

THE *HAPLOCHROMIS* SPECIES (PISCES : CICHLIDAE) OF LAKE RUDOLF, EAST AFRICA

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INTRODUCTION

LAKE RUDOLF is outstanding amongst the Rift Valley Great Lakes of Africa for the paucity of its endemic cichlid species, and particularly for the absence of a *Haplochromis* species flock (Trewavas, 1933). Whereas all other large Rift Valley lakes have a well-defined flock of endemic *Haplochromis* species (even if, like Lake Albert, the flock comprises only a few species), Lake Rudolf was thought to possess but a single *Haplochromis* species, the endemic *H. rudolfianus* Trewavas, 1933. The lake's one positive ichthyological peculiarity, the presence of an endemic species belonging to the west African genus *Pelmatochromis*, has now been shown to stem from a misidentification. The Rudolf *Pelmatochromis* is, in fact, a specimen of the widespread taxon *Hemichromis bimaculatus* Gill (see Trewavas, 1973).

Endemicity amongst the non-cichlid species is also at a low level (see Worthington & Ricardo, 1936 ; personal observations on collections recently made in the lake).

Various ideas have been advanced to explain the absence of a *Haplochromis* species flock in Lake Rudolf (see summaries and comment in Fryer and Iles, 1972). Of these, the most likely would seem to be the relative youth of the present lake fauna, an invasion from the Nile in post-Middle Pleistocene times. Coupled with this factor are the shape and recent history of the lake basin, neither of which would provide opportunities for the isolation (and subsequent speciation) of populations living in the lake. That until now the only *Haplochromis* known to inhabit the lake was of a structurally and ecologically generalized type similar to the fluviatile species of eastern Africa, would seem to agree with such a postulated lake history.

Recently, however, a second and anatomically specialized species has been discovered in the deeper waters of the lake. A few specimens of a third species (similar to *H. rudolfianus*, see p. 150) have also been collected, and there are indications of yet another taxon (see p. 149).

These and other specimens, made available through the efforts of the Lake Rudolf Fishery Research Project, have provided sufficient material to describe the new deep-water taxon, the new *Haplochromis rudolfianus*-like fish, and to redescribe in

greater detail *H. rudolfianus* itself. Unfortunately the putative fourth species is represented by so few and distorted specimens that I consider it inadvisable to describe it at present. Nevertheless, sufficient information has been gathered from these few specimens to show that this species too is like *H. rudolfianus*.

As part of a planned review of phyletic relationships within the *Haplochromis*-group cichlids, some consideration is also given to the relationships of the Lake Rudolf species with those of other lakes, especially Lakes Albert and Victoria.

***Haplochromis rudolfianus* Trewavas, 1933**

(Text-figs. 1-4)

Haplochromis rudolfianus Trewavas, 1933, *J. Linn. Soc. (Zool.)*, **38**: 321-322.

LECTOTYPE. A specimen, 51.0 mm standard length (BMNH reg. no. 1933.2.23: 163), from a weedy lagoon on the east shore of Lake Rudolf, near Mt El Moitat (station number 285, *see* Worthington, 1932). The specimen has been eviscerated, but judging from its preserved coloration it is probably an adult male.

PARALECTOTYPES. Three specimens (BMNH reg. nos. 1933.2.23: 164-166), 39.0-42.5 mm S.L., from the same locality as the lectotype (all are eviscerated), and one other specimen (BMNH reg. no. 1933.2.23: 167), 45.0 mm S.L. from Central Island (Worthington's station no. 264). This latter fish is also eviscerated but is probably an adult male.

Comment on the original description of H. rudolfianus

Trewavas' (1933) original description was based on 5 syntypes, but 25 other specimens were also examined although not included in the description. I have re-examined these fishes and would confirm their identification as *H. rudolfianus*. Dr Trewavas also included in this species, but with certain reservation, a larger specimen, 61.0 mm S.L. and 80 mm total length (BMNH reg. no. 1933.2.23: 169). The locality label for this fish reads '? Lake Rudolf', the uncertainty stemming from the collector's notes on the provenance of the specimen. A number of differences between this fish and other specimens of *H. rudolfianus* were noted by Trewavas. I can confirm these differences and would add others. The size discrepancy once existing between this specimen and others of *H. rudolfianus* is virtually obliterated by the larger specimens of the latter species now in the Museum's collections. Thus it seems very unlikely that the various differences listed by Trewavas are, as she then suggested, size correlated ones.

The specimen in question departs from *H. rudolfianus* in having a deeper body (37.4 per cent of standard length), somewhat deeper preorbital (17.7 per cent of head length), wider interorbital distance (25.6 per cent of head), a deeper cheek (25.6 per cent of head), a smaller eye diameter (30.0 per cent of head) and a markedly shorter caudal peduncle (14.7 per cent of standard length, *cf.* 16.5-19.7, mean 18.0 per cent in *H. rudolfianus*). The fish also differs from specimens of *H. rudolfianus* in having fewer gill rakers (7 *cf.* 8 or 9), larger scales on the nape and in the lateral line series (30), in lacking the characteristic dark vertical bars on the body and caudal

peduncle (*see* p. 147), in having no melanic pigment in the ovarian walls (*see* p. 146) and in having stouter and somewhat obliquely cuspidate outer jaw teeth. The lower pharyngeal bone is finer than in *H. rudolfianus*, and the median lower pharyngeal teeth are also finer (*see* p. 146).

In my opinion, this specimen cannot be identified as a member of *H. rudolfianus*, nor can it be placed in either of the other *Haplochromis* species from Lake Rudolf. All the evidence certainly suggests that it in fact belongs to the fauna of another lake. On this assumption, the specimen was compared with *Haplochromis* species from all the lakes sampled by the Cambridge University Expedition of 1930-31. It cannot be identified with any known Lake Albert *Haplochromis* species, nor does it closely resemble any of the described (or known but undescribed) species of Lakes Edward and George; *see* Greenwood, 1973. It does, however, closely agree in all morphometric and anatomical features (especially the dentition) with *H. velifer* Trewavas of Lake Nabugabo, Uganda (*see* Greenwood, 1965). Since extensive collections were made in this lake by the Cambridge Expedition, I would identify the fish as a specimen of *H. velifer* and suggest that the locality label be altered to read 'Lake Nabugabo'.

The redescription of *H. rudolfianus* given below is based on the 5 type specimens (39.0-51.0 mm S.L.) and 20 additional fishes (30.5-58.0 mm S.L.) collected in 1972 by the Lake Rudolf Fisheries Research Project team at Topi point, Allia Bay, and Ferguson's Gulf. Coloration and certain anatomical details were also checked on the other specimens from which meristic and morphometric data were not taken (BMNH reg. nos. 1973.11.13: 151-170).

All counts and measurements used in this description are those defined by Greenwood (1973).

Dorsal head profile straight or gently curved, sloping at an angle of 25-30 degrees with the horizontal; premaxillary pedicels rarely breaking the smooth outline of the profile.

Length of head 31.0-35.3 (mean, $M = 33.5$) per cent of standard length, depth of body 29.4-33.7 ($M = 32.1$) per cent.

Preorbital depth 12.5-17.9 ($M = 15.0$) per cent of head, least interorbital width 20.0-27.4 ($M = 22.7$) per cent, neither dimension showing allometry with standard length. Length of snout 26.6-32.3 ($M = 29.9$) per cent of head, 0.7-1.1 (mode 0.8) times its breadth. Eye diameter 30.5-35.7 ($M = 32.9$) per cent of head (showing ill-defined negative allometry), depth of cheek 17.4-25.8 ($M = 21.7$) per cent.

Caudal peduncle 16.5-19.7 ($M = 18.0$) per cent of standard length, 1.2-1.7 (modal range 1.3-1.5) times as long as deep.

Mouth horizontal or slightly oblique. Length of upper jaw 30.8-38.0 ($M = 33.7$) per cent of head, length of lower jaw 35.7-48.3 ($M = 39.7$) per cent, 1.4-1.8 (modal range 1.5-1.7) times as long as broad. Posterior tip of maxilla reaching a vertical through the anterior margin of the eye.

Gill rakers. Relatively stout, with the lower 1 or 2 on the first gill arch reduced; 9 (less frequently 8, rarely 10) on the lower limb of that arch. Well-developed 'pseudorakers' (fleshy protuberances between the inner and outer row of true rakers) are present on the first arch.

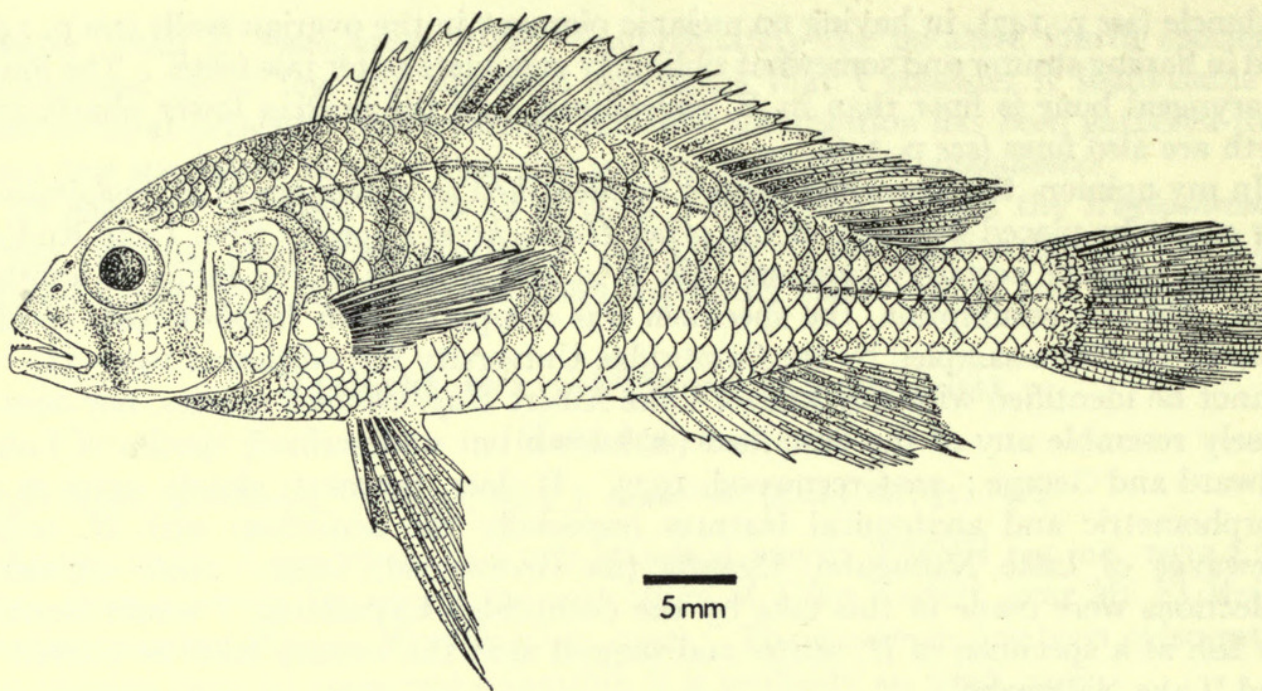


FIG. 1. *Haplochromis rudolfianus*. Lectotype. Drawn by Gordon Howes.

Scales. Strongly ctenoid, those on the anteroventral aspects of the thoracic region very small, with an abrupt size transition between them and the posterior scales of this region. Immediately anterior to the first dorsal fin spine there is a small naked area (about $1\frac{1}{2}$ or 2 scales in area), and often there is also a narrow naked strip below the ventral horizontal row of cheek scales. Lateral line with 30 (f2), 31 (f10), 32 (f12), or 33 (f1) scales, cheek with 3 (rarely 2 or 4) rows. Six or 7 scales between the dorsal fin origin and the upper lateral line, 6 or 7 (rarely 5) between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f12), 25 (f11) or 26 (f2) rays, comprising 14 (f3), 15 (f21) or 16 (f1) spinous and 9 (f9), 10 (f15) or 11 (f1) branched rays. Anal with 3 spinous and 8 (f3), 9 (f20), 10 (f1) or 11 (f1) branched rays.

First branched ray of the pelvic fin very slightly produced in both sexes, but relatively more so in adult males.

Caudal subtruncate, scaled on its basal quarter to third.

Teeth. The majority of teeth in the *outer row* of *both jaws* are unequally bicuspid and moderately stout (Text-fig. 2); the major cusp is acutely pointed and equilateral in outline. A few unicuspid teeth sometimes occur posteriorly in the upper jaw, but more often the posterior teeth are tricuspid; rarely are these teeth bicuspid. A noteworthy feature of the samples examined is the pronounced wear pattern seen on the outer teeth. Worn teeth have the major cusp either obliquely truncate or the wear may be so great that all demarcation between major and minor cusps has disappeared and the crown is spatulate.

There are 28–48 teeth in the outer premaxillary row, the number showing some positive correlation with the fish's length.

All *inner row* teeth are small tricuspid, and are arranged in 2 or 3 (mode), rarely 4, rows in the upper jaw and in 2 (mode) or 3 rows, rarely a single row, in the lower jaw.



FIG. 2. *Haplochromis rudolfianus*. Outer row jaw teeth (in labial view) from left dentary, anterolateral in position.

OSTEOLOGY. The *neurocranium* (Text-fig. 3A) of *H. rudolfianus* is of the generalized '*H. bloyeti*'-type (see Greenwood, 1974), with a moderately decurved profile and a relatively short preotic skull length (*ca* 62.5 per cent of total neurocranial length). None of the cephalic laterosensory canals or pores, nor any of the bones carrying the canals, is at all hypertrophied (*cf.* p. 155 ; Text-fig. 3B).

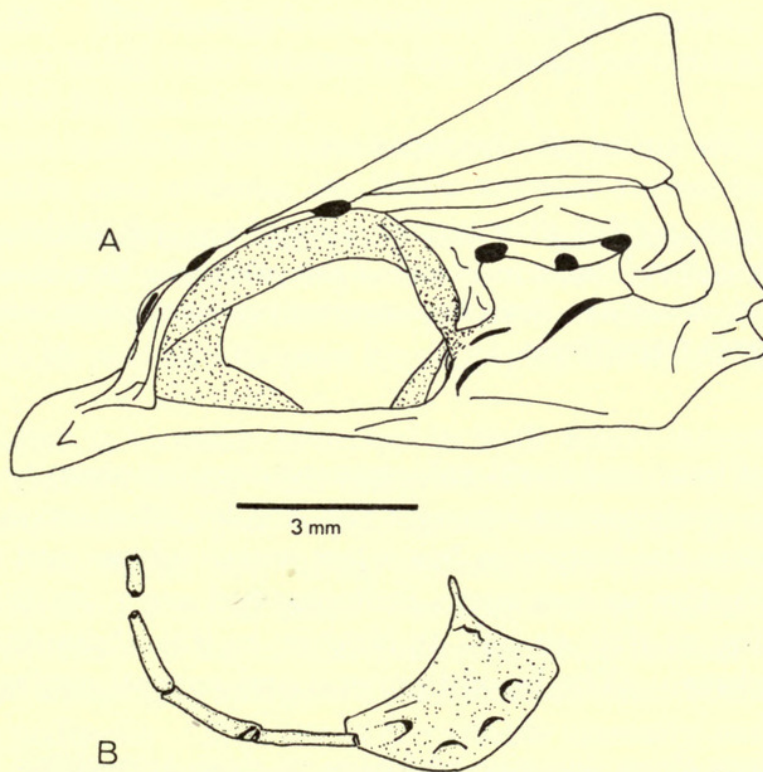


FIG. 3. *Haplochromis rudolfianus*. A : Neurocranium, left lateral view.
B : Bones in the infraorbital series of the right side.

The *lower pharyngeal bone* (Text-fig. 4) is triangular in outline, with the denticulous area a little broader than long (*ca* 1.1 times). In all specimens examined the bone is noticeably stout, especially compared with that of the other Rudolf species or that of the generalized species in other lakes and in the east African rivers. The degree of enlargement, however, varies between individuals.

The two median tooth rows are composed of teeth clearly stouter than their lateral congeners ; the degree of enlargement, like that of the bone itself, shows considerable individual variability. All five specimens in the type series have the stoutest bones and dentition of all the specimens examined ; the lectotype (51 mm S.L.) is exceptional even amongst the type series in having submolariform teeth posteriorly in the median rows (in all other specimens the bicuspid crown is still retained). The lectotype also has the relatively most massive lower pharyngeal bone (Text-figs. 4A and B).

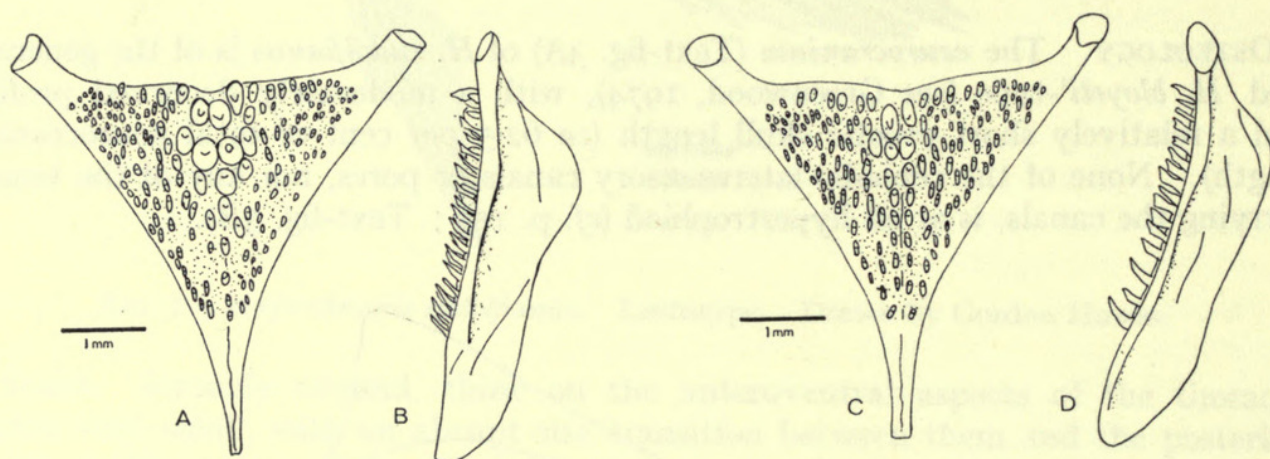


FIG. 4. *Haplochromis rudolfianus*. Lower pharyngeal bones to show variation in size of median teeth. A and B: Bone from one of the paratypes, in occlusal and left lateral views respectively. C and D: Bone from another specimen of the same size, in occlusal and left lateral views respectively.

Lower pharyngeal bone and tooth enlargement does not seem to be size correlated because some of the syntypes are amongst the smaller fishes examined, and a specimen 7 mm longer than the lectotype has a less massive bone and dentition.

Vertebral counts in the 30 specimens radiographed are : 27 (f1), 28 (f3), 29 (f18) or 30 (f8), comprising 11 (f1), 12 (f4), 13 (f23) or 14 (f2) abdominal and 16 (f23) or 17 (f7) caudal vertebrae. (The fused first ural and preural centra are not included in these figures.)

Only two specimens show any sign of fusion or close apposition between elements in the hypural series (*cf.* p. 158) ; in these two fishes the first and second hypurals seem to be fused.

VISCERA. The intestine is from $1\frac{1}{3}$ to $1\frac{1}{2}$ times the standard length ; the ovaries are of unequal size with the right ovary noticeably larger than the left in most specimens or, rarely, it alone shows signs of oogenesis. A very characteristic feature is the intensely melanic tissue of the ovary wall ; the testes, however, are but slightly pigmented. The entire peritoneum is also densely melanic. This extreme visceral melanism is probably correlated with the intense sunlight to which fishes living in the shallows of Lake Rudolf would be subjected.

COLORATION. In freshly killed specimens of *adult male H. rudolfianus* the ground colour is greenish-yellow (but whitish on the chest). Dark vertical bars cross the flank and caudal peduncle (*see* notes on preserved colours below). Each scale on the flanks has an opalescent centre in which yellow, blue and green colours can be detected; yellowish pigment predominates on the anterior body scales, especially those around the base of each pectoral fin. Posteriorly on the body the dominant colour in the scale centres is electric blue, and is especially noticeable around the base of the anal fin. The head, like the anterior part of the body, is an opalescent greenish-yellow and blue, the operculum marked with a golden yellow area on its lower part. The branchiostegal membrane is a delicate pale yellow except for a clearly demarcated black area anteriorly.

The dorsal fin membrane is dark golden-yellow, the lappets are scarlet and the soft part of the fin has a bright yellow basal streak and light yellow dots dorsally, the intervening areas melanic. Black spots also occur on the spinous part of the fin. Two dark basal blotches occur on the spinous dorsal; the first lies between the sixth to ninth spines, the second between the last two or three spines. The anal fin is yellow but with scattered black and red chromatophores, and with two or three light golden-yellow ocelli. The caudal is a marbled yellowish-green, with red and black spots, the red colour being most intense in the dorsal and ventral angles of the distal margin. The pelvic fins are dusky.

Adult females have a similar but more subdued coloration, with the whitish ventral areas more extensive and without the black anterior region to the branchiostegal membrane. The pelvic fins are hyaline tinged with yellow, and the red lappets and margin to the dorsal and anal fins respectively are barely discernible. On the anal fin there are pale yellow spots in the same position as the ocelli of males.

I am indebted to Mr and Mrs Hopson for supplying the notes on which this description is based.

Preserved coloration is virtually identical in both sexes, except that the pelvics in females are clear and not dusky, and the ground coloration is lighter than in males.

The ground coloration is a pale brown (fawn) shading to greyish-charcoal on the chest and belly. The flanks and caudal peduncle are crossed by 5-7 (rarely 8-10) dark and clearly defined vertical bars; the bars on the flanks reach almost to the ventral profile, but those on the caudal peduncle rarely extend to below the level of the midlateral line where they merge with a short and faint horizontal bar extending the length of the peduncle. This bar is of variable intensity and is barely visible in some specimens. Anteriorly there is a broad, sometimes ill-defined dark bar overlying the cleithrum and following the outline of that bone; dorsally the bar joins a dark, saddle-shaped blotch on the nape. A fainter bar is sometimes visible along the vertical limb of the preoperculum. The snout is crossed by a pair of parallel dark bars, and there is an intense and clearly demarcated lachrymal stripe.

All fins are a greyish-hyaline, the soft dorsal and the entire caudal are maculate, the dorsal with two distinct dark blotches basally (*see above*), and with dark lappets. Spotting on the caudal fin is most distinct proximally, the spots often arranged so as to produce two to four dark vertical bands on that part of the fin. The pelvics are dusky in males, greyish in females.

ECOLOGY. *Haplochromis rudolfianus* is apparently confined to the shallow and protected inshore areas of the lake, although there is a population inhabiting a crater lake on Central Island (*see below*). No data are yet available on the feeding habits of this species, nor whether it shows any particular substrate preferences.

Males appear to reach a larger size than do females, and are adult at a standard length of 45–47 mm. Females, however, mature at a smaller size, namely *ca* 30 mm. No data are available on the breeding habits or seasons of the species.

THE CENTRAL ISLAND POPULATION. One of the paralectotypes (*see* p. 142) and 12 additional specimens collected in 1965 by Dr R. L. Welcomme are from Central Island. The paralectotype is apparently from the shore of the island (station no. 264, *see* Worthington, 1932) but the other fishes are from one of the crater lakes in that island (*see* Beadle, 1932, for details of the lakes).

The Central Island fishes, particularly those from the crater itself, are of considerable interest since they are apparently isolated from other populations inhabiting the mainland shores of the lake. The apparent absence of *H. rudolfianus* from open-water localities suggests that it does not leave (or at least not frequently) its shallow-water inshore habitats.

A population of *Sarotherodon* living in Crater Lake A of Central Island is sufficiently distinctive for it to have been referred to a new species (*Tilapia vulcani*, Trewavas, 1933, *see also* Trewavas, 1973, for distinguishing features of the genera *Tilapia* and *Sarotherodon*). A population from the neighbouring Crater Lake C, however, did not differ significantly from the populations of *Sarotherodon niloticus* living in the main lake (Trewavas, 1933). The explanation for this seemingly anomalous situation appears to be that Lake C is, on occasion, connected with the main lake. (Personal communication from Dr K. E. Banister, based on information he was given by members of the Fishery Research Team on Lake Rudolf; the last interconnection was in 1972.) Lake A, on the other hand, is completely isolated from the main lake by a crater wall at least 10 m above current lake level.

It is the more regrettable then that the *H. rudolfianus* collected in 1965 bear no more precise locality data than 'Crater Lake, Central Island', and that all are distorted and poorly preserved. Allowing for the difficulty of measuring distorted specimens, I can find no meristic or morphometric differences between the Central Island fishes and those from the main lake. Several of the Island fishes are, however, larger than any recorded from the lake (maximum size 72 mm, *cf.* 58 mm for lake fishes). The largest Island fish has four or five unicuspid teeth situated posterolaterally in the upper jaw, but this could well be a size-correlated phenomenon (*see* Greenwood, 1974). Most of the Island fishes are much darker than are the lake fishes and consequently the vertical barring on the body is less obvious; in a few paler individuals, however, the bars are quite distinct. Like their main lake congeners, female Crater Lake fishes have only the right ovary well developed, but unlike the latter populations the ovarian wall in these fishes is but faintly melanized and then only on the dorsal and lateral aspects. These observations were paralleled by those I was able to make on specimens and colour photographs obtained by Dr Banister during his recent visit to the lake. Once again, the specimens are not well preserved and add little anatomico-morphological information to that already available.

However, the similarity in coloration between Dr Banister's fishes from Crater Lake A and those from the Welcomme sample strongly indicate that the latter are from the same source.

The dark coloration of Central Island *H. rudolfianus* seems to parallel that of '*Tilapia vulcani*' from Crater Lake A on the island (see Trewavas, 1933). In other characteristics the parallelism is not clearly apparent. That is to say, the *H. rudolfianus* specimens do not show the leanness, larger eyes, larger heads, longer dorsal fin spines and broader bands of inner teeth that Trewavas noted in the *Tilapia* specimens (Trewavas, 1933).

In contrast to the Central Island Crater Lake A specimens of *H. rudolfianus*, the paralectotype from the shore of the island does not show any marked darkening of the ground coloration. Unfortunately, it is eviscerated so no check can be made on the melanization of its gonads. The peritoneum is very dark.

Without more precise locality data, more material from different localities on the island and more details on live coloration, little can be said about the taxonomic status of Central Island populations of *H. rudolfianus*. It does, however, seem probable that, like the Crater Lake A population of *Sarotherodon niloticus* (with which species '*T. vulcani*' should now be synonymized; Dr Trewavas, personal communication), the Crater Lake A *Haplochromis* show some ecophenotypic response to their peculiar environment. The relative melanism shown by Crater Lake A *Haplochromis rudolfianus* populations is of particular interest because male coloration seems to be an important species recognition character (see Greenwood, 1974). Altered male coloration apparently is one of the first morphological differences seen in recently speciated *Haplochromis* (Greenwood, 1965).

DIAGNOSIS AND AFFINITIES OF *H. rudolfianus*. The distinctively barred colour pattern of this species immediately serves to distinguish it from all other *Haplochromis* species in Lake Rudolf (see footnote, below). From *H. macconneli* described on p. 154, *H. rudolfianus* is further distinguished by the absence of hypertrophied laterosensory canals and pores on the head, by several morphometric characters (see p. 155) and in having few, if any tricuspid teeth in the outer series of either jaw. In addition to the hypertrophied canal system, the neurocranium in *H. macconneli* is of a more derived type than that of *H. rudolfianus*. The nearest living relatives of *H. rudolfianus* are probably *H. turkanae* (see p. 153), and the fourth but as yet undescribed *Haplochromis* species in the lake.¹

The validity of these relationships can only be tested when more material of the putative relatives is available.

¹ Four specimens 37.0–64.0 mm standard length (and a fifth prepared as a skeleton) may represent a fourth *Haplochromis* species. Morphometrically these fishes are not distinguishable from *H. rudolfianus*, and the dentition is similar except for there being only a single row of inner teeth in each jaw. The principal 'interspecific' difference seems to be in the coloration, both that observed by Mr Hopson (*in litt.*) when the fishes were alive and that remaining in the preserved material. There is also an observable (but non-quantifiable) difference in head shape, and these fishes have a colourless (not black) peritoneum. The gonads show no sign of melanization, unlike those of *H. rudolfianus*.

All five specimens are from water between 15 and 35 m deep; that is, from somewhat greater depths than *H. rudolfianus*, but within the range of *H. turkanae*, from which species they differ in the same morphometric characters as does *H. rudolfianus*.

Since only five specimens are available and because all are in some way damaged or distorted, I would consider it inadvisable to describe a new taxon on this material.

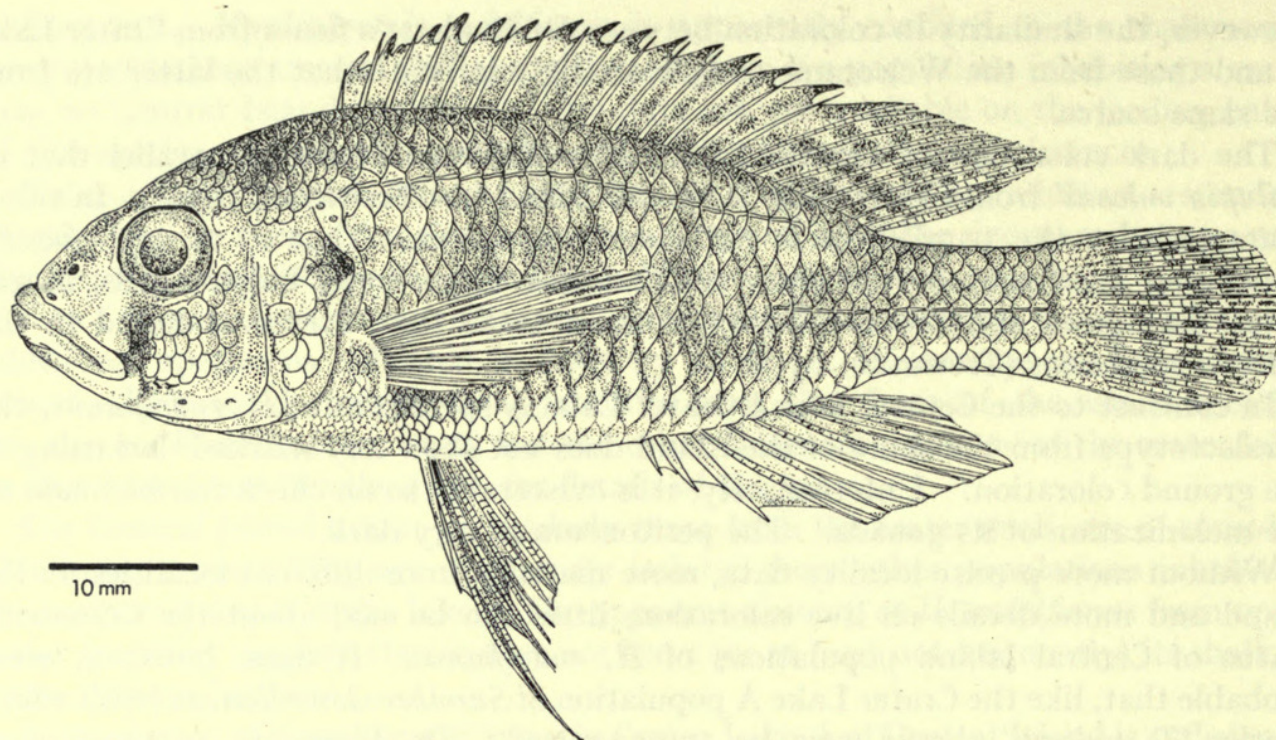


FIG. 5. *Haplochromis turkanae*. Holotype. Drawn by Gordon Howes.

In its gross morphology and in the details of its pectoral and predorsal squamation, *H. rudolfianus* resembles *H. albertianus* Regan, a species endemic to Lake Albert (see Trewavas, 1938). The two species differ in their preserved colour patterns, and in adult *H. albertianus* (of the same size as *H. rudolfianus*) having unicuspid outer jaw teeth and a more massive lower pharyngeal bone with a greater number of enlarged, submolariform teeth. In other words, *H. albertianus* shows a greater degree of specialization in those characters that are already somewhat specialized in *H. rudolfianus*.

STUDY MATERIAL

Register number BMNH	Locality : Lake Rudolf
1973.II.I3 : 151-154	Ferguson's Spit (shallow water, inshore)
1973.II.I3 : 155-170	Topi Point, Allia Bay

Haplochromis turkanae sp. nov.

(Text-figs. 5 and 6)

HOLOTYPE. An adult male, 73.0 mm standard length (BMNH reg. no. 1973.II.20:1), caught in a bottom trawl fished at a depth of 16 m, over a mud and rock bottom, 5.6 km north-west of Porr.

PARATYPES. Three adult males (BMNH reg. nos. 1973.II.20 : 2-4), 77.5-86.0 mm S.L. from the same locality and trawl as the holotype.

DESCRIPTION. Based on these four fishes, 73.0–86.0 mm S.L. With so few specimens available most of the morphometric data can be presented most conveniently in tabular form.

S.L.	Depth*	Head*	PO %	IO %	Snt %	Eye %	Cheek %	Lj %	Uj %	CP*
73.0	35.0	33.5	20.5	20.5	30.6	28.6	28.6	45.0	41.0	17.5
77.5	35.0	32.3	18.0	22.0	32.0	30.0	32.0	44.0	40.0	17.4
81.0	34.5	32.7	18.9	20.8	34.0	34.0	26.4	45.3	41.5	18.5
86.0	33.2	31.4	18.5	22.0	29.6	27.9	27.0	44.5	40.8	16.9

*=per cent of standard length. %=per cent of head length.

PO=preorbital depth; IO=least interorbital width; Snt=snout length; Lj=lower jaw, and Uj=upper jaw length. CP=caudal peduncle length.

Caudal peduncle 1.4–1.5 times longer than deep. Dorsal profile of head straight or gently curved dorsally, but straight anteriorly, sloping at an angle of 30–35 degrees with the horizontal. The ascending processes of the premaxillae barely interrupt the outline of the profile.

Mouth slightly (but noticeably) oblique, the lips a little thickened; posterior tip of the maxilla reaching a vertical through the anterior part of the eye. Jaws equal anteriorly, the lower 1.6–1.7 times longer than broad. Snout broader than long, its anterior profile, when viewed from above, smoothly rounded. None of the cephalic laterosensory canals (or their pores) is noticeably enlarged.

Gill rakers. Relatively stout, 8 (f3) or 9 (f1) on the lower part of the first arch, the lowermost one or two rakers reduced in size. Pseudorakers (*see* p. 143) are developed between the inner and outer rows of gill rakers, but are not conspicuous.

Scales. Ctenoid; lateral line with 31 (f3) or 32 (f1) scales, cheek with 4 (f1) or 5 (f3) imbricating rows. Six or 7 scales between the upper lateral line and the dorsal fin origin; a naked area (about $1\frac{1}{2}$ scales in extent) immediately before the first dorsal fin spine. Nine or 10 scales between the pectoral and pelvic fin bases; the scales of the chest are also very small and grade abruptly with the larger scales of the post-pectoral region.

Fins. Dorsal with 14 (f2) or 15 (f2) spinous rays and 9 (f4) branched rays, anal with 3 spines and 7 (f2) or 8 (f2) branched rays. The first pelvic ray is produced, very noticeably so in two specimens where it extends as far as the second branched anal ray. The caudal fin is strongly subtruncate, almost rounded, and scaled on its proximal quarter to half. Pectoral fin 25.6–28.7 per cent of standard length, 81.5–88.0 per cent of head length.

Teeth. In all four specimens the posterior three or four teeth in the *outer premaxillary row* are strong, dagger-like unicuspid. In two fishes the other teeth in this row are a mixture of caniniform unicuspid and weakly bicuspid, while in the other two specimens distinctly bicuspid teeth predominate, although a few unicuspid occur anterolaterally. There are 42–52 teeth in this row. There is a similar difference in the predominant tooth type of the outer row in the *lower jaw*. The first two specimens have mainly unicuspid teeth with a few bicuspid, the second

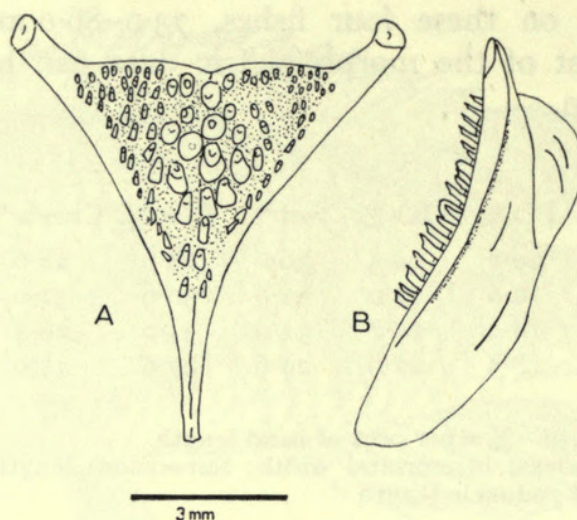


FIG. 6. *Haplochromis turkanae*. Lower pharyngeal bone of holotype in A : occlusal view ; B : left lateral view.

pair have a predominance of bicuspid. Bicuspid teeth in the lower jaw have their crowns more distinctly incurved than do the upper jaw teeth.

Bicuspid teeth in both jaws are of the typical generalized *Haplochromis* type, and closely resemble the teeth of *H. rudolfianus* (see p. 144 ; Text-fig. 2).

The *inner series* of teeth in both jaws are composed of small tricuspid arranged in 3 rows in the upper and 2 (or irregularly 2) rows in the lower jaw.

OSTEOLOGY. With only four specimens available, no skeletal preparations were possible. Vertebral counts made from radiographs are: 28 (f3) and 29 (fr), comprising 13 abdominal and 15 or 16 caudal vertebrae (the fused first preural and ural centra not included). No specimen has any fused elements in the caudal fin skeleton, but in two fishes hypurals 1 and 2 are closely apposed.

COLORATION. No information is available on the live colours of this species. The four adult (but not sexually active) male specimens (fixed in formalin) have a light grey to yellowish-grey ground colour that extends ventrally to a clearly demarcated horizontal line on the body and caudal peduncle, at which level it becomes pearly white. The line is at about the horizontal level of the lowermost insertion of the pelvic fin ; thus in lateral view little of the caudal peduncle shows the white ventral coloration. On the flanks, most dorsal, lateral and ventrolateral scales have a narrow margin of dark pigment. The lower jaw, branchiostegal membrane, suboperculum and the lower part of the cheek are also pearly-white.

About five very faint vertical dark bars are visible on the flanks, and another may also occur posteriorly on the caudal peduncle ; these bars are narrower dorsally than ventrally, and do not extend onto the white ventral coloration of the body. The vertical limb of the preoperculum is faintly to clearly dusky and there is a broad, intensely black lachrymal bar that, at about the level of the posterior maxillary tip, narrows abruptly and then continues ventrally and a little medially onto the lower jaw.

The entire soft dorsal fin and the posterior half of the spinous dorsal are densely and distinctly spotted, with the spots arranged in from four horizontal rows anteriorly to six or more rows posteriorly on the fin. On the anterior part of the spinous dorsal the spots are confluent and form vertically aligned, dark, interspinous streaks. The lappets of the dorsal fin are black. The entire caudal fin is covered with dark and discrete spots so arranged as to form wavy, vertical bars when the fin is not fully opened. The anal is hyaline except for three rather pale ocelli. The pelvics have the anterior half dusky, the posterior half hyaline; the elongate first pelvic ray is dead-white.

ECOLOGY. Virtually nothing is known about the biology of this species. The four specimens came from deeper water than is usual for *H. rudolfianus*, and shallower water than is usual for *H. macconneli* (see pp. 148 and 159).

All four specimens have the stomach and intestine packed with fragments of ostracod shells.

It is interesting to note that, unlike *H. rudolfianus* but like *H. macconneli*, there is no trace of dark pigment in the peritoneum and neither is there any on the gonads (cf. p. 146).

All four specimens are adult males, but judging from the size and shape of the testes, none is sexually active.

DIAGNOSIS AND AFFINITIES. *Haplochromis turkanae* is immediately distinguishable from *H. macconneli* because of its non-hypertrophied cephalic laterosensory canal system. There are also morphometric differences between the species, differences in their dentition and, apparently, in the preserved coloration of adult males (see below, pp. 156–159).

In its general appearance, its dentition and in several morphometric characters, *H. turkanae* closely resembles *H. rudolfianus*. It differs principally in having more rows of scales on the cheek (4 or 5, cf. 3), smaller scales between the pectoral and pelvic fin insertions (9 or 10, cf. 6 or 7), a deeper cheek (26.4–32.0 per cent of head, cf. 17.4–25.8, $M = 21.7$ per cent), longer upper jaw (40.8–41.5, cf. 30.8–38.0, $M = 33.7$ per cent of head), and a somewhat longer lower jaw (44.0–45.3, cf. 35.7–48.3, $M = 39.7$ per cent of head). *Haplochromis turkanae* also differs in having a more elongate first pelvic ray (which is distinctively coloured) and in its overall coloration. For example, it lacks the prominent vertical bars on the body, has more intensely and densely maculate dorsal and caudal fins, and has the peculiar dribble-like extension of the lachrymal bar onto the lower jaw. The lower pharyngeal bone and dentition of *H. turkanae* are somewhat more massive than those of most *H. rudolfianus*, but are quite comparable with those in the type series of that species (see above, p. 146, and cf. figs. 4 and 6).

Without more osteological information on *H. turkanae* it is difficult to say much about its affinities with *H. rudolfianus*. From what is known, however, the two species would seem to be very closely related phyletically. Indeed, the resemblance parallels that seen between many pairs of *Haplochromis* species in Lake Victoria. As in many of the Victoria pairs there is also an apparent ecological replacement involved, with *H. rudolfianus* being the inshore, shallow-water species and *H. turkanae* the species of deeper waters (see Greenwood, 1974).

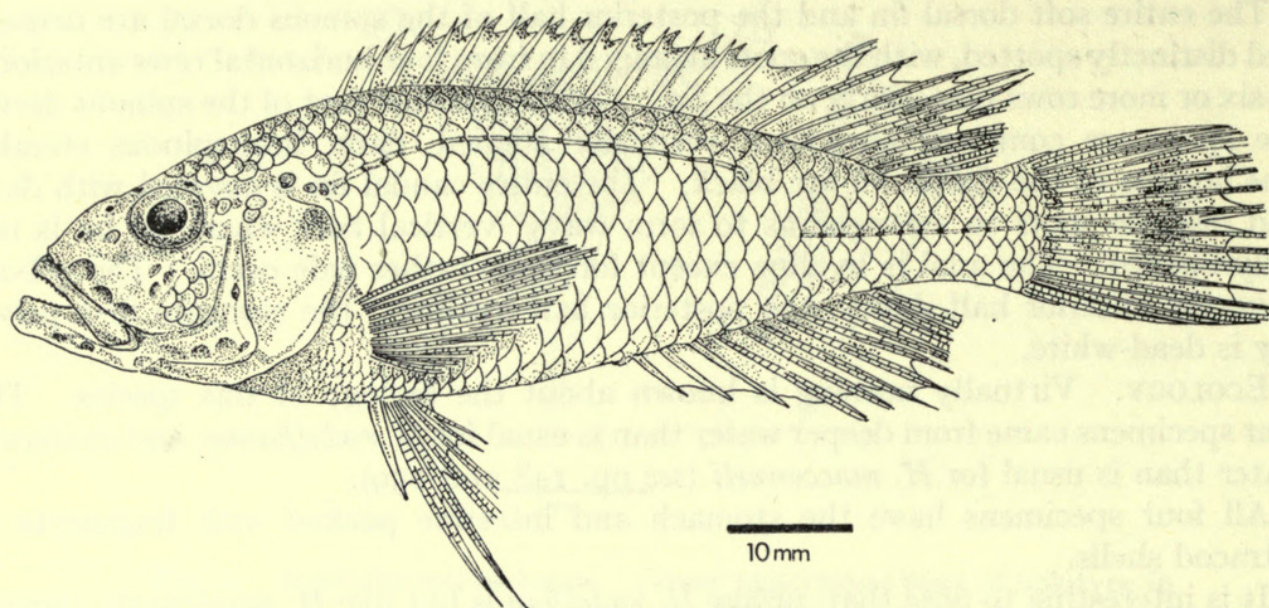


FIG. 7. *Haplochromis macconneli*. Holotype. Drawn by Gordon Howes.

***Haplochromis macconneli* sp. nov.**

(Text-figs. 7-10)

This most distinctive species was discovered by Mr and Mrs A. J. Hopson when the Lake Rudolf Research Project team began trawling operations in the deeper waters of the lake. Apparently it is confined to water more than 20 m deep and has been collected from depths down to 75 m.

Besides its various anatomical peculiarities, *H. macconneli* is also noteworthy for its marked sexual dimorphism in adult size. No males larger than 35.5 mm standard length have yet been recorded. Indeed, despite intensive efforts, only two males have so far been recognized amongst the several hundreds of specimens examined. Females, on the other hand, are common components of deep-water trawl catches.

The taxon is named for Mr R. B. McConnel, Officer in Charge of the Fisheries Department at Lake Rudolf, in grateful recognition of the assistance he has unstintingly given to Mr Hopson and his research team.

HOLOTYPE. A female, 77.0 mm standard length (BMNH reg. no. 1973.II.I3 : 37), caught near the bottom in 50-64 m of water 3 miles north-west of Central Island.

PARATYPES. (i) Twenty-one specimens (BMNH reg. nos. 1973.II.I3 : 38-58), 51.0-72.0 mm S.L., all females and from the same locality as the holotype ; (ii) 6 juveniles (of indeterminable sex), 22.0-38.0 mm S.L., caught in a bottom trawl at a depth of 20 m 1.6 km off Ferguson's Spit (BMNH reg. nos. 1973.II.I3 : 59-64 ; (iii) 2 adult males, 31.0 and 35.5 mm S.L., caught in a bottom trawl at a depth of 30 m, 2.4 km east of North Island (BMNH reg. nos. 1973.II.I3 : 65-66).

DESCRIPTION. Based on the holotype and 29 paratypes, 22.0-77.0 mm S.L. Various characters have been checked on the 78 additional specimens (size range 15.0-59.0 mm S.L.) from the Ferguson's Spit station and one other station 3.2 km

off-shore at a depth of 75 m. None of this extra material has, however, been included in the morphometric counts and measurements.

Because most of the proportional measurements used in this description show allometry with the fish's size, the material has been divided into two size groups, one of fishes 51–77 mm S.L. and the other of fishes 22–38 mm S.L. Ranges and means for the larger specimens ($N = 22$) are given first, followed in parentheses by those for the smaller fishes ($N = 8$).

Length of head 33.3–39.9, $M = 35.3$ (31.6–39.4, $M = 36.0$) per cent of standard length, depth of body 31.7–35.1, $M = 33.3$ (25.3–32.3, $M = 29.7$) per cent.

Dorsal profile of head clearly but gently concave above the eye, sloping at an angle of *ca* 35–40 degrees to the horizontal. The profile of the snout varies from straight to somewhat decurved, with the premaxillary pedicels always breaking the outline. The anterior tip of the lower jaw is usually produced into a symphyseal knob, which is most obvious in fishes over 65 mm S.L.

An outstanding feature of the head (in specimens of all sizes) is the greatly enlarged openings to all the laterosensory canals (Text-figs. 7 and 9). Particularly obvious are those on the preorbital and preopercular bones. The underlying canals are hypertrophied, with the result that the bones involved have a distinctly inflated appearance.

Laterosensory canals on the neurocranium, especially the temporal canal of the pterotic bone, are also inflated, particularly in comparison with those in *H. rudolfianus* and *H. turkanae*, and indeed with those of the generality of *Haplochromis* species (*see below*, p. 158). Canals, and their openings, in the extrascapular and supracleithrum are equally affected by this trend, as are the nasals although the latter are relatively the least cavernous of the cephalic laterosensory canal bones. In well-preserved specimens the canal openings are occluded by a thin membrane.

Depth of preorbital 16.6–22.2, $M = 20.1$ (12.5–16.7, $M = 15.4$) per cent of head, least interorbital width 18.8–24.2, $M = 21.8$ (14.7–25.0, $M = 21.2$) per cent. Snout slightly broader than long (rarely as long as broad) in specimens of all sizes, its length 27.8–38.1, $M = 33.8$ (26.1–33.3, $M = 29.6$) per cent of head for the size groups respectively. Diameter of eye 23.7–29.3, $M = 26.8$ (25.0–33.3, $M = 28.7$) and depth of cheek 22.8–29.3, $M = 26.7$ (18.1–25.0, $M = 21.2$) per cent of head.

Caudal peduncle 16.5–21.5, $M = 18.6$ (17.8–22.6, $M = 20.0$) per cent of standard length, 1.5–2.2 times as long as deep in fishes of all sizes.

Lower jaw with a distinct symphyseal knob in fishes of all sizes, the protuberance most marked in individuals of > 65 mm S.L. Length of lower jaw 40.8–51.0, $M = 45.6$ (37.6–46.2, $M = 42.0$) per cent of head, 1.6–2.0 (modal range 1.8–2.0) times longer than broad in specimens of all sizes. Length of upper jaw 31.8–44.0, $M = 38.4$ (30.6–37.6, $M = 33.3$) per cent of head.

Mouth slightly oblique, the posterior tip of the maxilla reaching a vertical through the anterior margin of the orbit, or to a point slightly posterior to that line.

Gill rakers. Of variable form, but usually with the upper 2 or 3 rakers on the first gill arch flattened and branched, those on the middle section of the arch relatively slender, and the lowermost 1 or 2 rakers reduced; no pseudorakers are developed

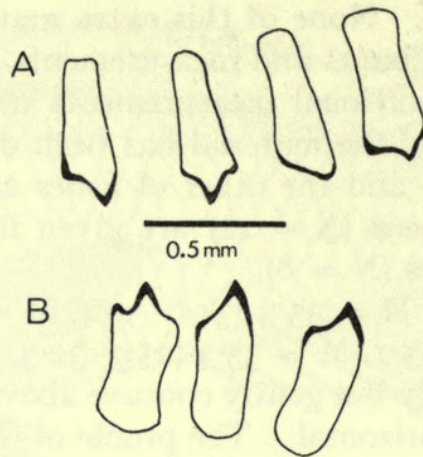


FIG. 8. *Haplochromis macconneli*. Dentition. A: Outer teeth from the premaxilla. B: Outer teeth from the dentary. In both, the teeth are from an anterolateral position in the jaw and are viewed labially.

(see p. 143). There are 7 (f1), 8 (f8) or 9 (f21) rakers on the lower limb of the first gill arch.

Scales. Ctenoid, those on the chest very small but grading in size with those on the subpectoral region (that is, the demarcation between small and large scales in this region is less abrupt than in *H. rudolfianus*; see p. 154).

Five and a half to 7 (mode 6) scales between the dorsal fin origin and the lateral line, 7–9 (modes 8 and 9), rarely 5, between the pectoral and pelvic fin bases. Cheek with 3 or 4 rows of imbricating scales. In most specimens there is a small naked area (about the area of one scale) in front of the first dorsal fin spine.

Fins. Dorsal with 22 (f6), 23 (f16) or 24 (f8) rays, comprising 13 (f2), 14 (f16), 15 (f11) or 16 (f1) spinous and 8 (f11), 9 (f18) or 10 (f1) branched rays. Anal with 3 spines and 7 (f2), 8 (f25) or 9 (f3) branched rays. First ray of the pelvic fin slightly produced, more so in larger fishes. Caudal truncate, scaled on its proximal quarter (mode) to third. Pectoral fin 25.8–34.5, $M = 28.6$ (23.7–28.3, $M = 26.1$) per cent of standard length, and 73.0–92.5, $M = 81.1$ (63.5–77.0, $M = 72.3$) per cent of head.

Teeth. In fishes more than 50 mm S.L. the outer row of premaxillary teeth is composed of unequally bicuspid teeth anteriorly, but of tricuspid teeth laterally and posteriorly (Text-fig. 8); the median cusp of the tricuspid teeth, and the major cusp of the bicuspid teeth is slightly incurved. Many specimens have some tricuspid teeth intercalated amongst the bicuspid teeth anteriorly, and in a few fishes almost the entire outer row is composed of tricuspid teeth. When there is a mixture of bi- and tricuspid teeth the latter predominate. At all positions in the tooth row the bi- and tricuspid teeth are of equal size.

Tooth morphology and arrangement in the lower jaw are similar to those in the upper, although more individuals have only tricuspid teeth present; a predominantly bicuspid outer row is rarely encountered.

Fishes in the size range 20–40 mm S.L. have mainly bicuspid teeth in the upper jaw, with those tricuspid teeth present restricted to a posterolateral position in the row.

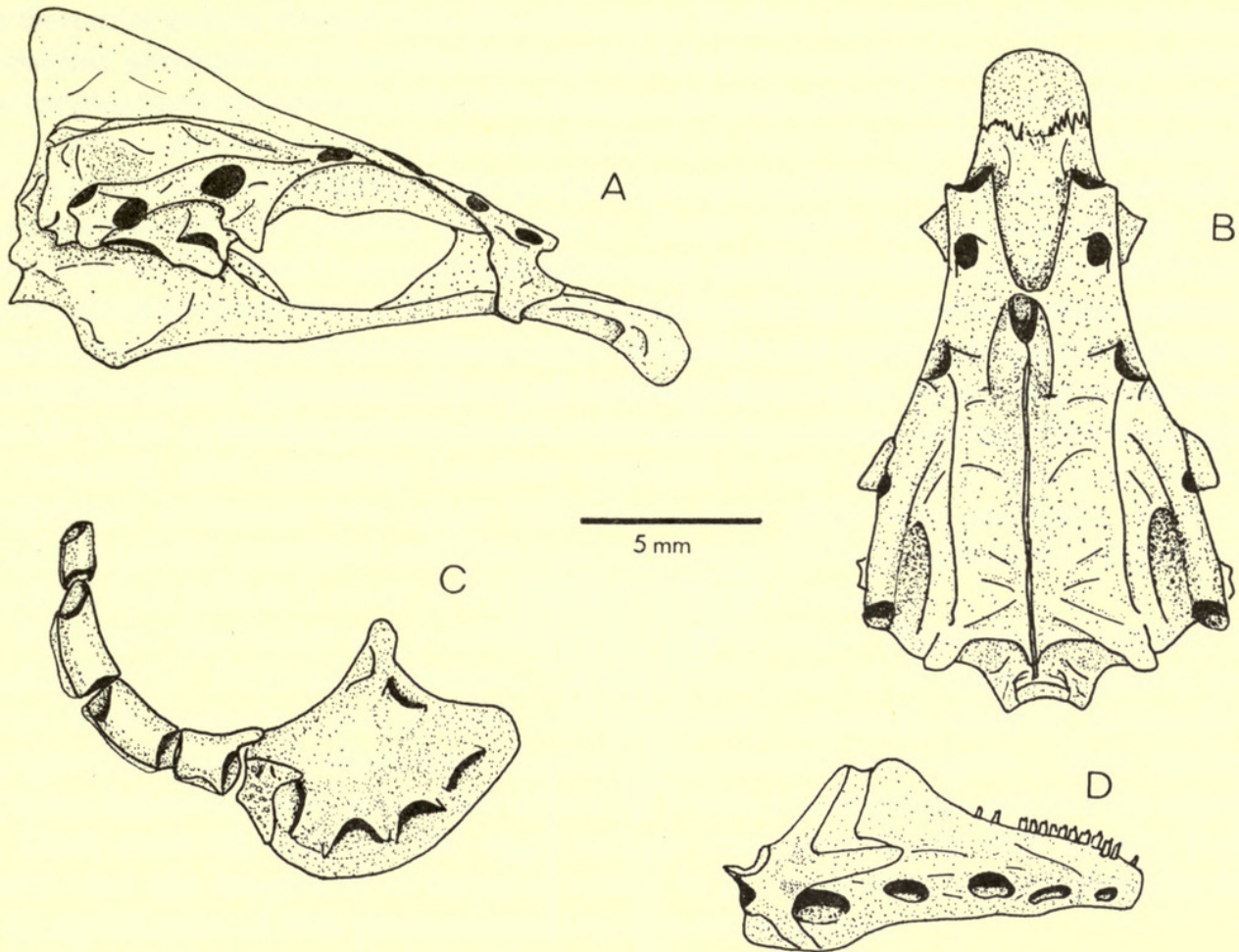


FIG. 9. *Haplochromis macconneli*. A : Neurocranium in right lateral view. B : Neurocranium, dorsal surface. C : Bones of the infraorbital series, right side. D : Right lower jaw, viewed from a slightly ventrolateral position.

Bicuspid teeth also predominate in the lower jaw, but some unicuspid (and slender) teeth may occur posterolaterally. Tooth form is like that of the larger fishes.

There are 41–64 ($M = 52$) outer premaxillary teeth in fishes 50–77 mm S.L., and 24–42 in specimens 22–39 mm long.

Irrespective of a fish's size, the *inner teeth* in both jaws are all tricuspid and small, and are usually arranged in a single series but double rows are encountered occasionally.

OSTEOLOGY. The characteristic hypertrophy in the cephalic laterosensory canal system has been commented upon above (*see also* Text-figs. 7 and 9). Canal bones in the pectoral skeleton are also affected, and the otic region of the skull is noticeably inflated (*see* Text-fig. 9).

The *neurocranium* (Text-fig. 9) departs from the generalized *Haplochromis* type (as seen in *H. rudolfianus*, Text-fig. 3) and clearly approaches that found in *H. saxicola* and allied species in the Lake Victoria species flock (Greenwood, 1974). In other words, the preotic region of the skull is slightly more elongate than in the generalized type, and associated with this and the shallower braincase, the preotic skull roof is straighter and slopes upwards at a smaller angle. The supraoccipital

crest is lower than in most generalized types of skull, and the otic region is narrower.

Although all the canal bones of the skull (and also those bones encasing the inner ear) are noticeably inflated, the dermopterotics show the greatest hypertrophy of all (see Text-fig. 9A and B).

The *lower pharyngeal bone* (Text-fig. 10) is triangular in outline (length and breadth of the dentigerous surface almost equal), is relatively slender, and has an anterior blade that is neither noticeably long nor noticeably short. The teeth on this bone are rather sparsely arranged in 16–20 irregular rows. Without exception, the teeth are weakly bicuspid, with a low, blunt or even barely visible anterior cusp and a crown that slopes gently into the sharper and larger posterior cusp; all are fine and compressed but those in the two median rows are somewhat coarser.

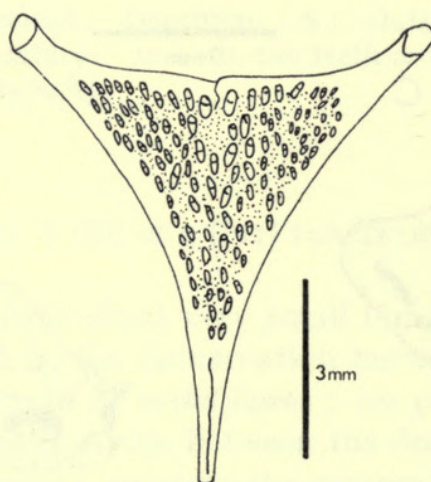


FIG. 10. *Haplochromis macconneli*. Lower pharyngeal bone in occlusal view.

Vertebrae and the caudal fin skeleton. Vertebral counts for the 24 specimens radiographed are: 27 (f1), 28 (f8), 29 (f14) or 30 (f1), comprising 12 (f16) or 13 (f8) abdominal and 15 (f1), 16 (f15) or 17 (f8) caudal centra. The fused first ural and first preural centra are excluded from these counts.

The caudal fin skeleton is unusual in showing a high degree of fusion between various hypurals (or if not fusion, such extremely close apposition as to be indistinguishable from fusion on radiographed specimens). The extent of fusion or apposition is generally complete, but in a few fishes there are short unfused sections between the otherwise conjoined elements.

About 77 per cent of the 26 specimens radiographed showed some degree of fusion between various hypurals. Only 6 specimens (*ca* 23 per cent of the sample) had all 5 hypurals completely free from each other. Most frequently (i.e. in 20 fishes) hypurals 1 and 2 are fused. In the upper part of the skeleton the commonest pattern of fusion is to have hypurals 3 and 4 fused, but hypural 5 free (11 specimens); only 4 specimens had all 3 upper hypurals fused, and 5 fishes showed no fusion between any of the 3 upper hypurals. In *H. rudolfianus*, it will be recalled, only 2 out of 30 specimens (i.e. about 7 per cent) had any fused hypurals; in both these fishes fusion was between hypurals 1 and 2 (see p. 146).

For comparison with the situation in Lake Rudolf, the caudal skeleton in several endemic *Haplochromis* species from other lakes was examined. Of 174 specimens (representing 12 species) from Lake George, Uganda, about 8 per cent showed some (but never complete) fusion between elements in both the upper and the lower parts of the skeleton. The frequency of fusion seems equally distributed amongst the species examined.

In Lake Victoria, too, hypural fusion is relatively rare. One hundred and seventy-eight specimens representing 22 species (with a modal sample size of 10 specimens per species) were examined. Of these, 20 specimens (i.e. about 13 per cent) had fused hypurals. The commonest pattern here is of fusion between hypurals 3 and 4, less frequently it occurs between hypurals 1 and 2, and only once was it recorded, with certainty, between hypurals 1 and 2, and 3 and 4 in the same individual (although two other individuals may show this pattern). The Lake Victoria species examined are from several phyletic lineages within the *Haplochromis* flock of that lake and cover a wide range of body forms.

Far fewer specimens are available of the four endemic *Haplochromis* species from Lake Albert. Of these, *H. bullatus* Trewavas has 3 out of 18 fishes (i.e. about 17 per cent) with hypurals 1 and 2 fused (or very closely apposed), while *H. avium* Regan (9 specimens) and *H. albertianus* Regan (15 specimens) have none. Both the latter species, however, have some individuals in which the hypurals are closely apposed.

Thus, even allowing for the small sample sizes involved in this survey, it does seem that the frequency of hypural fusion in *H. macconneli* is exceptionally high. The significance of this phenomenon remains unexplained.

VISCERA. Because of poor preservation it is impossible to measure precisely the length of the gut in *H. macconneli*; I would estimate the intestine to be about $1\frac{1}{2}$ times longer than the standard length. In strong contrast to *H. rudolfianus* there is no trace of melanin in the peritoneal tissue and neither are the gonadal walls pigmented (see p. 146 above).

COLORATION. In life, *adult females* are a pale greenish-fawn with traces of greenish iridescence on the flanks. All fins are colourless except for three conspicuous and bright yellow spots on the anal.

Live colours for *males* have not been recorded.

Preserved colours. I suspect that the material I have examined is somewhat bleached and thus the coloration is probably lighter than it might otherwise have been.

There is apparently little sexual dichromatism. In both sexes the ground colour of the body and head is a pale yellowish-fawn with no tonal variation between dorsum and venter. All fins are hyaline with, in both sexes, dark maculations on the proximal third to half of the caudal fin. The males examined have the dorsal fin somewhat darker than that of the females, and there is a fairly dense aggregation of melanophores on the anterior third of the pelvic fins. (These specimens may, however, be less bleached than are the females.)

ECOLOGY. Judging from Mr Hopson's records, *H. macconneli* is confined to water more than 20 m deep, and is probably most abundant in deeper water (i.e. at depths

of 50–70 m). Some of the smallest specimens collected (15–20 mm S.L.) were caught at a depth of 75 m, and none, of any size, has been recorded from littoral habitats. The pale coloration of this species and the absence of melanic pigments in the peritoneum and gonads may well be correlated with this deep-water distribution.

No data are available yet on the feeding habits of the species.

Breeding biology. The marked sexual dimorphism in adult size has been noted already (p. 154). Despite a very thorough search, Mr and Mrs Hopson were at first unable to find any males amongst the several hundreds of *H. macconneli* they examined. Eventually two males, 31.0 and 35.5 mm S.L., were identified in a catch made some 2.4 km east of North Island at a depth of 30 m. Both these fishes appear to be sexually adult; one is probably in an advanced stage of ripening, the other at a slightly earlier stage of development. Females are certainly adult at a length of *ca* 50 mm and it seems likely that they may mature at a smaller size (Hopson *in litt.*). Be that as it may, females seem to grow to a much greater length than do males.

In a sample of 21 adult females examined, only 2 have both ovaries equally developed. Eleven fishes have the right ovary much larger than the left one (at all stages of oogenesis), and 8 have only the right ovary developed. Unlike *H. rudolfianus*, there is no trace of melanization in the ovarian wall of *H. macconneli*.

No details are available on the breeding habits or seasons of the species.

DIAGNOSIS AND AFFINITIES. *Haplochromis macconneli* is readily distinguished from the other Lake Rudolf species by the hypertrophy of its cephalic laterosensory canal system, its dentition (*see* p. 156), and in specimens > 35 mm S.L., from *H. rudolfianus* by several morphometric characters (deeper cheek and preorbital, longer snout, smaller eye and longer jaws).

Indeed, *H. macconneli* is so distinct morphologically from *H. rudolfianus* and *H. turkanae* (and the putative fourth species) that it is difficult to establish its phyletic affinities with these other taxa. In addition to the characters listed above, *H. macconneli* also differs from *H. rudolfianus* (and from the undescribed species too) in the shape of its neurocranium, which is of a more specialized type (*see above*, p. 157 and Greenwood, 1974). Almost certainly the hypertrophy of the cephalic lateral line canals is an adaptation associated with the deep-water habitat of *H. macconneli*, and strongly suggests that the species evolved within the lake. No fluvial *Haplochromis* exhibits this specialization.

It is interesting to note that the cephalic lateral line canal hypertrophy seen in *H. macconneli* is much greater than that found in any known *Haplochromis* species living at comparable depths in Lake Victoria (Greenwood & Gee, 1969). Amongst *Haplochromis*-group species an equivalent hypertrophy is seen only in *H. bullatus* of Lake Albert, and in species of the endemic Lake Malawi genus *Trematocranus* (Trewavas, 1935). Species of another Malawi endemic, *Aulonocara*, show greater development in certain parts of the system (the infraorbital series for example), but otherwise exhibit a level of hypertrophy comparable with that of *H. macconneli*.

Trematocranus and *Aulonocara* are manifestly more closely related to each other and to other taxa from Lake Malawi (Trewavas, 1935; personal observations) than

to any species occurring outside the lake. Neither need be considered further in the possible phylogeny of *H. macconneli*.

On purely morphological grounds *H. bullatus* of Lake Albert could be considered the nearest living relative of *H. macconneli*. Both species share the specialization of enlarged laterosensory canals on the head, and both share (with other species from Lakes Albert and Rudolf) certain peculiarities in the predorsal and thoracic squamation patterns (see above, p. 144). The latter character is, however, difficult to assess with respect to its being a primitive or a derived one. At present all that can be said is that the pattern is not encountered amongst the *Haplochromis* species of Lake Victoria nor is it seen in the fluviatile *Haplochromis* of Kenya, Uganda and Tanzania. It is rarely encountered in the *Haplochromis* species flock of Lakes Edward and George (where it is known from two species, *H. pharyngalis* Poll and *H. petronius* Greenwood; see Greenwood, 1973), but it does seem to characterize the *Haplochromis* of the River Nile, Lake Albert, Lake Rudolf and the River Zaire (personal observations; also Greenwood, 1971).

Haplochromis macconneli differs from *H. bullatus* in the shape of its neurocranium (see p. 157 above) which is like that found in the moderately specialized insectivore-piscivore radiation in Lake Victoria (see Greenwood, 1974, pp. 80-93). This difference would not, of course, debar *H. bullatus* from consideration as the living plesiomorph sister species of *H. macconneli*. But the fact that the Lake Rudolf and Lake Albert basins have never been interconnected (and if there had been some riverine connection, the probability that any presumed common ancestor of the two species would itself have been abyssal in habits) seems to rule out any such close phyletic relationship. Interspecific similarities in laterosensory canal hypertrophy are thus to be interpreted as the product of parallel evolution. The shared peculiarities in squamation patterns may well reflect a common ancestry but this is likely to be a relatively distant one (see below, p. 162).

It seems probable, therefore, that the relationships of *H. macconneli* should be sought amongst the species of Lake Rudolf. Two interpretations seem possible. First, *H. macconneli* may be an immediate derivative of an *H. rudolfianus*-like ancestor (i.e. *H. rudolfianus* and *H. macconneli* may be true sister species). Alternatively, *H. macconneli* might be the apomorph survivor of another lineage the relatively plesiomorph, that is *H. rudolfianus*-like members of which have become extinct (unlike the situation in Lake Victoria, for example, where it is possible to follow, from species still extant, the specialization of a lineage; see Greenwood, 1974).

DISCUSSION

Even with the discovery of two and possibly three new *Haplochromis* species, the total fish fauna of Lake Rudolf still stands low on the scale of endemism in African lakes. Its *Haplochromis* species flock also shows a low level of adaptive radiation, probably lower than that of Lake Albert (see Trewavas, 1938; Greenwood, 1971) where an anatomically specialized mollusc-eater, a specialized grazer on epiphytes and a species adapted for life in deep water have evolved.

This comparison must, however, be interpreted with care. For one thing, *H. mahagiensis* David & Poll (the mollusc-crushing species) of Lake Albert may well belong to a different lineage from that of the other species in the lake. It could be the local representative of a fluviatile mollusc-crushing species represented elsewhere by *H. straeleni* Poll and *H. vanderhorsti* Greenwood (see Greenwood, 1954 & 1959a, for discussion). Furthermore, a temporal element is probably involved. There is little evidence of Lake Albert having dried out at any time in its history, but Lake Rudolf probably was severely reduced, or even completely desiccated, during the middle part of the Pleistocene (see Fryer & Iles, 1972, for review). Refilling of the Rudolf basin appears to have been through what is now the River Sobat at some time within the later Pleistocene. Subsequently the connection was broken and has never been re-established. Such an historical background has two consequences, namely that Lake Rudolf is to be considered a relatively young lake, and that its colonizers (or, perhaps more accurately, its recolonizers) were species of Nilotic origin.

The relative youth of Lake Rudolf, coupled with the nature of its basin may, as Fryer & Iles (1972) suggest, account for the paucity of endemic species and, I would also suggest, for the muted adaptive radiation seen amongst the three or four *Haplochromis* species that evolved there.

With two exceptions, all the *Haplochromis* species of Lake Albert are apparently confined to the basin of that lake. The two more widely distributed species, *H. wingatii* (Blgr.) and *H. loati* Greenwood, both have dental specializations that are not shared with any Lake Rudolf taxa (Greenwood, 1971). Thus, it seems unlikely that an extant Albertine *Haplochromis* species was the original recolonizer of Lake Rudolf in later Pleistocene times. Nor does it seem probable that the recolonizer closely resembled any species from the Nile (amongst which must be considered *H. wingatii* and *H. loati* or their ancestors). In this situation the only conclusion that can be drawn is that some fluviatile species, now extinct, provided the founder population for the Lake Rudolf microflock.

It is, of course, possible that the present-day Rudolf species (or some part of them) are descendants from the relicts of a previous flock, possibly a more complex one, that inhabited the early Pleistocene lake and which survived the subsequent period of desiccation. The neurocranial differences between *H. rudolfianus* and *H. macconneli* might be explained in this way. If this was the history of the present-day species then it follows that their ancestors were derived not from the Nile (which did not then exist in its present form; see Berry & Whiteman, 1968), but from a river that originated in the eastern highlands and emptied into the developing Nile system in the region of the present River Sobat.

Shared peculiarities in the squamation pattern of the thoracic and predorsal regions hint at a common ancestry for the Lake Rudolf and Lake Albert *Haplochromis* species (see above, p. 161). This character complex is not found in the *H. bloyeti*-like species group that is widespread in the rivers of Uganda, Kenya and Tanzania. Members of this species complex are thought to be close relatives of the ancestral species which gave rise to the sister species flocks in Lake Victoria and Lakes Edward and George (see Greenwood, 1973 & 1974). Fishes in these flocks, with one exception in Lake George and one in Lake Edward, all lack the Albert-Rudolf scale

pattern. The exceptional species, *H. petronius* and *H. pharyngalis*, resemble the Nilotic *H. wingatii* in several features as well as the one of scale pattern, and they may represent an exotic element amongst the otherwise *H. bloyeti*-like derivatives inhabiting these lakes (Greenwood, 1974). The possible phyletic relationship of *Haplochromis* species from Lakes Rudolf and Albert raises some interesting points of zoogeography. The lakes are several hundred kilometres apart and any form of past interconnection they may have had would have been of an indirect nature (see above, p. 162). In contrast, Lake Albert is close to Lake Edward and the lakes are in direct contact through the River Semliki. Yet, their faunas, both cichlid and non-cichlid, are quite distinct (Greenwood, 1959b). The present barrier to faunal interchange, principally the Semliki rapids, is clearly an effective one.

I have argued elsewhere for a close phyletic relationship between the *Haplochromis* species of Lakes Edward and Victoria and for their derivation in parallel from a common ancestor that once inhabited the westward flowing rivers of eastern Africa during the Pleistocene (Greenwood, 1973). It seems now that perhaps this concept should be qualified by postulating an ancestral species that lived in some but not all of those rivers. The reasoning behind this qualification is, of course, the presence of species in Lake Albert that would seem to be derived from a different lineage, a lineage that also gave rise to the species of the Nile and, possibly, Lake Rudolf as well (see above, p. 161). Furthermore, it is possible that the *Haplochromis* species of the River Zaire may share ancestry with these species (p. 161).

The evidence upon which these postulated phylogenies are based, a shared scale pattern, is admittedly tenuous, particularly since it is not yet possible to determine which of the two types is to be considered the primitive condition. Further research is planned to investigate the phylogeny of *Haplochromis*-group species and I would certainly not consider the ideas expressed here as more than a working hypothesis.

The presence of two species with Albert–Rudolf scale patterns (*H. petronius* and *H. pharyngalis*) in Lakes George and Edward demands explanation. Three possible explanations can be considered. First, the ancestor of these species made its way into the Lake Edward basin in fairly recent times and *via* the River Semliki. The likelihood of this, however, is reduced by the fact that no reciprocal exchange of *Haplochromis* seems to have taken place (although the two lakes share another cichlid *Sarotherodon leucostictus* [Trewavas]). Second, the prerift rivers each may have contained species of both squamation types. The absence of species with the Albert–Rudolf pattern from most rivers in eastern Africa (and probably from Lake Victoria as well) would seem unlikely if both types had been represented there previously. The third possibility is one based on the assumption of there having been a single basin in which the proto-Lakes Albert and Edward developed, probably as a series of partly interconnected small and swampy lakes. The northern region of this basin (the future Lake Albert) could have been fed by rivers in which the *Haplochromis* species had an Albert–Rudolf facies, while the southern end (future Lakes Edward and George) was fed by rivers with *Haplochromis* of a Victoria–Edward facies. The next assumption would be that only a limited exchange of species took place between the two regions before their continuity was broken. Victoria-type species, if any penetrated to the north, were, presumably, unsuccessful in that

environment or in competition with the Albert-Rudolf types. Such a general contact between the early lakes may also account for the similarity in their Pleistocene fish faunas (see Greenwood, 1959b; also new and unpublished observations), although one can equally argue that a fauna of this type was widespread in the prerift river systems.

Whatever the explanation, it does seem that both Lake Albert and Lake Rudolf have, since their inceptions, been relatively isolated from each other and from other water bodies in eastern Africa.

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