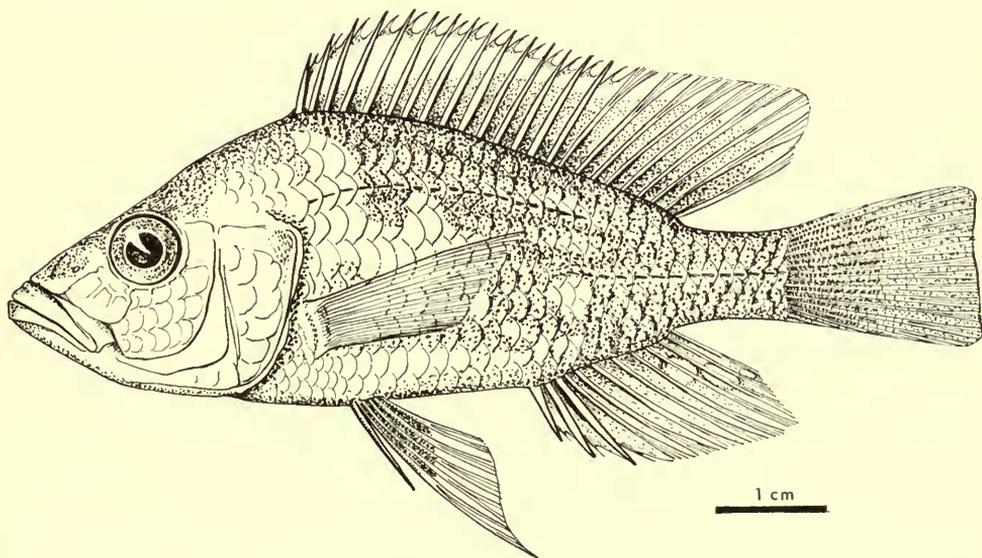
(Text figs. 4 and 5)

H. velifer (part) Trewavas, 1933, *J. Linn. Soc. Soc. (Zool.)*, **38** : 322. (See list of study material.)

HOLOTYPE. An adult male 88 mm. standard length (B.M.[N.H.] reg. no. 1964.7.1.12) collected by the C.N.B.S.

Named in honour of Mr. M. Simpson, one of the members of the Cambridge Nabugabo Biological Survey.

DESCRIPTION. Based on the holotype and twenty-one additional specimens, 76–114 mm. S.L.; data on dentition were also derived from eighty further specimens, collected by Capt. C. R. S. Pitman.

Depth of body 32.7–42.0 ($M = 37.6$) per cent of standard length, length of head 31.6–37.6 ($M = 34.9$) per cent. Dorsal profile of head straight (without a noticeable concavity above the eye), sloping at about 45° to the horizontal.Preorbital depth 16.1–20.5 ($M = 17.8$) per cent of head, least interorbital width 18.8–24.7 ($M = 22.3$) per cent, length of snout 28.8–34.3 ($M = 32.2$) per cent; snout longer than broad. Eye diameter 25.6–32.4 ($M = 29.4$) per cent of head (not showing any allometry in the sample studied), depth of cheek 22.4–28.2 ($M = 25.0$) per cent.Caudal peduncle 15.3–18.5 ($M = 16.7$) per cent of standard length, 1.1–1.6 (mode 1.4) times as long as deep.Mouth horizontal (rarely, slightly oblique); jaws equal anteriorly, the lower 37.5–45.0 ($M = 41.4$) per cent of head, 1.5–2.1 (mode 2.0) times as long as broad. Posterior tip of maxilla reaching or almost reaching the vertical through the anterior orbital margin or even to slightly beyond this point.FIG. 4. *Haplochromis simpsoni*. Drawn by Barbara Williams.

Gillrakers variable, from stout to moderately slender, both extremes often occurring on the same arch; 6–9 (mode 7) on the lower part of the first arch, the lowermost 1 to 3 rakers reduced.

Scales ctenoid; lateral line with 30 (f.1), 31 (f.2), 32 (f.10) or 33 (f.8) scales; cheek with 3 (f.13) or 4 (f.9) rows; 5–7 (modal range $5\frac{1}{2}$ –6) scales between the upper lateral line and the dorsal fin origin; 5 or 6 (mode) between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.8) or 25 (f.14) rays, comprising 15 (f.8) or 16 (f.14) spinous and 8 (f.1), 9 (f.20) or 10 (f.1) branched rays. Anal with 11 (f.12) or 12 (f.10) rays, comprising 3 spinous and 8 (f.12) or 9 (f.10) branched rays. Pectoral 26.4–33.2 ($M = 27.6$) per cent of standard length. First and second pelvic rays produced, proportionately more so in adult males. Caudal subtruncate.

Teeth. There are three forms of teeth in the outer row of both jaws; all are slender and recurved, and all have an acutely pointed major cusp. The commonest form has a very weakly developed minor cusp which appears as little more than a lateral spur at the base of the protracted, slender and curved major cusp (text fig. 5); a variant of this type lacks the minor cusp, either through wear or because the tooth develops without it (as can be determined from erupting teeth). The third form is relatively stouter than the other two types, has a small but distinct minor cusp and a less protracted and less acutely pointed major cusp; this form is usually restricted to a posterolateral position in the row. An admixture of all forms of tooth may occur in any fish and usually there is no difference in the proportion of the two commoner types as between upper and lower jaws. However, in some individuals the unicuspid occurs in the upper jaw and the weakly cuspidate form in the lower (where there may also be a few of the stouter, more definitely bicuspid teeth). No obvious correlation exists between the sex or size of the fish and the type of dentition present.

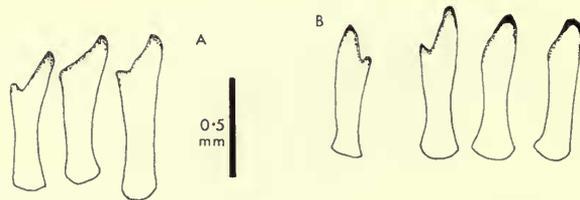


FIG. 5. *Haplochromis simpsoni*. Outer teeth (labial aspect) from: A, dentary, and B, premaxilla.

There are 50–70 (mean 60) teeth in the outer row of the upper jaw; the tooth number has a weak positive correlation with the size of the specimen.

The inner rows (2 [mode] or 3 in the upper jaw and 1–3 [mode 2] in the lower) are also made up of three different types of teeth. A tricuspid tooth with a protracted middle cusp is the commonest form, but weakly bicuspid and even unicuspid also occur, although much less frequently and in fewer numbers.

In many specimens the teeth are coarsely disfigured by a dark brown thickening of the crown which, in many cases, almost obscures the nature of the cusp. A similar (? pathological) condition was found in *H. empodisma* of Lake Victoria (Greenwood, 1960), a species thought to be related to *H. simpsoni*; it is also seen in the very distantly related *H. obliquidens* of Lake Victoria (Greenwood, 1956).

Lower pharyngeal bone slender; its dentigerous surface triangular and slightly longer than broad. The pharyngeal teeth are slender and cuspidate, and are arranged in 26–28 rows; the median rows may contain a number of somewhat coarser teeth but in the majority of specimens examined no such differentiation was apparent.

Vertebrae: 29, comprising 12 (f.1) or 13 (f.8) abdominal and 16 (f.8) or 17 (f.1) caudal elements.

Coloration in life. Adult males: dorsal surface of body cobalt, that of the head dark umber to black; flanks with light turquoise sheen, the ventral body surface sooty except for the chest which is silvery-white with a diffuse sooty overlay.

Dorsal fin pale grey with small blotches of dull red between the spines, and darker, more irregular red blotches between the branched rays; lappets and margin to soft part black. Caudal fin dark turquoise on its proximal half, followed by a broad, pinkish vertical band and, distally, a blackish area extending to the margin; the posterior angles are sometimes outlined in red. Anal greyish-white, lappets sooty; a faint pink flush extends along the distal margin of the soft part and spreads, but less definitely, to below the black lappets of the spinous portion. Pelvics olivaceous with a sooty wash.

Females: body olive-green, with a suggestion of blue dorsally, becoming lighter on the flanks (which have a turquoise iridescence) and shading to blue-grey ventrally. Cheek and opercular region with turquoise high-lights.

Dorsal fin olive-green basally, the posterior part lightest; dull red blotches occur between the spines and give an impression of a broad red stripe along this part of the fin and even to the more distal region below the black lappets. Similar but smaller blotches occur between the soft rays so that the band is continued posteriorly where, however, it is narrower and less intense. Caudal fin with a reddish to olive-brown blotch at its base, the blotch becoming brighter red distally; the area around the blotch is olive-yellow as is the middle third of the fin; the distal third is either sooty or olive-yellow. Anal fin olive-yellow except for a dull crimson basal streak. Pelvics pale olive-yellow, the elongated rays dead white.

Coloration in preserved specimens. Adult males (sexually active) are light brown, with the belly, isthmus, flanks (to the level of the upper lateral line) and caudal peduncle (except dorsomedially) sooty to black; the cheeks are dark but with a pearly lustre. Two narrow transverse bars are usually visible across the snout but apparently only one nuchal band is developed; the latter originates at the anterior upper angle of the operculum and is usually interrupted medially. The lower jaw is pale but the branchiostegal membrane is black. The dorsal fin is hyaline with a sooty overlay most concentrated in the middle third of the fin and least concentrated on the distal region of the soft part. Caudal fin is dark on its proximal quarter, lighter over the remainder except along a moderately wide band outlining its ventral and posterior

margins. The anal fin is faintly white to hyaline except for a narrow, intensely dark basal streak and four greyish ocelli (arranged in a single row). The pelvics are black to sooty, being lightest on the posterior third.

Sexually quiescent males are light brown, the chest, belly, branchiostegal membrane and the lower half of the caudal peduncle dusky and overlaid with a pearly sheen; the two snout- and single nuchal-bands are as in active males. Five or six vertical bars of variable intensity are visible on the flanks; these do not reach the origin of the dorsal fin and ventrally they merge with the dark ventral coloration. Dorsal fin hyaline with dark lappets, caudal dark hyaline, darkest proximally; anal dusky, darkest (almost black) in the area of the spines, two to four greyish ocelli arranged in one or two rows. Pelvic fins black to sooty.

Females are silvery-grey; a short, broad lachrymal stripe or blotch is present, as are a faint nuchal bar and an even fainter transverse bar across the snout. Six or seven faint but moderately broad bars are visible on the flanks and caudal peduncle, those on the flanks reaching neither the dorsal nor ventral body outlines. All fins are hyaline, the base of the caudal slightly darker; in one specimen there is a faint darkening between the rays of the dorsal fin (especially over the soft part) and over the proximal two-thirds of the caudal fin. In all specimens there are two dark spots on the anal in the position of the ocelli in males.

Ecology. Habitat. This species seems to have a wide distribution within the lake, being found inshore over a variety of substrata, amongst the emergent vegetation, over exposed sandy beaches and even at some distance offshore over a muddy bottom. It does not appear to inhabit isolated pools in the swamps, nor does it extend for any distance up the inlets into the swamps. Thus, it will be seen that *H. simpsoni* and *H. velifer* do not differ in their broad ecological requirements or restrictions.

Food. From the C.N.B.S. field notes, supplemented by further gut analyses on five specimens, I can find no clear-cut differences in the feeding habits of this species and *H. velifer* (see p. 322); that is, *H. simpsoni* is an omnivorous bottom feeder preying chiefly on insect larvae.

Breeding. No data are available. All the specimens examined are adult, the smallest male and female being 76 and 85 mm. S.L. respectively. The largest fish is a female (114 mm. S.L.) and the largest male is 105 mm. S.L.

Distribution. Known only from Lake Nabugabo.

Affinities and diagnosis. The nature of the dentition, together with the relative size of the eye and snout, serves to distinguish *H. simpsoni* from the generalized species of Lake Edward (i.e. *H. eduardii*, *H. engystoma*, *H. nigripinnis*, *H. elegans* and *H. schubotzi*). On the basis of its dentition, *H. simpsoni* cannot be included in the same category as these generalized species (although though trophically it should be considered generalized). Rather, it should be grouped with *H. empodisma* of Lake Victoria, a species with which it shows fairly close affinities.

The body form and, particularly, the dentition of *H. empodisma* and *H. simpsoni* are similar as are the feeding habits and broad ecological requirements of the two species (Greenwood, 1960). *Haplochromis simpsoni* is, anatomically, more closely

related to *H. empodisma* than it is to the small, undescribed, species which I mentioned in connection with the affinities of *H. empodisma* (see Greenwood, *op. cit.*). *Haplochromis simpsoni* differs from *H. empodisma* in having somewhat fewer jaw teeth (50–70, $M = 60$ cf. 54–82, $M = 70$), the triangular dentigerous surface of the lower pharyngeal bone equilateral and not isoscelean, a slightly narrower head (15.0–16.7, $M = 15.9$ per cent of standard length, cf. 15.6–19.8, $M = 17.4$ per cent in *H. empodisma*) and a straighter dorsal head profile. The modal number of dorsal rays in *H. empodisma* (24) is lower than in *H. simpsoni* (25) although the ranges overlap; however, the range in *H. empodisma* includes a number of specimens with only 23 rays and but one fish with 25. The two species differ in the coloration of adult males, especially in the absence of red pigment on the head of *H. simpsoni*; the red head of *H. empodisma* is a characteristic feature.

Haplochromis simpsoni also resembles *H. velifer*; the diagnostic characters separating these species are discussed on page 324. In sum, it seems that *H. simpsoni* shares more characters with *H. empodisma* than with *H. velifer*.

STUDY MATERIAL

<i>B.M. (N.H.) reg. no.</i>	<i>Collector</i>
1964.7.1.12 (Holotype)	C.N.B.S.
1964.7.1.13–24 (Paratypes)	C.N.B.S.
1964.7.1.25–27 (Paratypes)	Pitman
1933.2.23.195–199 (Paratypes of <i>H. velifer</i>)	
Paratypes	Worthington
1964.7.1.28–33 (Paratypes)	Pitman
1935.8.23.34–63	Pitman
1935.8.23.81–100	Pitman

Haplochromis annectidens Trewavas, 1933

(Text figs. 6 and 7)

H. annectidens (part) Trewavas, 1933, *J. Linn. Soc. (Zool.)*, **38** : 323.

HOLOTYPE. An adult male, 67 mm. S.L. from Lake Nabugabo (collected by E. B. Worthington), B.M. (N.H.) reg. no. 1933.2.23.210.

DESCRIPTION: based on the holotype, seven paratypes and thirteen additional specimens, 43–67 mm. S.L.

Depth of body 31.3–40.0 ($M = 36.9$) per cent of standard length, length of head 30.6–36.0 ($M = 33.8$) per cent. Dorsal profile of head straight, sloping moderately steeply (ca 40°–45° with the horizontal).

Preorbital depth 11.1–15.8 ($M = 13.5$) per cent of head, least interorbital width 21.0–29.2 ($M = 25.3$), snout length 25.0–31.6 ($M = 27.9$), eye diameter 30.4–37.5 ($M = 33.3$) and depth of cheek 12.5–21.7 ($M = 18.1$) per cent, the latter character showing slight positive allometry with standard length.

Caudal peduncle 14.7–18.6 ($M = 16.3$) per cent of standard length, 1.1–1.6 (mode 1.4) times as long as deep.

Mouth horizontal, lips sometimes slightly thickened. Jaws equal anteriorly, the lower 31.3–42.2 ($M = 37.4$) per cent of head length, 1.5–2.0 (modal range 1.5–1.6) times as long as broad; posterior tip of the maxilla reaching the vertical through the anterior orbital margin (the modal condition) or to below the anterior part of the eye.

Gillrakers variable, from short and stout to relatively slender, but usually of uniform shape in any one individual; 8–10 (mode 9) on the lower part of the first arch, the lowermost 1–3 rakers reduced.

Scales ctenoid; lateral line with 30 (f.1), 31 (f.6), 32 (f.12) or 33 (f.1) scales; cheek with 2 or 3 (mode) rows; 5–6 (mode) scales between the dorsal origin and the upper lateral line, 4–5½ (mode 5) between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.2), 24 (f.8), 25 (f.10) or 26 (f.1) rays, comprising 15 (f.8) or 16 (f.13) spinous and 8 (f.5), 9 (f.14) or 10 (f.2) branched rays. Anal with 11 (f.2), 12 (f.17) or 13 (f.2) rays, comprising 3 spinous and 8 (f.2), 9 (f.17) or 10 (f.2) branched. Caudal subtruncate or truncate. Pectoral 25.4–30.8 ($M = 27.6$) per cent of standard length. First two soft pelvic rays produced, proportionately more so in males.

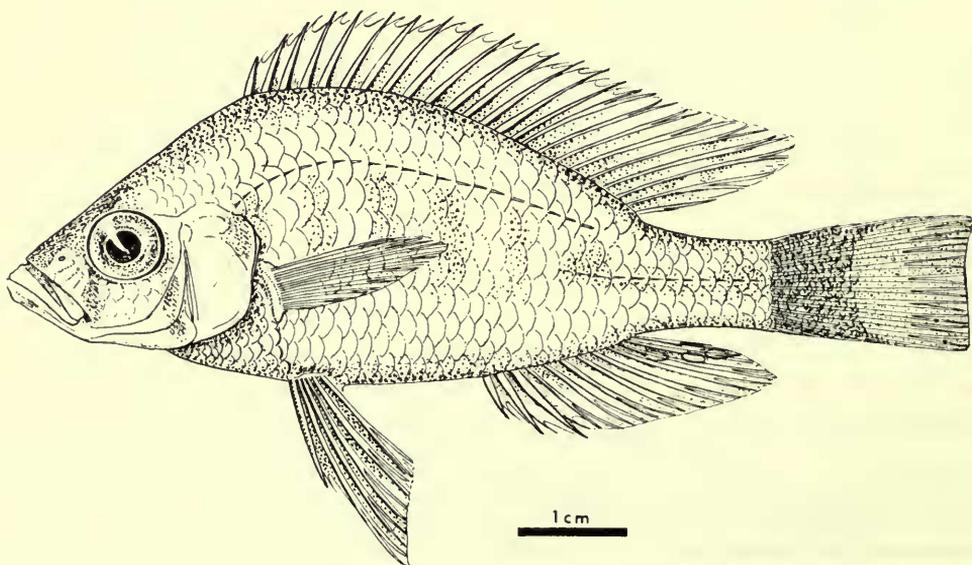


FIG. 6. *Haplochromis annectidens*. Drawn by Barbara Williams.

Teeth. The outer teeth in this species are highly characteristic. Except for a few teeth situated posteriorly in each jaw, the teeth are moveably implanted; each tooth has an elongate, slender neck and base but a flattened and expanded crown which is derived almost entirely from the enlarged major cusp (see fig. 7a, b). The occlusal margin of this cusp is obliquely truncate so that the thin occlusal surface

is slightly convex and almost horizontal in position; the minor cusp is minute and acutely pointed. The anterior tip of the crown is drawn out, so that this margin of the tooth is concave; the posterior margin is curved in parallel with the anterior one (*i.e.* it is convexly arched). A few posterior teeth in the upper jaw are much smaller than their anterior congeners and are but weak replicas of them; in the dentary, the posterior teeth are tricuspid. The number of teeth in the outer, upper row shows some positive correlation with the size of the fish, *viz.* in fishes 43–50 mm. S.L. ($N = 6$), 38–50 ($M = 45$) and 48–68 ($M = 56$) in larger specimens ($N = 15$).

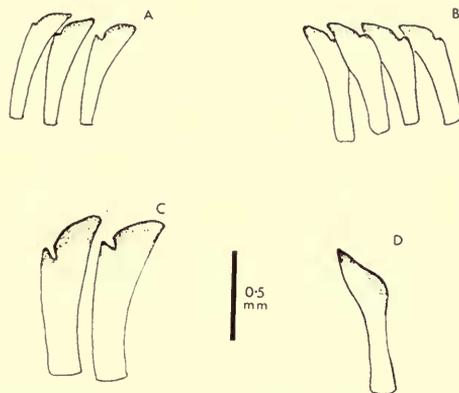


FIG. 7. A and B: *Haplochromis annectidens*, outer teeth (labial view) from, respectively, the premaxilla and the dentary. C, outer premaxillary teeth of *H. lividus* (labial view), D, outer tooth (premaxilla) in labial view, of *H. obliquidens*.

All teeth in the inner rows are small and tricuspid; in a few specimens the teeth of the outermost row may be noticeably enlarged but are still clearly tricuspid, unlike the enlarged inner teeth of *H. obliquidens* (see below p. 334) which are also obliquely cuspidate. There are 2–4 (mode) inner rows of teeth in the upper jaw and 2–4 (mode 3) in the lower; a fairly distinct interspace usually separates the inner rows from the outer row, but in some specimens it is obscured.

Lower pharyngeal bone and teeth. The lower pharyngeal bone is slender, its denticerous surface triangular and somewhat broader than long (occasionally equilateral). The teeth are slender, weakly cuspidate, slightly curved and fairly close set in 30–36 rows. In the largest specimen examined (the holotype) a few of the posterior teeth in the median rows are slightly enlarged; in all other specimens there is no such differentiation.

Vertebrae: 28 or 29, comprising 13 abdominal and 15 (f.1) or 16 (f.5) caudal elements.

Coloration in life. The C.N.B.S. field notes on this species are extensive and cover a number of different sexual and emotional states. Overall coloration of *adult males* shows considerable variation both in intensity and in the extent of any one pigment, and is apparently correlated with the emotional state of the fish. However,

the predominance of pink and red in fin coloration, irrespective of these factors, is an obvious feature, as is the amount of red on the flanks in sexually active individuals.

Quiescent males are light blue-grey above the lateral line; the flanks are orange-buff shading to light green on the ventral body surface and the lower half of the caudal peduncle. Traces of five indigo bars are visible on the mid-flank region but do not extend to the body outline. Dorsal surface of the head dark olive to reddish, cheeks and operculum greenish-yellow, sometimes with faint red blotches at the angles of the preoperculum and operculum. Lachrymal, trans-snout and nuchal stripes (see notes on preserved colours) are sometimes visible but only faintly so. Dorsal fin with a pink flush on the spinous part (lappets black), the soft part hyaline with red spots and streaks between the rays, and a narrow basal band of orange-yellow. Caudal fin grey-green, sometimes with pinkish-red streaks between the rays. Anal faintly grey, becoming sooty in the region of the spines and with a very faint pink flush over the soft part, becoming more intense at the distal margin of the anterior part of the fin; ocelli orange red. Pelvic fins dusky.

Sexually active males. Dorsal body surface intense ultramarine to purple with a faint sooty overlay especially along the base of the dorsal fin and over the nuchal region; ventral part of body, from just before the vent to the posterior tip of the caudal peduncle, dark greenish-indigo. Belly, chest and flanks below the level of the lower lateral line crimson, the belly scales with or without a narrow black margin; lower jaw and ventral surface of the head light blue to greenish-blue. Faint traces of transverse bars are sometimes visible on the mid-flank region of the body. The intensity and extent of the red flank and belly colours vary with the emotional state and may be restricted to a small triangular area on the chest extending thence dorsally to a level at about the midpoint of the operculum. The dorsal head surface is always ruddy although the intensity and the area involved are variable; however, the snout and cheeks are invariably reddish. A lachrymal stripe of variable intensity and width is always visible. Dorsal fin is pink to crimson, the colour most intense between the rays; lappets sooty. Caudal fin pink to dusky pink, the colour most concentrated proximally; posterior angles sometimes scarlet with a faint sooty overlay. Anal pink, the margins of the spinous part with a sooty overlay; ocelli orange yellow. Pelvic fins dusky with, usually, a faint pink flush.

Female coloration is also variable. Basically, the body is olive-yellow, darkest dorsally (even becoming grey-blue) and on the cheeks, lightest ventrally on the belly and jaws (almost peach-colour), the flanks sometimes with a pinkish glow. Faint traces of vertical bars are often visible on the flanks and caudal peduncle, the bars usually dark olive green and extending to the dorsal outline of the body.

In excited fishes the colours darken so that the back, dorsal head surface and the vertical flank marks appear very dark olive whilst the flanks and belly become an olivaceous yellow-green; in this condition a dark lachrymal stripe develops. Dorsal fin pale olive yellow with a faint pink flush most concentrated between the spinous and anterior branched rays. In excited individuals the pink colour darkens to scarlet and appears as blotches between the anterior soft rays. Caudal olive-yellow,

darker (olive-green to sooty) proximally. Anal buff, sometimes with a faint sooty overlay in the region of the spines; spots (in the position of the ocelli in males) orange. Pelvic fins buff, the anterior half sometimes orange.

Coloration in preserved specimens. *Adult males (sexually active)* light brown, the chest, branchiostegal membrane, lower half to three-quarters of the caudal peduncle and the entire belly sooty, the latter with a silvery overlay. A broad, nearly vertical lachrymal stripe runs from the angle of the jaws to the orbit; the snout is crossed by two transverse bars and there is a medially interrupted nuchal band running upwards from the posterior margin of the orbit. The flanks are crossed by six or seven dark bars, each broadest at its midpoint and narrowing more markedly dorsally than ventrally where it merges with the dark ventral body coloration. All fins (except the pelvics) are hyaline; the lappets of the spinous dorsal are dark, as is the base of the caudal; along the base of the anal fin there is a faint, sooty crescent and near its posterior tip two or three large, circular, greyish ocelli. The pelvics are black.

Sexually quiescent adult males have a similar coloration except that the pearly-silver overlay on the belly is brighter and the lower part of the caudal peduncle is brownish rather than black. The lachrymal, nuchal and cheek stripes are as in active fishes as are the vertical flank bars except that some of the latter extend to the base of the dorsal fin; none extends to the ventral body outline. The fins are as described above but the base of the anal and caudal may be hyaline and the posterior margin of the pelvics light sooty.

Females are grey-brown above, shading to silvery white on the belly and ventral flanks. The lachrymal bar is short (not extending to the jaw angle), the nuchal stripe and snout bars very indistinct or absent. There are five or six faint vertical bars on the flanks, each bar reaching the base of the dorsal fin but not the ventral body outline. All fins are hyaline, the lappets of the spinous dorsal dark.

Ecology. Habitat. *Haplochromis annectidens* is an inshore species occurring mainly in the vicinity of or amongst the marginal vegetation, and only rarely over exposed sandy beaches away from rooted plants; apparently it does not penetrate deeply into the marginal swamps and is rarely recorded at the swamp ends of inlets.

Food. Data on the food of *H. annectidens* were obtained principally from fourteen preserved specimens which I examined; these observations were supplemented by notes made on four specimens by the C.N.B.S. Despite the small size of these samples the variety of organic material found in the stomach and intestines is high, suggesting that the feeding habits of the species are also varied. Perhaps the commonest gut content is a barely recognisable mush of plant debris, both algal and phanerogamic, with blue-green algae predominating. Such material often forms the flocculent "mud" which covers the bottom in inshore regions of the lake; this leads one to conclude that many fishes had fed from the bottom. This supposition gains support from the presence of dipteran larvae in the stomach contents of the same individuals. Less frequently, the guts contain fragments of plant epidermis (and sometimes the bladders of *Utricularia*) together with large quantities of epiphytic algae, especially diatoms and filamentous green algae (e.g. *Oedogonium*).

These remains suggest that the fishes had been grazing epiphytic algae off submerged plants. Sand grains and fragmentary insect remains also occur in gut contents of this type; it is impossible to tell whether the sand grains were derived from the bottom or whether they were derived from the broken-down cases of Trichoptera larvae. Likewise it is difficult to suggest the provenance of the insect larvae.

As far as could be told from the preserved guts there is little digestion of the phanerogamic material, the blue-green algae or the filamentous green algae; diatom frustules, by contrast, were always empty.

In one specimen the stomach was packed with sand grains but it also contained two larval fishes. Since the larvae were small and not Cichlidae they should, presumably, be listed amongst the food organisms of this species.

Haplochromis annectidens has the long gut ($2\frac{1}{2}$ – $2\frac{3}{4}$ times the standard length) and the dentition of a herbivore. It was somewhat surprising, therefore, to find such ill-defined feeding habits. However, it may be recalled that the similar species *H. lividus* and *H. obliquidens* of Lake Victoria are also somewhat facultative in their feeding habits, although in these species there is a predominance of algal grazing over other feeding methods (Greenwood, 1956).

Breeding. One female with embryos in the mouth is recorded by the C.N.B.S. (June 1962); this specimen was not amongst those brought back to the Museum. The sex of the smallest specimen available (43 mm. S.L.) could not be determined, but a male 44.5 mm. S.L. is sexually active although another of 46 mm. is juvenile; the smallest female (50 mm. S.L.) is of undeterminable state but is probably maturing. The largest fishes examined (both 67 mm. S.L.) are of opposite sexes.

Distribution. Known only from Lake Nabugabo.

Affinities and diagnosis. The slender, obliquely cuspidate teeth of *H. annectidens* place it in the well-defined group of East African *Haplochromis* comprising the following species: *H. obliquidens* and *H. lividus* (Lake Victoria) and *H. astatodon* (Lake Kivu). Apart from their peculiar teeth and their long guts, these species have a generalized anatomy. Each differs from the others in a number of characters, including dental morphology. From *H. obliquidens*, with its invariably unicuspid anterior and anterolateral teeth, *H. annectidens* is distinguished by having bicuspid teeth in these positions, and in having teeth which are stouter and with somewhat differently shaped crowns (see fig. 7*d*); the interorbital is narrower in *H. annectidens* (21.0–29.2, $M = 25.2\%$, cf. 27.8–34.7, $M = 31.8$ in *H. obliquidens*) and the cheek shallower (12.5–21.7, $M = 18.1\%$ of head, cf. 19.0–25.0, $M = 21.5$). Although the range for the lateral line scale count is identical in both species, the modal number for *H. annectidens* (32) is higher than in *H. obliquidens* (31).

The teeth in *H. lividus* are bicuspid, but crown form serves to distinguish them from those of *H. annectidens*; indeed, the condition in the latter species is almost perfectly intermediate between *H. lividus* and *H. obliquidens* (see fig. 7*c*). *Haplochromis annectidens* and *H. lividus* also differ in certain morphometric characters; the interorbital of *H. lividus* is broader (26.2–33.3, $M = 29.7\%$ of head, cf. 21.0–29.2, $M = 25.2$), the cheek is slightly deeper (17.0–24.1, $M = 20.1\%$ of head) and the range of lateral line scale counts extends to 34, although the modal

number is identical in both species (32). The most pronounced difference lies in the coloration of adult males. *Haplochromis lividus* is probably unique within the genus (and certainly is unique amongst the *Haplochromis* of Lakes Victoria and Nabugabo) for the intense, almost fluorescent blue colour of the head and snout of adult males. This coloration contrasts strongly with the ruddy head tones of *H. annectidens*. (Male coloration also seems to distinguish *H. obliquidens* and *H. annectidens*; cf. p. 332 above with p. 229 of Greenwood, 1956).

The dental morphology of *H. annectidens* is very similar to that of *H. astatodon* from Lake Kivu, but there are fewer inner tooth rows in *H. annectidens*. The species also differ in head shape, the gently sloping head profile of *H. annectidens* contrasting with the declivous snout and rounded upper profile of *H. astatodon*; also, in *H. annectidens* the interorbital is markedly smaller than the eye, but in *H. astatodon* of a comparable size the two measurements are equal or the interorbital width is slightly greater.

Trewavas (1933) mentions *H. plagiodon* (a Lake Victoria species) when discussing the affinities of *H. annectidens*, but notes that the teeth of the former are "much larger and fewer", a description with which I concur (see Greenwood, 1959b). However, in the introduction to her paper, Trewavas suggests that *H. annectidens* "represents the stock from which *H. obliquidens* and *H. plagiodon* of Lake Victoria seem to have diverged in separate directions". Certainly, *H. annectidens* represents a dental and anatomical grade which could be ancestral to that of *H. obliquidens* but the level of its dental specialization is higher than that likely to be ancestral to the peculiar teeth found in *H. plagiodon* (see Greenwood, 1959b). Rather, I would support Trewavas' idea (1933, p. 324) that *H. plagiodon* evolved from a stock resembling *H. velifer* in its dental morphology. The anatomical status of *H. velifer* is that of a generalized *Haplochromis* but it does differ from many of the other generalized species in having somewhat obliquely cuspidate teeth. The *H. plagiodon*-type of tooth represents but a slight modification of the *H. velifer*-type, the *H. lividus-annectidens-obliquidens* types are much more extreme developments involving both the neck and the crown of the tooth.

STUDY MATERIAL

<i>B.M. (N.H.) reg. no.</i>	<i>Collector</i>
1933.2.23.210 (Holotype)	Worthington
1933.2.23.211-220 (Paratypes)	Worthington
1935.8.23.III-II3	Pitman
1964.7.1.41-79	C.N.B.S.

Haplochromis beadlei Trewavas, 1933

(Text fig. 8)

H. beadlei Trewavas, 1933, *J. Linn. Soc. (Zool.)*, **38** : 324.

HOLOTYPE: An adult male 106.0 mm. S.L., from Lake Nabugabo (E. B. Worthington collection), B.M. (N.H.) reg. no. 1933.2.23.221.

Although *H. beadlei* is easily distinguishable from other species of *Haplochromis* in Lake Nabugabo, its systematic status is uncertain. It closely resembles *H. labiatus* of Lake Edward and *H. crassilabris* of Lake Victoria; neither of these species is sufficiently well-known to allow for a full assessment of the characters by which *H. beadlei* differs from them. As is usual amongst related *Haplochromis* species there is no single trenchant diagnostic character; since various combinations of characters (differing for large and for small specimens) seem to distinguish *H. beadlei*, it is retained as a distinct species pending a full revision of *H. crassilabris* and *H. labiatus*, especially the latter.

DESCRIPTION based on the holotype, nine paratypes and thirteen additional specimens, 72–118 mm. standard length.

Depth of body 36.0–40.3 ($M = 38.1$) per cent of standard length, length of head 31.4–35.8 ($M = 33.8$) per cent. Dorsal head profile straight or faintly concave, sloping at about 35° – 40° with the horizontal; snout straight, not decurved.

Preorbital depth 14.8–18.0 ($M = 15.9$) per cent of head length, least interorbital width 23.2–28.0 ($M = 25.0$), snout length 29.6–36.0 ($M = 31.7$) per cent, snout slightly broader than long or, rarely, as long as broad. Eye diameter 25.0–32.0 ($M = 27.8$) per cent of head, depth of cheek 17.8–25.6 ($M = 22.1$) per cent.

Caudal peduncle 13.4–17.0 ($M = 15.2$) per cent of standard length, 1.1–1.6 (modal range 1.2–1.4) times as long as deep.

Mouth horizontal, both lips markedly thickened, usually to a comparable degree or with the upper lip slightly thicker; in one specimen there is an incipient median lobe developed on the upper lip. Jaws equal anteriorly in most specimens but in a few fishes >85 mm. S.L. the lower jaw projects slightly so that the upper teeth

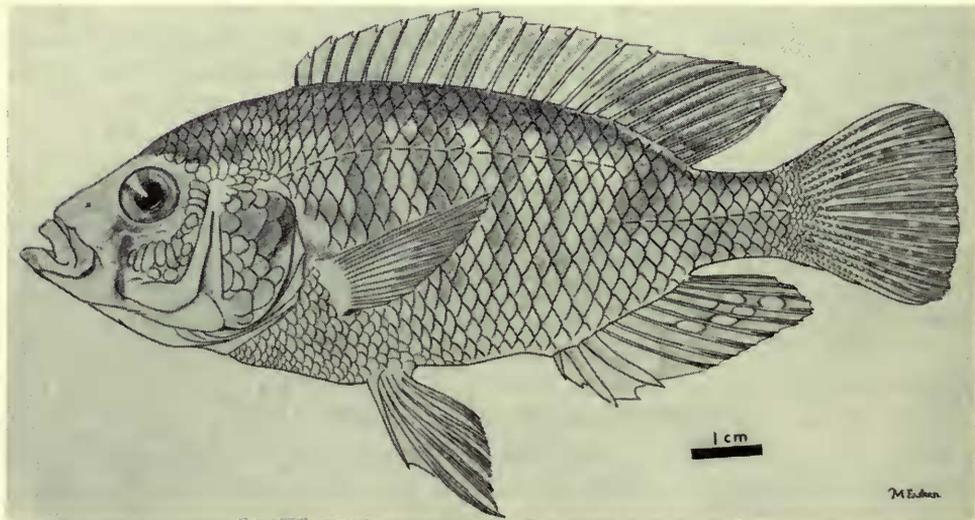


FIG. 8. *Haplochromis beadlei*. Drawn by Miss M. Fasken.

occlude behind the lower. Lower jaw 34.5–39.6 ($M = 36.9$) per cent of head, 1.3–1.7 (mode 1.4) times as long as broad. Posterior tip of the maxilla somewhat bullate, reaching the vertical through the anterior orbital margin in most specimens but not quite reaching this point in others (33% of the sample examined), rarely extending to below the anterior part of the eye.

Gillrakers variable (except for the lowermost one to three), from moderately slender to moderately stout, but of constant form in any one individual; 7 (f.3), 8 (f.16) or 9 (f.4) on the lower part of the first gill arch, the lowermost one to three rakers reduced.

Scales ctenoid; lateral line with 30 (f.3), 31 (f.14) or 32 (f.5) scales; cheek with 2 (f.4), 3 (f.18) or 4 (f.1) rows; 5–7 (modes 6 or 7) scales between the dorsal fin origin and the upper lateral line, 5–7 (mode 6) between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.11), 25 (f.11) or 26 (f.1) rays, comprising 15 (f.15) or 16 (f.8) spinous and 8 (f.1), 9 (f.16) or 10 (f.6) branched rays; anal with 10 (f.1), 11 (f.4) or 12 (f.18) rays comprising 3 spines and 7 (f.1), 8 (f.4) or 9 (f.18) branched rays. Caudal subtruncate, scaled on its basal half. First two rays of the pelvic fin barely produced in females but greatly elongate in males. Pectoral 23.3–28.0 ($M = 26.0$) per cent of standard length.

Teeth. The nature of the dentition changes with the size of the individual but is always characterized by the teeth being stout and slightly curved, with the anterior teeth somewhat procumbent (those of the upper jaw most obviously so). The outer, upper teeth are all bicuspid in most fishes < 85 mm. S.L. (and in all individuals < 75 mm.), those situated anteriorly have subcylindrical crowns but those laterally and posteriorly are more flattened. The anterior and anterolateral teeth in most specimens > 85 mm. S.L. are cylindrical in section and are unicuspid or with a poorly developed minor cusp; the crown, especially in unicuspid, is slightly recurved. In exceptional individuals over 85 mm. S.L. (the holotype is one of these) the entire upper outer row is composed of distinctly bicuspid teeth.

The outer row of the lower jaw is, in general, like that of the upper except that the anterior teeth are less procumbent and are often implanted vertically; variations in tooth form follow the same size-correlated trends described above.

There are 24–32 ($M = 28$) teeth in the outer row of the upper jaw.

Teeth of the inner series are tricuspid and small, and are arranged in 2 or 3 (mode) rows in each jaw. In one exceptional specimen, some of the teeth in the outermost inner row of the lower jaw are enlarged and weakly tricuspid.

The shape of the dental arcade in all specimens is a broadly rounded U.

Lower pharyngeal bone moderately slender, the triangular dentigerous surface slightly broader than long. The lower pharyngeal teeth are compressed, cuspidate and slender, and are arranged in 22–26 rows. In fishes over 80 mm. S.L. the two median rows are composed of coarser and weakly cuspidate teeth. Some of the posterior teeth in neighbouring rows are also enlarged and form a small, roughly triangular zone of enlarged teeth at the posterior end of the median tooth rows; the degree of enlargement undergone by these teeth is positively correlated with the size of the individual.

Vertebrae 28 or 29, comprising 13 abdominal and 15 (f.5) or 16 (f.6) caudal elements.

Coloration in life. Sexually active male. The dorsal surface of the body is greeny-blue (rather more green than blue), the head darkest; flanks lighter, the ventral surface of the chest sooty but the lateral aspects with a red flush. Dorsal fin sooty along its base and over the whole spinous part, the soft part being pink. Anal pink, with a sooty overlay which becomes intensely black over the spinous part; ocelli orange-yellow. Pelvic fins uniformly sooty.

Females are bright olive-green, the flank scales with turquoise margins; belly blueish-green, chest golden olive to silvery white. Dorsal surface of the head dark amber, cheek with golden lights. Dorsal fin pale olive, with a sooty overlay. Anal clear olive-yellow, spots (when present occupying the place of ocelli in males) bright yellow. Caudal fin light olive with dark red maculae between the rays. Pelvics olive with a sooty overlay, the first two rays dead white.

N.B. These colour notes are based on many fewer fishes than are those for the other species; only one sexually active male is described in the C.N.B.S. field-notes.

Coloration of preserved specimens. Adult males (sexually active) are dark brown, almost black, with a pearly sheen on the belly. Lower jaw and branchiostegal membrane are greyish, the cheeks brownish and the operculum dark with a pearly overlay. The snout and dorsal aspect of the head is blackish; there is a distinct lachrymal stripe but no trace of a nuchal band; an ill-defined, blotchy stripe runs along the opercular-preopercular junction. The flanks are crossed by six vertical bars which merge dorsally and ventrally with the dark ground colour of the body. The base of the caudal fin is black, the remainder of the fin becoming progressively lighter towards its posterior margin. The entire spinous dorsal and the basal quarter of the soft dorsal are black to sooty, the remainder of the soft part darkly maculate. Anal fin hyaline, with five large, grey ocelli each outlined by a dark ring. Pelvics with anterior third black, remainder whiteish, the demarcation not well defined.

Sexually quiescent males are brownish, shading to dusky silver on the belly. Lower jaw and branchiostegal membrane are silvery white. A broad, dark lachrymal stripe originates slightly ventral to the jaw angle and continues to the anterior orbital margin; this stripe extends through the eye to form a transverse nuchal band. A weaker, posterior nuchal band is also present and originates at the junction of the operculum and body. The flanks are crossed by six, moderately broad vertical bars which extend to the base of the dorsal fin but do not reach the ventral body outline. The greater part of the dorsal fin is dusky, the soft part weakly maculate. The base of the caudal fin is dark, the rest hyaline. The anal is hyaline with three oval, dead-white ocelli. The pelvics are black on the anterior third, whiteish posteriorly, the demarcation being clear cut.

Females are light brown, becoming silvery white on the belly and ventral aspects of the flanks. The lachrymal stripe is very faint as are the nine, ventrally incomplete vertical bars on the flanks and caudal peduncle; dorsally these bars merge with the base of the dorsal fin, the latter being hyaline with a slight darkening between the posterior spines and between all the soft rays. The distal part of the soft dorsal is

often darkly maculate. Caudal fin hyaline with dark maculae; anal hyaline, with three to six small, dead-white ocelli often arranged in two rows. Pelvic fins also hyaline.

Ecology. Habitat. This species is apparently confined to shallow, inshore regions of the main lake and the lakeward ends of inlets to the marginal swamps. The substrate in these places varies, and includes sand, sand with a mud-detritus overlay and deep mud.

Food. The gut contents of eight specimens containing ingested material were examined. All except one contained fragments of insect larvae (chironomid and trichopteran); in one of these fishes the gut yielded numbers of undamaged cases of Trichoptera larvae but in all the others containing identifiable trichopteran remains, no trace of the cases was found. Fragments of undigested plant epidermis were recorded in two specimens. The exceptional fish noted before contained a large amount of unidentifiable sludge.

Breeding. No data are available on the breeding habits of *H. beadlei*. One specimen (a male paratype, 77 mm. S.L.) has cichlid embryos and larvae in its mouth. Because these are at such disparate stages of development it seems unlikely that they represent a brood; rather, I suspect that the adult had snatched at young jettisoned by parents as they were captured, a not uncommon phenomenon (personal observations on the behaviour of netted *Haplochromis* in Lake Victoria).

With one exception, all the specimens examined are obviously adult; the exceptional fish, a female 72 mm. S.L., may be a juvenile or it could be a spent and quiescent adult. There is no sexual dimorphism in the size attained by fishes in this sample.

Distribution. Known only from Lake Nabugabo.

Affinities and diagnosis. The peculiar oral dentition, heavy lips and general morphology of *H. beadlei* indicate a strong affinity with *H. paucidens* (Lake Kivu), *H. crassilabris* (Lake Victoria) and *H. labiatus* (Lake Edward). Unfortunately none of these species is well-known morphologically or ecologically despite, in the case of *H. crassilabris*, intense field studies on the Lake Victoria *Haplochromis*.

The description of *H. labiatus* is based on three specimens of rather disparate sizes (60, 74 and 107 mm. S.L.); no information is available on live colours or ecology. The present concept of *H. crassilabris* stems from twelve specimens and does not agree entirely with that published by Regan (1922); my revision of *H. crassilabris* is still unpublished but will be used here as the basis for comparison with *H. beadlei*. Comparative data for *H. paucidens* were obtained from four specimens in the British Museum (N.H.).

Haplochromis beadlei differs from *H. crassilabris* in the following characters:

(i) In fishes of a comparable size, *H. beadlei* has a relatively smaller proportion of unicuspid to bicuspid outer teeth, and the teeth are more compressed and less cylindrical in cross-section (especially through the neck); also, in *H. crassilabris* some unicuspid teeth appear anteriorly in smaller specimens.

(ii) There are more teeth in the outer row of the upper jaw (24-32, $M = 28$ cf. 20-30, $M = 24$ for *H. crassilabris*).

(iii) The height of the teeth in the upper jaw of *H. beadlei* is gently graded postero-anteriorly but in *H. crassilabris* the anterior teeth are markedly larger than the lateral ones.

(iv) The lower jaw in *H. beadlei* is somewhat longer (34.5–39.6, $M = 36.9\%$ of head, cf. 31.0–34.0, $M = 32.4$ in *H. crassilabris*).

(v) In *H. beadlei* the female has well-defined spots on the anal fin, corresponding in position with the ocelli of males; no spots are developed in *H. crassilabris*.

The orodontal characters of *H. beadlei* appear less specialized than those of *H. crassilabris*. However, it is difficult to determine whether the “*beadlei*” condition represents an evolutionary stage intermediate between the generalized *Haplochromis* condition and the “*crassilabris*” level, or whether it is a slightly regressive development from a species which had already achieved the “*crassilabris*” stage. The possibility of such regressive changes must be given serious consideration because this phenomenon has been demonstrated in the cichlid *Astatoreochromis* (Greenwood, 1965). An aquarium bred specimen of *A. alluaudi*, derived from a typical Lake Victoria population, failed to develop the hypertrophied pharyngeal structures characteristic of its ancestors. The degree of hypertrophy shown by the aquarium fish resembled an intermediate stage in the development of this particular specialization. Thus, it seems possible that *H. beadlei* could have evolved from a “*crassilabris*”-like ancestor if environmental conditions in Lake Nabugabo were such that selection pressure did not demand the full expression of the specialized “*crassilabris*” dentition.

From *H. labiatus*, *H. beadlei* is distinguished by the following:

(i) The large specimen of *H. labiatus* (107 mm. S.L.) has its lower jaw shorter than the upper; in *H. beadlei* of a comparable size the jaws are equal anteriorly or the lower projects slightly.

(ii) At all sizes the eye is about equal to the interorbital width in *H. beadlei* but in *H. labiatus* the eye is distinctly larger.

(iii) In small specimens of *H. labiatus* (60 and 74 mm. S.L.) the teeth are more compressed than those in comparable sized *H. beadlei*; in larger specimens the teeth are identical.

(iv) The upper dental arcade in the large *H. labiatus* is more acutely rounded than in *H. beadlei* but the arcade in small specimens is identical.

(v) The dorsal head profile of small *H. labiatus* is more rounded than in *H. beadlei*, and the snout is more declivous (ca 60° cf. 35°–40° for *H. beadlei*); in larger fishes these differences are less marked but the profile still slopes more steeply in *H. labiatus*.

Haplochromis paucidens of Lake Kivu is very similar to *H. crassilabris* in gross morphology and dental characters. Thus, it may be distinguished from *H. beadlei* by the same characters (see above); from the few specimens available, the teeth appear to be finer than those of *H. crassilabris* and therefore stand in even greater contrast with those of *H. beadlei*.

The lower pharyngeal bone and its dentition is identical in all three species.

Live coloration is unknown for *H. labiatus* and the only record for *H. crassilabris* is from a 35 mm. colour-transparency (kindly lent to me by N. Mitton of Nairobi).

As far as I can determine, there is a general similarity between the coloration of *H. crassilabris* and *H. beadlei*.

Two other species from Lake Victoria, *H. chromogynos* and *H. chilotes*, should be considered since both species have thickened lips and a dentition obviously related to that of *H. beadlei*. Of the two, *H. chromogynos* has the greater similarity to *H. beadlei*. It is distinguished from the latter species by its fewer teeth, shorter lower jaw (30.0–34.4, $M = 32.5\%$ of head) and the fact that all females have a piebald black and silver coloration (Greenwood, 1959b). *Haplochromis chilotes* represents a more extreme development of *H. chromogynos*, particularly with regard to the hypertrophy of the lips; most specimens have both lips drawn out medially to form large lobes, although in others there is only an incipient lobation and in a few the lips are little more developed than in *H. beadlei*. (It will be recalled that one specimen of *H. beadlei* has an incipient lobe developed from the upper lip.) Several morphometric characters of *H. chilotes* are correlated with the degree of lip hypertrophy, but even specimens with poorly-developed lips may be distinguished from *H. beadlei* by having a more acute dental arcade, finer teeth and a shorter lower jaw (30.0–36.6, $M = 33.2$ cf. 34.5–39.6, $M = 36.9\%$ of head, in *H. beadlei*). On the other hand, the lower jaw of *H. chilotes* with lobed lips is slightly longer than in *H. beadlei* (36.0–49.0, $M = 39.6\%$ head). Finally, there are distinctive differences in the live colours of adult males (cf. p. 338 above with p. 209, Greenwood, 1959b).

As Trewavas (1933) noted, the morphological affinities between *H. beadlei*, *H. crassilabris*, *H. paucidens* and *H. labiatus* are strong; to this complex may now be added *H. chromogynos* which, in turn, bridges the morphological gap between this complex and the more extreme *H. chilotes*. This species complex will be discussed again; for the moment it is only necessary to point out that *H. beadlei* does seem most closely related to *H. labiatus* of Lake Edward and not, as might be expected, to *H. crassilabris* of Lake Victoria. As a corollary to this paradox, the known specimens of *H. paucidens* (Kivu) seem closer to *H. crassilabris* than to the geographically near *H. labiatus* of Lake Edward.

Trewavas (*op. cit.*) also suggested that *H. beadlei* is closely related to *H. sawagei* of Lake Victoria, a species which, on Regan's revision of the Victoria species, is related to *H. crassilabris*. However, recent studies (Greenwood, 1957) show that *H. sawagei* belongs to a different lineage and one not closely related to *H. crassilabris*. The jaw structure, skull architecture and dental characters of the *H. sawagei* line are distinctive and are not even foreshadowed in the *H. crassilabris*-*H. beadlei* species group.

STUDY MATERIAL.

<i>B.M. (N.H.) reg. no.</i>	<i>Collector</i>
1933.2.23.221 (Holotype)	Worthington
1933.2.23.222–230 (Paratypes)	Worthington
1933.2.23.231–3	Worthington
1935.8.23.114–134	Pitman
1964.7.1.1–11	C.N.B.S.

Haplochromis venator sp. nov.

(Text fig. 9)

H. pellegrini: (non Regan) Trewavas, 1933, *J. Linn. Soc. Lond. (Zool.)*, **38** : 326.

Trewavas (1933) identified seven specimens of a predatory *Haplochromis* from Lake Nabugabo as *H. pellegrini* Regan on the basis of a comparison with the two syntypes of *H. pellegrini*. Since 1933 many more specimens of *H. pellegrini* have been obtained and a revised description of the species has been prepared (Greenwood, 1962). It is now clear that the Nabugabo fishes, although showing some affinity with *H. pellegrini*, should be recognised as a distinct species for which the name *venator* is proposed (*Venator*, Latin, a hunter).

HOLOTYPE: an adult female 158 mm. standard length (B.M. (N.H.) reg. no. 1933.2.23.240) collected by Dr. E. B. Worthington.

DESCRIPTION based on the holotype and twelve paratypes, 59–178 mm. S.L.

Depth of body 28.8–35.5 ($M = 32.9$) per cent of standard length, length of head 34.6–36.8 ($M = 35.5$) per cent; dorsal head profile straight or slightly concave (the depression increasing with size and accentuated by the prominent premaxillary pedicels), sloping at 30°–35° to the horizontal.

Preorbital depth 16.3–21.0 ($M = 18.9$) per cent of head length, least interorbital width 16.8–21.8 ($M = 19.0$), snout longer than broad, its length 33.6–38.5 ($M = 35.3$) per cent, probably showing slight positive allometry with standard length. Eye diameter 21.9–28.6 ($M = 24.1$) per cent of head, showing very slight negative allometry; cheek 19.0 (in the smallest specimen) –28.2 ($M = 25.6$) per cent and showing very slight positive allometry.

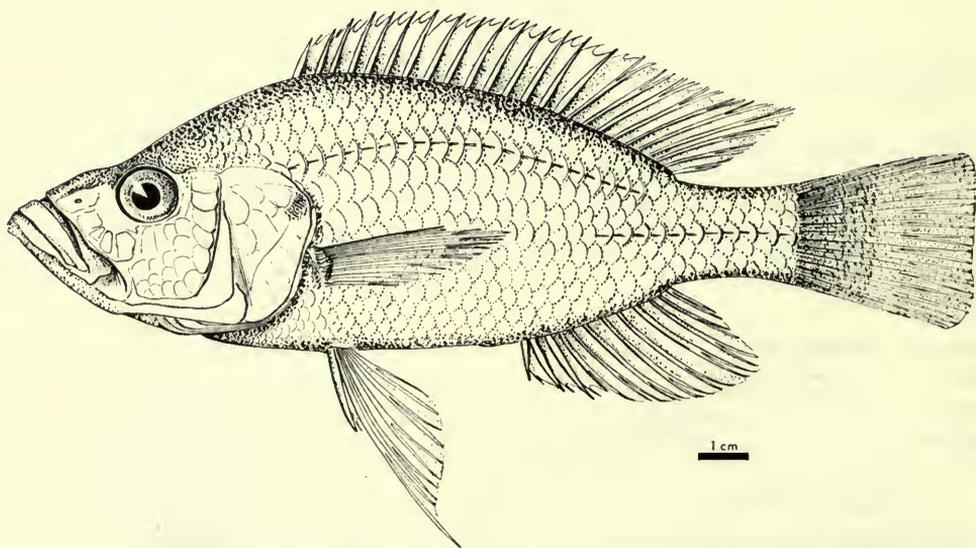


FIG. 9. *Haplochromis venator*. Drawn by Barbara Williams.

Caudal peduncle 14.3–17.5 ($M = 15.8$) per cent of standard length, 1.2–1.6 (modal range 1.3–1.4) times as long as deep.

Mouth oblique, sloping upwards at about 30° – 35° , lips not thickened but the dentigerous surface of the premaxilla expanded antero-posteriorly in the midline. Jaws either equal anteriorly or the lower projecting slightly (both conditions equally common), its length 47.6–54.0 ($M = 50.6$) per cent of head length, 2.1–2.5 (mode 2.3) times as long as broad. Posterior tip of the maxilla usually not reaching the vertical through the anterior orbital margin (but nearer this point than to a vertical through the nostril), sometimes reaching that point.

Gillrakers moderately stout, the upper three or four usually flattened and anvil-shaped, the lower one to three reduced; 8–10 (mode 9) on the lower limb of the first gill arch.

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

Fins. Dorsal with 24 (f.5), 25 (f.7) or 26 (f.1) rays, comprising 14 (f.3), 15 (f.8) or 16 (f.2) spinous and 9 (f.3) or 10 (f.10) branched rays. Anal with 12 (f.9) or 13 (f.4) rays, comprising 3 spines and 9 (f.9) or 10 (f.4) branched rays. Pectoral 23.7–27.5 ($M = 26.0$) per cent of standard length. Caudal subtruncate, the posteroventral corner often obliquely truncate. Pelvics with the first ray produced in both sexes.

Teeth. Throughout the size-range examined, the outer row of teeth in both jaws is composed of slender unicuspid, those situated anteriorly and laterally being slightly recurved, whilst those posterolaterally are more strongly curved and are directed medially. There are 46–64 ($M = 53$) teeth in the outer row of the upper jaw in fishes 59–128 mm. S.L. ($N = 6$) and 52–80 ($M = 63$) in larger individuals ($N = 7$).

The inner rows are composed of small, unicuspid teeth in fishes > 110 mm. S.L., and of small tricuspid, weakly tricuspid and, predominantly, unicuspid teeth in individuals 59–107 mm. S.L.; the inner teeth are implanted obliquely so that their crowns may come to lie almost horizontally. Inner teeth are arranged in 2 or 3 rows in the upper jaw and 1 or 2 rows in the lower.

Lower pharyngeal bone triangular, the length of the dentigerous surface equal to its breadth or, rarely, slightly longer. The pharyngeal teeth are slender, compressed and weakly cuspidate (some almost caniniform in the median rows of larger fishes) and are arranged in 20–22 rows.

Neurocranium. The neurocranium of *H. venator* closely resembles that of *H. longirostris* and *H. mento*, being intermediate between the two (see Greenwood, 1962); in other words, it has a skull type characteristic of the group of moderately specialized predatory *Haplochromis* in Lake Victoria.

Vertebrae: 29, comprising 13 (f.4) or 12 (f.1) abdominal and 16 (f.4) or 17 (f.1) caudal elements.

Coloration in life. *Adult males* are bright blueish-green dorsally, shading to silvery on the lower flanks and on the ventral surfaces; operculum and cheek with

a pinkish flush. Dorsal fin smokey-grey with a dull red blotch basally at the junction between the spinous and soft parts. Caudal fin sooty grey, the rays darker. Anal sooty at the base of the soft part, the remainder of the fin neutral; ocelli light vermilion-orange surrounded by a narrow white ring, each ocellus set on a transparent area of membrane. Pelvics sooty, darker along the anterior edge.

Adult females have a similar coloration to that of males but the body is a darker, more olivaceous green and the anal fin is olive with a faint salmon-pink flush over the spinous part; as many as five pale red spots occupy the position of the ocelli in males.

Preserved colours. Adult male (sexually active): dusky brown except on the belly and chest, which are silver with the scales outlined in black. Dorsal surface of snout dark as are the anterior and anterolateral aspects of the lips, and the branchiostegal membrane; an ill-defined, dark lachrymal blotch is present, and there are very faint traces of six dark, vertical bars on the flank and caudal peduncle. Dorsal fin grey, with black lappets and a narrow black basal stripe along the origin of the branched rays and the last few spines; the membrane between the soft rays is dark except for a narrow, whiteish band immediately above the dark basal one. Anal fin with a black basal band which is capped by a narrower, dead-white band; the ocelli are very faint. Caudal fin greyish to sooty. Pelvics sooty, darkest along the anterior quarter.

Females: greyish-brown to silvery brown (depending on fixative used, the former for formol, the latter for alcohol), shading to silvery white on chest and belly. Snout, lips and dorsal head surface dark grey or brown. A broad mid-lateral band visible on the flanks in formol fixed specimens only; the band is faint and appears interrupted at about its mid-point.

All fins are hyaline, the anal with faint spots in the position of the ocelli in males; the membrane between the caudal rays is maculate, the spots darkest proximally.

Ecology. Habitat. *Haplochromis venator* is widely distributed in the lake but appears to be more abundant in open, off-shore areas than in other regions. It has been caught in surface gill-nets set in the middle of the lake over a deep mud bottom (water depth 10 ft.) but is not recorded from bottom nets in the same places, nor from the inlets to swampy areas. Specimens caught in beach operated seines are smaller (30–90 mm. S.L.) than those caught off-shore but this may be a reflection of the type of gear used in the two places.

Food. In addition to data from the C.N.B.S. field-notes, I have examined seven preserved specimens. From these records it is clear that *H. venator* is predominantly a piscivorous predator, although insects (especially adult Ephemeroptera) are also eaten. Only two specimens of the fourteen for which detailed gut analyses are available contained other ingested material, in both cases a few fragments of plant tissue. *Haplochromis* (of ca 20–40 mm. total length) and small *Barbus* species seem to be the commonest prey species but in some cases the fish remains were too fragmentary to allow for further identification. One fish (a juvenile 59 mm. S.L.) contained twelve larval cichlids of various sizes but all were within the size range at which larvae are carried by the parent; it is impossible to tell whether such small

individuals represent "normal" prey for *H. venator* or whether they were jettisoned young swallowed whilst the seine net was being brought to the shore.

Breeding. No data are available. The two smallest specimens (59 and 82 mm. S.L.) are juveniles; all others are adults (and predominantly females) in differing states of sexual activity.

Distribution. Known only from Lake Nabugabo.

Diagnosis and affinities. The resemblance between *H. venator* and *H. pellegrini* of Lake Victoria has been noted already (p. 342). Several small differences serve to distinguish the two species. In addition, *H. venator* reaches a much larger adult size than does *H. pellegrini* (178 mm. S.L. cf. 104 mm.); considering the ecological differences obtaining in the two lakes, this difference is difficult to evaluate. This size difference may underlie a number of the observed morphometric differences between the species. *Haplochromis venator* has a longer lower jaw than *H. pellegrini* (47.6–54.0, $M = 50.6\%$ of head, cf. 42.3–51.5, $M = 46.8$ in *H. pellegrini*), a longer pectoral fin (23.7–27.5, $M = 26.0\%$ of standard length, cf. 19.4–25.3, $M = 21.3$), and a slightly narrower head as measured by interorbital width (16.8–21.8, $M = 19.0\%$ of head, cf. 18.2–24.0, $M = 21.0$ in *H. pellegrini*). In dental morphology the species hardly differ except that unicuspid teeth occur in the inner rows of *H. venator* at all sizes. No inner unicuspid teeth are found in *H. pellegrini*, although in some specimens a few inner teeth may be only weakly tricuspid. The pharyngeal dentition is similar in both species.

A most marked difference is the coloration; live female *H. pellegrini* are a dark chocolate-brown (shading to light brown ventrally) and have greyish-black fins (see Greenwood, 1962). The body of *H. venator* females is olivaceous green shading to silver, the fins are olivaceous to sooty and the anal has a pink flush. Live colours of male *H. pellegrini* are unknown but the dark brown coloration of preserved specimens contrasts with the lighter colours of preserved male *H. venator*.

Neurocranial architecture differs in the two species, the neurocranium of *H. pellegrini* being of a rather distinctive type (see Greenwood, *op. cit.*), whereas that of *H. venator* is closely allied to the *H. mento* and *H. longirostris* types.

The overall morphology of *H. venator* is not closely similar to that of *H. longirostris* from which species it is distinguished by its deeper body, longer and less oblique lower jaw, medially expanded premaxilla and, most obviously, by its shorter and deeper caudal peduncle (14.3–17.5, $M = 15.8\%$ of standard length, length/depth ratio 1.2–1.6, modal range 1.3–1.4, cf. 17.2–22.2, $M = 19.2$, 1.9–2.0 modal range, for *H. longirostris*). There are also interspecific differences in dental morphology, especially the finer and more numerous outer teeth of *H. longirostris*.

Haplochromis mento is so obviously distinct from *H. venator* that no detailed comparison is required (see Greenwood, *op. cit.*).

Some resemblance exists between *H. venator* and the group of Lake Victoria *Haplochromis* comprising the "species" *H. macrodon*, *H. taeniatus* and *H. lamprogenys*. This group is under revision, hence the uncertainty as to the specific status of its members. *Haplochromis venator* differs in having more numerous teeth, a somewhat larger eye and narrower interorbital (eye diameter equals interorbital

width in the *H. macrodon* group but is larger than the interorbital in *H. venator* and a longer and more oblique jaw; there are also differences in preserved coloration. Looked at in relation to the morphological groupings of the Lake Victoria predatory *Haplochromis*, *H. venator* belongs to a more specialized grade than does the *H. macrodon* group.

STUDY MATERIAL

<i>B.M. (N.H.) reg. no.</i>	<i>Collector</i>
1933.2.23.240 (Holotype)	Worthington
1933.2.23.234-239 (Paratypes)	Worthington
1964.7.1.80-85 (Paratypes)	C.N.B.S.

Haplochromis nubilus (Blgr.) 1906

(Text fig. 10)

Tilapia nubila Blgr., 1906, *Ann. Mag. nat. Hist.*, (7), **17** : 450.

Haplochromis nubilus (part): Regan, 1922, *Proc. Zool. Soc.*, 164 (excluding *Paratilapia victoriana* Pellegrin, 1903, for which see Greenwood, 1962).

Haplochromis annectidens (part) Trewavas, 1933, *J. Linn. Soc. Lond. (Zool.)*, **38** : 323.

This synonymy is by no means definitive since a revision of the species is still incomplete; it is given here especially to include the two paratypical specimens of *H. annectidens* which are now identified as *H. nubilus*.

From the information I already have on this rather widely distributed east African species there are indications that the various geographical groups may be differentiable on certain anatomical and morphometric characters (see also Trewavas, 1933). Thus, a brief description and tabulation of these characters is given for the five specimens from Lake Nabugabo. The paratypes of *H. annectidens* are indicated with an asterisk.

S.L.	Depth†	Head†	Po.%	Io.%	Snt.%	Eye%	Cheek%	Lj.%	C.P.†
62.5*	39.2	33.6	14.3	28.6	28.0	28.6	23.8	38.1	14.4
65.0*	35.4	32.3	14.6	26.2	31.0	29.2	23.8	38.4	16.8
72.0	37.5	34.7	16.0	24.0	30.0	28.0	20.0	40.0	13.9
86.0	37.2	35.0	16.7	24.4	31.7	26.7	21.7	40.0	15.2
86.0	34.9	35.5	14.7	23.0	31.1	29.6	19.7	39.3	14.0

† = per cent of standard length.

% = per cent of head length.

Caudal peduncle 1.1-1.6 times as long as deep.

Dorsal head profile straight but usually with a marked concavity above the orbit.

Mouth horizontal or very slightly oblique, the lips somewhat thickened; posterior tip of the maxilla reaching the vertical through the anterior margin of the orbit. Jaws equal anteriorly, the lower 1.6–2.0 times as long as broad.

Gillrakers: 8 or 9 (7 in one specimen), relatively stout, on the lower part of the first gill arch, the lowermost 3 or 4 rakers reduced.

Scales ctenoid; lateral line with 31 (f.4) or 32 (f.1) scales, cheek with 3 rows; 6 scales between the dorsal fin origin and the upper lateral line, 5 (f.3) or 6 (f.2) between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.2) or 25 (f.3) rays, comprising 15 (f.3) or 16 (f.2) spinous and 9 (f.4) or 10 (f.1) branched rays. Anal with 12 (f.3) or 13 (f.2) rays comprising 3 spines and 9 (f.3) or 10 (f.2) branched rays. Pectoral 23.6–28.8 per cent of standard length. Caudal distinctly subtruncate or rounded. Pelvics with the first branched ray slightly produced in both sexes.

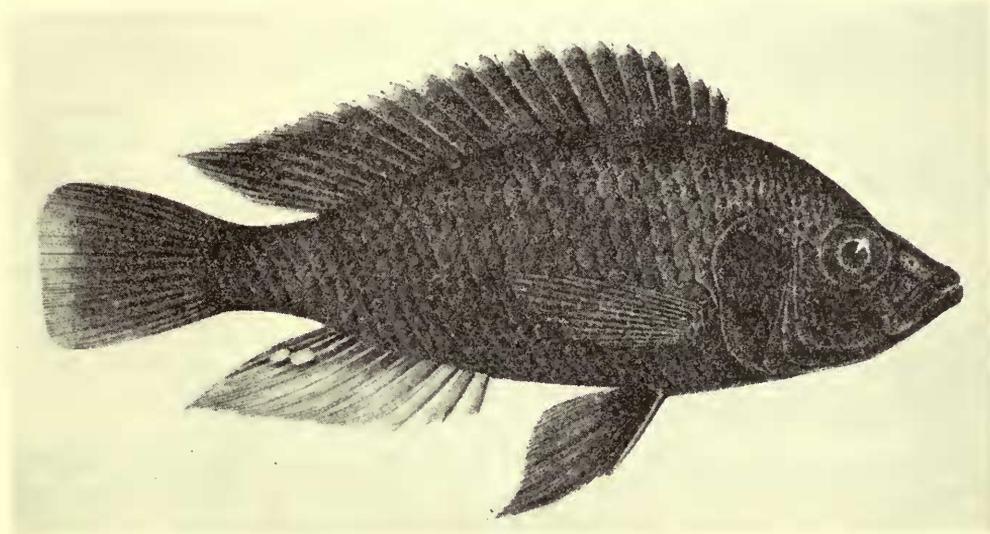


FIG. 10. *Haplochromis nubilus*. From Boulenger, *Fishes of the Nile*: a Lake Victoria specimen is depicted.

Teeth in the outer row of both jaws relatively stout, immovably implanted and unequally bicuspid; the major cusp slopes somewhat obliquely (*cf. H. velifer*). The posterior three or four teeth on either side of the upper jaw are stouter than the anterior teeth and are unicuspid. The number of upper, outer teeth in the five specimens is 40, 42 and 46 (f.3).

The inner rows in both jaws are composed of small tricuspid teeth arranged in 2, 3, 4 or 5 series in the upper jaw and 2 or 3 series in the lower jaw; with one exception, the inner series are separated from the outer row by a distinct interspace; in the exceptional specimen the gap is obscured by the irregular arrangement of the inner series.

Lower pharyngeal bone slender and triangular, its dentigerous surface broader than long. The pharyngeal teeth are slender, bicuspid and laterally compressed, those of the two median rows somewhat coarser. The teeth are fairly close-set (especially in the upper corners of the bone) and are arranged in 24-26 rows.

Coloration. Judging from the few notes prepared by the C.N.B.S. there does not seem to be any noticeable difference in the colours of Nabugabo fishes. Adult males have an overall velvety black colour, with a bright scarlet margin to the entire dorsal fin, scarlet maculae on the soft part, a scarlet distal half of the caudal fin and a similar colour spread over the entire anal fin; the anal ocelli are orange-yellow. The pelvic fins are black.

Ecology. Because so few specimens of *H. nubilus* were recorded by the C.N.B.S. little is known about the habits of this species in Lake Nabugabo. The one locality at which *H. nubilus* was caught is in shallow water (about 3 ft. deep) over a sand and mud bottom and a few feet away from a swamp shore.

No data are available on the food of the Nabugabo population, nor is anything known about their breeding biology except that all five specimens described above are adults (4 males, 1 female).

III. *HEMIHAPLOCHROMIS* Wickler, 1963

See Wickler (1963) for a full discussion of this genus.

Hemihaplochromis multicolor (Schoeller) 1903

(Text fig. 11)

Chromis multicolor Schoeller, 1903, *Bl. Aq. Terrk.*, **14** : 185.

Paratilapia multicolor: Hilgendorf, 1903, *Sitzber. Ges. Naturf. Fr. Berlin*, 429-32.

Haplochromis multicolor: Regan, 1922, *Ann. Mag. nat. Hist.* (9), **10** : 249-64.

Hemihaplochromis multicolor: Wickler, 1963, *Senk. biol.*, **44** : 83-96.

As yet, insufficient revisional work has been done on this widespread species to determine the relationships of the Nabugabo population. The C.N.B.S. field notes on coloration certainly do not suggest that the Nabugabo fishes differ in this important character.

Hemihaplochromis multicolor is recorded from the White Nile, Lower Nile, Bahr el Jebel, Lake Albert, the Semliki river, Lakes Victoria and Kyoga, the Malawa and

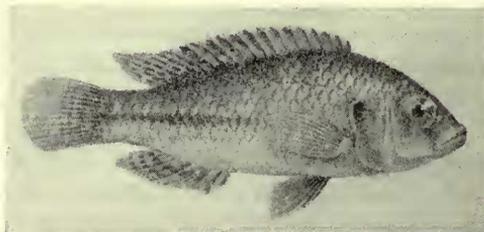


FIG. 11. *Hemihaplochromis multicolor*. From Boulenger, *Fishes of the Nile*: a Lake Victoria specimen is depicted.

Aswa rivers (Uganda) and the small, swampy lakes Kachira, Kijanebalola and Nakavali which lie between Lakes Edward and Victoria. The C.N.B.S.'s material constitutes the first record of the species from Lake Nabugabo.

In Nabugabo, *H. multicolor* was collected from a range of habitats; indeed, it is probably the only *Haplochromis*-group species to occur in the isolated pools of the floating border swamp and in the sand-bar swamp at the eastern lake edge. It is found frequently amongst the rooted vegetation fringing the main lake, and there are records of it from the deep inlets, which penetrate into the swamps. A few specimens were caught amongst flooded tree roots at the mouth of the Juma river. There are no records from the open lake but limitations imposed by the gear used there, coupled with the small size of the fishes, would reduce the chances of their being captured.

The C.N.B.S. concluded that *H. multicolor* are most common in areas where the water is relatively sheltered and where there is a good growth of water-weed, particularly *Utricularia* and *Ceratophyllum*. Of all the species in Lake Nabugabo, *H. multicolor* seems to be peculiar in exploiting *Utricularia* as a food source; presumably it is the animals trapped by the plant, and not the plants, which provide the nourishment.

The feeding habits of *H. multicolor* are diverse. Data from the C.N.B.S. notes indicate that many individuals had fed exclusively on other fishes, especially the cyprinodont *Aplocheilichthys pumilus* and species of the cyprinid *Barbus*. Insects (particularly chironomid and ephemeropteran larvae) and Crustacea (*Cyclops* and Ostracoda) are also recorded, as are some specimens in which the entire gut is packed with filamentous and blue-green algae, or with a mixture of algae and the remains of *Utricularia*. In these latter fishes remains of small Crustacea are also found, suggesting that they were derived from the *Utricularia* bladders since similar animals are trapped by these plants. A few specimens contained, in addition to the plant matter, a number of small oligochaet worms.

No breeding females were recorded by the C.N.B.S., but several females had ovaries in an advanced stage of oogenesis.

IV. *ASTATOREOCHROMIS* Pellegrin, 1903

See Greenwood (1959a) for a complete generic synonymy and a discussion of generic characters; also, see Greenwood (1965) for further comments on the generic diagnosis.

Astatoreochromis alluaudi Pellegrin, 1903

(Text fig. 12)

For synonymy see Greenwood (1959a and 1964).

A single specimen of this species was collected by the C.N.B.S. and it represents the first record from Lake Nabugabo. Unfortunately it is impossible to be certain that *A. alluaudi* forms a natural element in the Nabugabo fauna. In recent years this species has been introduced into several ichthyo-faunal regions of east Africa

as a biological control agent against snails. However, I can find no definite record of introduction to Lake Nabugabo and since it does occur naturally in other small lakes (Greenwood, 1959a) and because snail control in Nabugabo would not be necessary (snails are reputedly rare) the evidence does seem to favour the consideration of *A. alluaudi* as a natural element.

The specimen available is an adult male 85 mm. S.L. (85 + 22 mm. total length) and does not differ in any morphometric characters from specimens described before (Greenwood, 1959a).

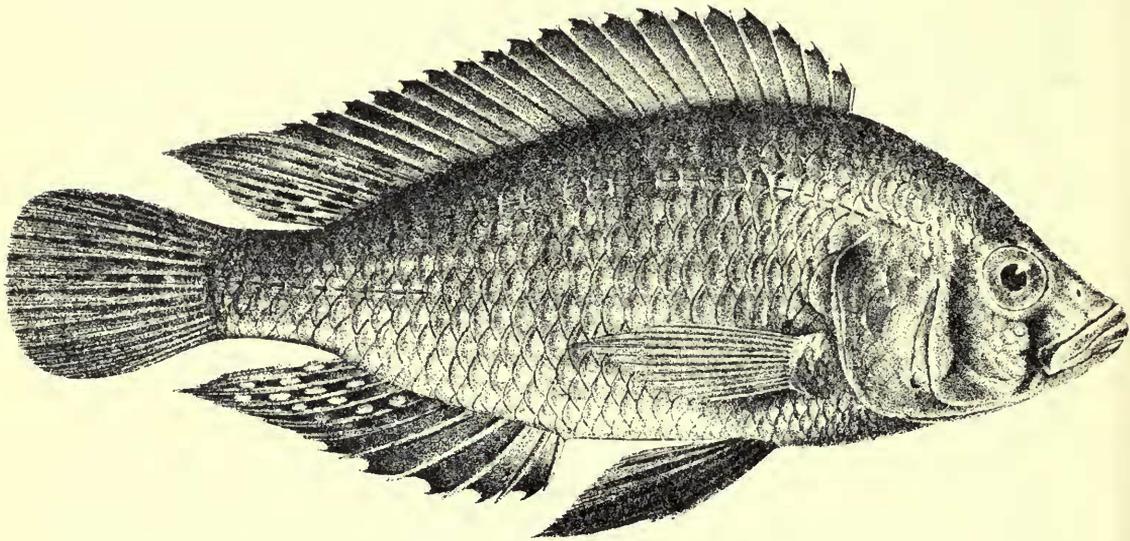


FIG. 12. *Astatoreochromis alluaudi*. From Boulenger. *Fishes of the Nile*.

The oral dentition is likewise typical. The pharyngeal bones and teeth are directly comparable with the greatly reduced type characterizing fishes from Lakes Edward, George, Nakavali and Kachira (*i.e.* of the populations formerly described as the subspecies *A.a.occidentalis*; but see Greenwood, 1965). The lower pharyngeal bone is weak and only slightly enlarged but the upper pharyngeal bones are relatively stouter. The two median rows of lower pharyngeal teeth are composed of slightly enlarged teeth still with remnants of the smaller cusp (*i.e.*, not of the broad-crowned unicuspid type found in specimens from Lake Victoria and in some from Lake Edward). The remaining teeth are small, compressed and weakly bicuspid with the major cusp very prominent. Some enlarged teeth occur on the upper pharyngeal bones and these are relatively stouter than their counterparts on the lower bone; however, they are distinctly bicuspid.

The neurocranial apophysis for the upper pharyngeal bones is markedly reduced in size, with proportionately much smaller basioccipital facets than are found in any other natural population of the species. Indeed, the morphology of the apophysis

is comparable with that of an aquarium raised specimen which was fed on a snail-free diet (see Greenwood, 1965).

Unfortunately, the gut of the unique Nabugabo specimen is empty so no data are available on its feeding habits. The extreme scarcity of snails in the lake suggests, however, that the food of these fishes would not be at all like the predominantly snail diet of the Lake Victoria population, and it probably contains even fewer snails than does the diet of populations from Lake Edward.

It is clear from the C.N.B.S. notes that the coloration of the Nabugabo fish is identical with that of specimens from other areas. Like males from Lake Kachira, the Nabugabo fish is adult at a smaller size than has been recorded from Lake Victoria. No data are available on the minimum sizes of adult males from other localities.

DISCUSSION

Before discussing the evolutionary aspects of the Lake Nabugabo *Haplochromis*, it is necessary to consider the status of the five endemic "species", particularly their status *vis à vis* related species in Lake Victoria.

But for one exceptional species pair, the endemic *Haplochromis* are easily distinguished from each other both anatomically and with regard to male breeding coloration. No intermediate specimens are encountered and there is no *prima facie* evidence to suggest that interspecific crossing takes place.

The exceptional pair is *H. simpsoni* and *H. velifer*. There, the overall level of morphological differentiation, although appreciable, is slight and concentrated in dental characteristics. Two specimens out of a total of seventy have a dentition which could be considered a mixed "*velifer-simpsoni*" type; however, each fish has a greater ratio of "*simpsoni*" to "*velifer*" characters. In other respects the morphology of these fishes is "*simpsoni*"-like, but it must be remembered that it is in dental characters that specimens of the two species show the greatest divergence. With only this evidence on which to work, one cannot decide if specimens with apparently interspecific dental characters are of hybrid origin. Whatever their origin, their frequency is very low.

The real problem posed by the Nabugabo species flock is to estimate the degree of biological separation existing between the endemic Nabugabo species and those *Haplochromis* endemic to Lake Victoria which are morphologically closest to them and from which the Nabugabo species were probably derived. Phenotypically, as we have seen, there is every reason to consider them specifically distinct. Indeed, the morphological gaps between any one Nabugabo species and its counterpart in Victoria are as great as those between any two related *Haplochromis* in Lake Victoria. Similar differences are apparent when Nabugabo species are compared with species from Lake Kivu or Lake Edward.

I believe that the marked differences in male coloration between the anatomically nearest species of Nabugabo and Victoria suggest that members of each pair or

group would behave as biological species should they ever become sympatric. Ethological studies (Baerends and Baerends van Roon, 1950; Wickler, 1963) all stress the importance of male coloration in species discrimination amongst cichlids; indirect evidence from the multispecific *Haplochromis* flock of Lake Victoria adds support to the experimental studies because one repeatedly finds distinctive male colours characterising otherwise phenotypically similar species.

This evidence is inferential with regard to the extralacustrine validity of the Nabugabo species but it seems as well-grounded as any such evidence can be.

The history of Lake Nabugabo (see page 316) makes it seem unlikely that its fishes were derived from any source other than Lake Victoria, a conclusion amply supported by the non-cichlid fishes.

If this source is accepted, it then remains to consider the stage of speciation which the Victoria *Haplochromis* had reached 4,000 years ago. Allowing for some inevitable genetical differences, it seems likely that there was little major difference between the species then and now. The reasons for my thinking this are based mainly on the difficulty of understanding how any significant number of species could have evolved in Lake Victoria during that short period. If it be argued that some degree of habitual isolation would allow for the differentiation of species, then one is faced with the problem of how the species then became widely distributed around the extensive shores of Victoria. Also militating against the concept of habitual isolation is the fact that no morphologically distinct populations are recognisable in any present-day Victoria species. This does not, of course, deny the possibility of there being genetically distinguishable populations (particularly since Victoria *Haplochromis* species are usually restricted in their habitat preferences) but the present argument is concerned with the morphological expression of the genotype and the recognition of species in that way.

If habitual segregation be ruled out, what of isolation through changes in the topography of the Lake basin? Again there is nothing to support the hypothesis; all the geological and climatological evidence strongly suggests that there has not been any great change in the form of Lake Victoria during the past four thousand years. The problem of intralacustrine distribution after speciation is also relevant.

Thus, it seems reasonable to conclude that at the time of its formation Lake Nabugabo would have been populated by *Haplochromis* similar to those inhabiting a comparable bay in the Lake Victoria of today.

Trewavas (1933) implies that the Nabugabo endemics are relict species. Her views were influenced by the fact that the extreme youth of Nabugabo had not then been fully appreciated, and also by the lack of knowledge about the *Haplochromis* species-flock of Lake Victoria. For instance, it was not realised that there are species in Victoria which, anatomically speaking, are of stock status when compared with the more specialized species existing alongside them, often in the same habitat. This ancestor-descendant relationship is found in all the trophic groups of Victoria *Haplochromis* but is seen especially well amongst the algal grazers, mollusc crushers, mollusc shellers and the piscivorous predators. There is no reason

to consider *H. annectidens* anatomically more "basal" than its relative in Lake Victoria, *Haplochromis lividus* (see above, p. 334); *Haplochromis venator* belongs to the Lake Victoria species group containing some of the more advanced piscivorous predators, and there is nothing about *H. simpsoni* or *H. velifer* either more or less specialized than in similar species of Lake Victoria.

The case of *H. beadlei* is equivocal (see p. 340) since although the dental characters of this species seem less specialized than those of *H. crassilabris* in Victoria, they could be interpreted as having evolved, through regression, from a "*crassilabris*"-like condition.

If the endemic *Haplochromis* of Lake Nabugabo were evolved from Lake Victoria *Haplochromis* virtually identical with those of the present day, the evolutionary process was simply one of speciation. It did not involve the development of new adaptive lines from the point of view of feeding mechanisms; indeed, this could hardly have been possible since the Victoria flock had already exploited this field to saturation. Adaptation seems more likely in those physiological characters concerned with respiration and osmoregulation, because the hydrology of Lake Nabugabo certainly differs from that of Victoria.

Historically, Nabugabo is a cut-off bay of Lake Victoria. If, on this basis, it is compared with a bay of comparable size in Victoria, one of the more remarkable features is the reduction in the number of *Haplochromis* and *Haplochromis*-group species: eight species compared with at least thirty in Victoria (i.e. ca. 25 per cent of species one might expect to find). There is also a reduction in the number of trophic types amongst the species (four compared with six in Lake Victoria). The broad specializations not represented in Lake Nabugabo are the embryo and larval-fish eaters and the mollusc shellers; there is, also, a reduction in the number of intra-group specializations represented in the Nabugabo flock. Another difference is in the proportions of the various trophic types; the number of insectivorous species in Nabugabo is proportionately much higher than would be found in a bay of Lake Victoria. There, piscivorous species would be most numerous, followed by phytophagous, mollusc-eating and insectivorous species in about equal proportions. These proportions are based on adult and subadult fishes because the feeding habits of immediately post-larval individuals are still unknown.

The non-cichlids of Lake Nabugabo, on the other hand, show much less depauperization, with about seventy-three per cent of the Victoria species also occurring in Nabugabo (figures based on the C.N.B.S. collections now deposited in the B.M. [N.H.]).

There is no indication of the fate of those Lake Victoria trophic groups which are not represented in Lake Nabugabo. Some may have retreated from the embryo lake before it was completely sealed-off and others may have been unable to survive the hydrological changes which took place once the bar was completed, hydrological changes directly affecting the water chemistry or acting indirectly through altered food chains.

The history and ultimate differentiation of the surviving isolated populations provide a text-book case of geographical isolation resulting in speciation. The rate at which speciation occurred shows how rapidly a genetic revolution (*sensu* Mayr, 1963) can be achieved. In relation to the species of Lake Victoria, those of Nabugabo must be considered inferential but it is significant that the degree of morphological differentiation achieved is as great as that existing between related sympatric species in Lake Victoria. The marked differences in male coloration between similar species in the two lakes is striking and, I believe, an important element in providing interspecific barriers. In Lake Nabugabo there could have been no selection in favour of strengthening such potential interspecific barriers because the species evolved there were derived from fully differentiated Victoria species. In such circumstances differences in male coloration must be looked upon as coincidental results of the genetical revolution undergone by the isolates, possibly even byproducts of selection acting on other components of the genotype directly concerned with adaptation to altered and altering environmental conditions.

If these suppositions are accepted, they throw some light on the rate at which genetical isolating mechanisms could evolve in isolated populations of *Haplochromis*. This is one of the principal problems involved in any attempt to explain the evolution of such multispecific flocks as that of Lake Victoria.

Recently, Hubbs (1961) has criticized the emphasis I placed on the role of spatial isolation (i.e. geographical and physical) in accounting for the history of the Lake Victoria *Haplochromis* flock. Lake Nabugabo seems to provide a "pertinent indication" (Hubbs' phrase) of speciation through geographical isolation which Hubbs did not consider when arguing against this concept in favour of essentially sympatric speciation within cichlid flocks. Hubbs believes that "in general, shallow ponds are not scenes of extensive speciation . . ." and that "No great diversity has arisen within small lakes and ponds over Africa". Perhaps Hubbs was placing much emphasis on the qualifying words "extensive" and "great"; neither, I agree, applies to Nabugabo. However, the fact that speciation seems to have occurred in Nabugabo should be considered and the evidence for it is as good as it is for any allopatric species; it could hardly be more pertinent to the problem of cichlid speciation in Lake Victoria (see Greenwood, 1959c). The question of diversity is another issue if the word is taken to cover more extensive evolution than just the multiplication of species. Because of the highly differentiated species-flock from which it arose one would not expect to find great new diversity amongst the Lake Nabugabo species. Nabugabo provides evidence for phylogenesis and not anagenesis. The latter will always be a function of the adaptive levels attained by the ancestral stock or stocks and the environmental conditions obtaining during the evolutionary period under consideration.

The effects of ecological segregation (and with it in many cases spatial but not physically insuperable segregation) on the species of Lake Victoria has certainly been much less marked than has the effect of physical isolation on the ancestors of the present-day Nabugabo species. Lake Nabugabo was cut off about four thousand

years ago and in that period the physiography of Lake Victoria has remained unchanged. The Victoria *Haplochromis* species must then have had virtually the same intralacustrine distribution and habitat preferences as at present, yet none has shown any differentiation comparable with that undergone by the populations isolated in the bay that was to become Lake Nabugabo. Any argument that the present-day Victoria species-flock has also evolved and reached the present pattern of species distribution (no species shows a geographically restricted intralacustrine distribution) in the last four thousand years, seems inconceivable in the light of evidence we have on the *Haplochromis* of Lakes Victoria and Edward (particularly the species common to both lakes), and the geological history of the area (Greenwood, 1951, 1959a and c).

KEY TO THE GENERA OF *CICHLIDAE* IN LAKE NABUGABO

- | | | |
|---|---|-------------------------|
| | Scales ctenoid | 1 |
| | Scales cycloid | TILAPIA |
| 1 | Anal fin with three spines | 2 |
| | Anal fin with more than three spines | ASTATOREOCHROMIS |
| 2 | Many scales in lateral line series without pores; no ocelli on anal fin in adult males but posterior tip of fin with pigmented spot | HEMIHAPLOCHROMIS |
| | All scales in the lateral line series with pores; ocelli on anal fin in adult males, no pigment spot on posterior tip | HAPLOCHROMIS |

KEY TO THE SPECIES OF *HAPLOCHROMIS*

- | | | |
|---|---|-----------------------|
| | Lower jaw more than 47 per cent of head length; teeth unicuspid and moderately stout, more than 40 in the upper jaw | H. venator |
| | Lower jaw less than 47 per cent of head length; teeth generally bicuspid or if unicuspid, either slender and numerous or stout and fewer than 40 in upper jaw | 1 |
| 1 | Caudal truncate or weakly subtruncate | 2 |
| | Caudal distinctly subtruncate or, more usually, rounded; adult males jet black | H. nubilus |
| 2 | Teeth bicuspid or unicuspid (or a mixture of both); if predominantly unicuspid, then slender and more than 30 in upper jaw; lips not markedly thickened | 3 |
| | Teeth unicuspid or bicuspid, stout and procumbent, less than 34 in upper jaw; lips markedly thickened (upper sometimes thicker than lower). | H. beadlei |
| 3 | Teeth distinctly bicuspid | 4 |
| | Teeth weakly bicuspid or unicuspid or a mixture of both types, slender; more than 50 in upper jaw | H. simpsoni |
| 4 | Teeth moderately stout, distinctly bicuspid, immovably implanted; major cusp not protracted towards symphysis, and occlusal surface not horizontally aligned | H. velifer |
| | Teeth with slender shafts, weakly bicuspid, major cusp expanded, obliquely truncated so that occlusal surface is almost horizontal and produced towards the symphysis; moveably implanted | H. annectidens |

SUMMARY

1. Lake Nabugabo, a small swampy lake, is separated from Lake Victoria by a relatively narrow sand-bar and swamp. The sand-bar is estimated to be about 4,000 years old; prior to that date the lake was a bay of Lake Victoria. A short description of the lake and its history is given.
2. The cichlid fishes are reviewed, mainly on the basis of new material collected by the Cambridge Nabugabo Biological Survey of 1962.
3. Six species of *Haplochromis* (five endemic to the lake) are now recorded; of these, two are new (*Haplochromis simpsoni* and *H. venator*; the latter was previously confused with *H. pellegrini* of Lake Victoria) and one (*H. nubilus*) is recorded for the first time.
4. Two other new records are: *Hemihaplochromis multicolor* and *Astatoreochromis alluandi*. The latter species shows certain interesting osteological differences when compared with specimens from Lakes Victoria and Edward.
5. The evolutionary history of the Nabugabo *Haplochromis* is discussed. The evidence strongly suggests that the endemic species were derived from Lake Victoria species similar to, if not identical with species still extant in Lake Victoria. The significance of this rapid speciation in understanding speciation in Lake Victoria *Haplochromis* is considered.

ACKNOWLEDGEMENTS

In many respects this paper should be regarded as a joint effort between the members of the Cambridge Nabugabo Biological Survey and myself. I have drawn heavily upon their extensive and detailed field-notes as well as on the numerous coloured drawings they made of live fishes. Without their painstaking attention to detail and deep appreciation of the *Haplochromis* problem it would have been almost impossible to gain a full impression of the Nabugabo species. To the members of the C.N.B.S., Alan Roberts, Barney Hopkins, Michael Simpson and Robin Sturdy, I express my warmest thanks.

My thanks are also due to my colleagues, Dr. Ethelwynn Trewavas for the numerous discussions we have had about these fishes, and Mr. A. C. Wheeler for making several radiographs.

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