A REVISION OF THE LAKE VICTORIA HAPLOCHROMIS SPECIES (PISCES, CICHLIDAE), PART III

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INTRODUCTION

FIVE of the seven species described in the first part of this paper are known to feed almost exclusively on the embryos and larvae of other cichlid fishes, especially *Haplochromis*. Data on the food of the sixth species are very inadequate but are nevertheless indicative of similar habits. The seventh species is known from only a few specimens, but various morphological similarities between it and two other species of this group suggest embryo and larval fish-eating habits.

If the species on which these fishes prey are mouth-brooders, it can be said that none of the young found in the stomachs of the predators was of a size at which it

would normally have left the parental mouth.

Despite identical feeding habits, the members of this species group are morphologically heterogeneous and exhibit convergence only in a tendency for the teeth to be deeply embedded in the oral mucosa and in having capacious mouths. Furthermore, in most species there is a marked intra-specific variability in gross morphology, especially of the head. It seems that the group is of polyphyletic origin.

The four species dealt with in the second part of the paper are, morphologically speaking, somewhat isolated from the other Haplochromis of Lake Victoria. All are insectivores.

Haplochromis cronus sp. nov.

(Text-fig. 1)

Holotype. A female, 135 mm. standard length, from Buka Bay, Uganda.

Description, based on eight specimens, including the holotype, 114-135 mm. standard length.

Depth of body 39·5-43·5 per cent of standard length, length of head 30·3-34·6 per cent. Dorsal head profile strongly curved, with a well-defined but localized

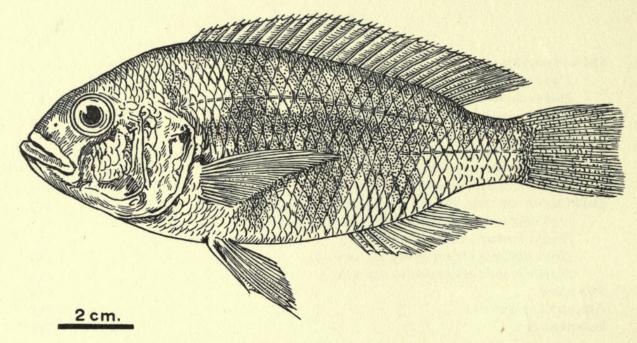


Fig. 1. Haplochromis cronus; holotype. Drawn by Miss D, Fitchew.

swelling above the anterior part of the eye. Preorbital depth 16·7-18·2, mean (M) 17·5 per cent of head length; least interorbital width 31·9-35·5 (M = 33·1) per cent. Snout slightly broader than long, its length 31·6-35·7 (M = 33·7) per cent of head; eye diameter 23·1-26·3 (M = 25·2), depth of cheek 29·3-34·2 (M = 30·1) per cent. Caudal peduncle 15·2-17·3 per cent of standard length, 1·1-1·3 (mode 1·3) times

as long as deep.

Jaws equal anteriorly; lips thickened; posterior tip of the maxilla not bullate and almost completely hidden beneath the preorbital, extending to the vertical through the anterior part of the eye. Lower jaw stout and deep, its length 29·3-34·2 (M = 30·1) per cent of the head, 1·2-1·4 times as long as broad.

Gill rakers stout; 8-10 on the lower limb of the first arch.

Scales ctenoid; lateral line with 32 (f.5), 33 (f.1) or 34 (f.2) scales. Cheek with four or five series. Five to 8 scales between the dorsal fin origin and the lateral line; 8 or 9 between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.7) or 25 (f.1) rays, anal (damaged in one specimen) with 12 (f.7), comprising XV or XVI, 9-10 and III, 9 spinous and branched rays for the fins respectively. Pectoral fin shorter than the head; pelvic fins with the first soft ray produced and extending to the vent in females and to the anal fin in males. Caudal truncate, the rays noticeably coarse; densely scaled over about four-fifths of its length (a most unusual character in Lake Victoria Haplochromis species).

Teeth. The outer row in both jaws is composed of unicuspid, fairly stout teeth, implanted vertically and not hidden by thickened oral mucosa; there are 40-56 teeth in this series of the upper jaw. The inner teeth are small and unicuspid, arranged in two rows (three in one specimen) in both jaws, and are separated from the outer

series by a distinct space.

Lower pharyngeal bone triangular, the dentigerous area about 1.3 times as broad as long; the teeth are slender and cuspidate.

Syncranium. The syncranium is noticeable for its short and deep neurocranium (comparable with H. obesus; see p. 185) and for the stout but otherwise unspecialized dentary. These characters were determined from a radiograph B.M. (N.H.) Reg. No. 957 and the partial dissection of one specimen.

Vertebrae: 13 + 16 in the single specimen radiographed.

Coloration of preserved material: Adult females and sexually quiescent males. Ground colour dark golden above, lighter below, with traces of a golden-yellow flush on the operculum: a broad, mid-lateral stripe of variable depth and intensity crossed by four or five broad but faint transverse bars on the flanks; a well-defined lachrymal stripe. Dorsal fin hyaline, with dark spots and bars on the soft part (probably deep red in life); caudal hyaline (densely maculate in males); proximal two-thirds of anal fin dark, remainder light; pelvic fins dark (black laterally in males).

One of the three females available has a typical "bicolor" (piebald black and yellow) coloration, similar to that described in several other and apparently unrelated Haplochromis species and in two monotypic genera (Greenwood, 1957, and p. 213).

Sexually active male. Dark brown above, sooty-grey below; transverse and lateral stripes faint except at their junction mid-laterally. Dorsal fin dusky, the soft part maculate; caudal dusky and densely maculate; anal dark, except for its extreme tip and two colourless ocelli. Pelvic fins black on the lateral half and dusky mesially.

Distribution. Known only from Lake Victoria.

Ecology: Habitat. Five of the eight specimens are from an exposed beach habitat, one is from the sandy littoral of a sheltered gulf, one from the mud-bottom sublittoral of a sheltered bay and one from shallow water near a reed bed (no other data available). In no locality was the water more than 20 feet deep.

Food. Four specimens contained food in the stomach; in each, only larval cichlid fishes were found (in three fishes these were identified as Haplochromis); the number of larvae in each fish was: 127 (ca. 11 mm. long); 50 (ca. 11 mm.) and 41 (ca. II mm.). The remains found in the fourth fish were too fragmentary to allow even an estimate of numbers.

Breeding. Two females were found with, in one, larvae and in the other, newly

hatched embryos in the buccal cavity. Since the ovarian condition of these fishes was clearly "spent" it can be assumed that the young were the fishes' own brood and not prey.

Affinities. Haplochromis cronus belongs to the small group of deep-bodied, broad-headed Haplochromis whose adult size is ca. 100–140 mm. S.L. The specialized mollusc-eating species H. pharyngomylus Trewavas and H. ishmaeli Boulenger may be cited as examples of this morphotype. H. cronus differs from all other members of the group in having a densely and extensively scaled caudal fin. The species shows some affinity with H. obesus and H. maxillaris, forms which may have evolved independently from an H. cronus-like ancestor.

Diagnosis. From other species with a similar gross morphology, H. cronus can be distinguished, primarily, by its almost completely scaled caudal fin (four-fifths scaled in H. cronus cf. two-thirds scaled in other species). The relatively large, completely exposed, caniniform and recurved teeth of H. cronus, together with an unmodified lower pharyngeal dentition and the presence of a supra-orbital swelling, also serve to distinguish H. cronus from other morphologically similar species.

Study material and distribution records

Museum and Reg. No.	Locality Uganda	Collector
B.M. (N.H.).—1958.1.16.85 (Holotype)	Buka Bay	E.A.F.R.O.
B.M. (N.H.).—1958.1.16.86–89 ,, 1958.1.16.90 ,, 1958.1.16.91	Napoleon Gulf near Jinja Pilkington Bay	,, ,,
,, 1928.5.24.408	Kenya Port Victoria (Graham's St. No. 84)	M. Graham

Haplochromis obesus (Boulenger) 1906 (Text-figs. 2 and 3)

Pelmatochromis obesus (part) Boulenger, 1906, Ann. Mag. nat. Hist. (17) 17, 447 (type specimen, by restriction [specimen figured in Fish. Nile], only); Idem, 1907, Fish. Nile, 491, pl. LXXXIX fig. 5; Idem, 1915, Cat. Afr. Fish. 3, 414, fig. 283.

Lipochromis obesus (Boulenger), Regan, 1920, Ann. Mag. nat. Hist. (9) 5, 45 (foot-note).

Haplochromis obesus (Boulenger), Regan, 1922, Proc. zool. Soc. London, 170.

Paratilapia gestri Boulenger, 1911, Ann. Mus. Genova (3), 5, 67, pl. I, fig. 3.

Paratilapia gestri (part, holotype only). Boulenger, 1915, Cat. Afr. Fish. 3, 318, fig. 211.

Haplochromis gestri (part, holotype of P. gestri only), Regan, 1922, Proc. zool. Soc. London, 170.

The union of *H. obesus* and *H. gestri* might be questioned if only the type specimens of the two species were available; indeed, for a long time I thought that the species were distinct. However, after examining a large series of *H. gestri*-like specimens, I am forced to conclude that the type and unique specimen of *H. obesus* is merely an aberrant individual from a species whose modal morphotype is "gestri"-like.

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In my opinion, the critical specific character-complex is the broad and stout lower jaw, combined with a relatively fine premaxilla and a stout, posteriorly bullate maxilla. These characters are easily verified in the type specimens of *H. obesus* and *H. gestri*, and have been further confirmed in a radiograph of the former.

In its gross morphology and partly in its physiognomy, the type of H. obesus differs from all except one of the 46 specimens now referred to this species; these differences may be partly attributable to post-mortem changes and poor preservation. In Boulenger's figure (reproduced here as Text-fig. 2) the mouth is shown as it appeared when closed artifically, with the result that the gape is very oblique. With the passage of time, the specimen has softened and it is now possible to close the mouth more easily. If this is done, it will be seen that the angle of the mouth is only slightly

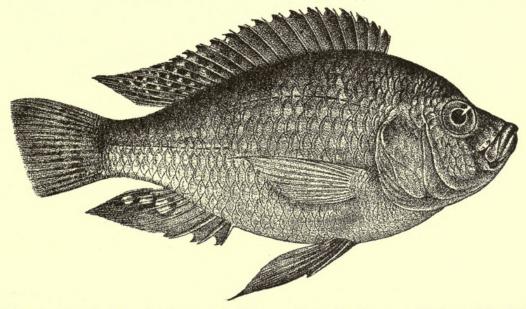


Fig. 2. Haplochromis obesus; holotype (from Boulenger, Fishes of the Nile).

oblique and that the dorsal head profile, although sloping steeply, is not so markedly concave as it appears in the figure. The lower jaw closes within the upper and only the anterior part of the maxilla is covered by the preorbital. Whether or not this is due to a natural deformity or to *post-mortem* distortion, I cannot say.

Although, in appearance, the majority of specimens resemble the holotype of *H. gestri*, there are several others which depart from that mode but still retain the diagnostic dentary, upper jaw elements and dentition of the species.

Description, based on 48 fishes (71–170 mm. S.L.) including the type, and the holotype of *H. gestri*.

Depth of body 33.6-47.3 per cent of standard length; length of head 30.3-35.9 per cent. Physiognomy variable, the dorsal head profile straight or very slightly concave in the interorbital region, sloping steeply (Text-fig. 4); most fishes resemble the figured specimen. Preorbital depth 12.5-17.3 (M = 15.4) per cent of head length, least interorbital width 27.3-37.0 (M = 32.2) per cent. Snout 1.20-1.33 times as broad as long, its length 28.0-39.5 (M = 33.5) per cent of head; eye diameter shows negative allometry with standard length, being 23.7-30.4 (M = 27.6) per cent in

23 fishes less than 125 mm. S.L. and 20.5-27.9 (M = 23.6) per cent in 25 larger individuals; depth of cheek 21.8-31.8 (M = 27.6) per cent.

Caudal peduncle 12·8-17·9 per cent of standard length, its length 1·0-1·6 (modal range 1·0-1·2) times its depth.

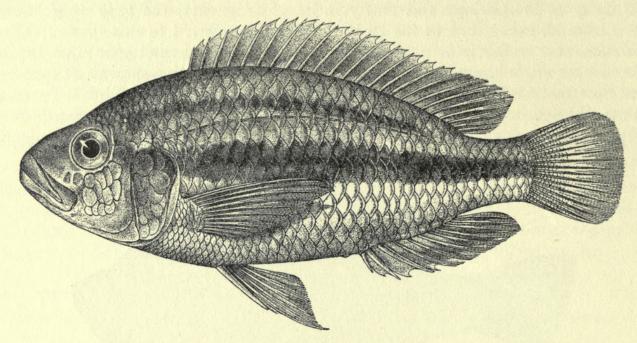


Fig. 3. Haplochromis obesus; typical form (holotype of Paratilapia gestri). From Boulenger, Ann. Mus. Genova, 1911.

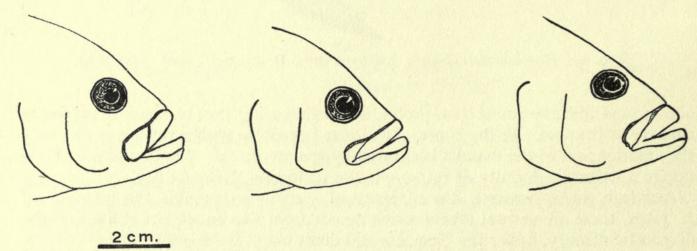


Fig. 4. Haplochromis obesus; individual variability of head profile.

Mouth slightly oblique, maxilla bullate posteriorly and only partly covered by the preorbital, reaching the vertical through some part of anterior half of eye. Lips somewhat thickened; jaws equal anteriorly, the length of the lower showing a positive but widely scattered allometry with standard length, 40·0–54·5 per cent of head length. Length/breadth ratio of the lower jaw I·0–I·6 (mode I·3).

Gill rakers short and stout, 9 or 10 (rarely 8 or 11) on the lower part of the first arch.

Scales ctenoid; lateral line with 29 (f.1), 31 (f.11), 32 (f.18), 33 (f.15) or 34 (f.2) scales; cheek with 3 or 4 (rarely 2) series. Six or 7 (rarely 8) scales between the dorsal fin origin and the lateral line; 6–8 between pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.21), 25 (f.26) or 26 (f.1) rays, anal with 10 (f.2), 11 (f.23), 12 (f.21) or 13 (f.1), comprising XV-XVI (rarely XVII), 8—10 and III, 8 or 9 (rarely 10) spinous and branched rays for the fins respectively. Pectoral shorter than the head. Pelvic fins with the first soft ray produced, more particularly so in adult males. Caudal subtruncate or less commonly, obliquely truncate.

Teeth. Both the inner and outer series of teeth are deeply embedded in the oral

mucosa, so that only the tips protrude.

Except for the smallest specimens, the outer teeth in both jaws are relatively stout and unicuspid with conical crowns. In small specimens most teeth are unequally bicuspid, or there may be an admixture of uni- and bicuspid forms. There are 34–52 teeth in the outer series of the upper jaw.

The shape of the teeth is variable; in most specimens the anterior and some lateral outer teeth in the lower jaw have the crown bent so that its tip is directed anteriorly. In the upper jaw there is an admixture of such teeth with the more usual recurved and conical types. Teeth with anteriorly directed crowns are known only in *H. obesus*, *H. maxillaris* and *H. melanopterus*.

The inner teeth are unicuspid and slenderly conical in fishes over 100 mm. S.L.; in smaller individuals there is a combination of unicuspid and weakly tricuspid teeth. Anteriorly in both jaws the inner teeth are arranged in one or, less commonly, two series; the interspace between inner and outer teeth is greatly reduced or even absent.

Lower pharyngeal bone short and broad, the dentigerous surface 1.2-1.6 times

as broad as long; pharyngeal teeth cuspidate and laterally compressed.

Syncranium. The most outstanding skeletal characteristic of H. obesus is the broad and stout lower jaw (Text-fig. 5A). The "obesus"-type dentary is unique amongst the Haplochromis of Lake Victoria. When compared with one of the larger but generalized species the dentary of H. obesus is noticeably bullate in the region where each ramus divides into ascending and horizontal rami.

Departure from a generalized *Haplochromis* condition is also seen in the maxilla, which is deeper and more bullate posteriorly. The neurocranium closely resembles that of *Hoplotilapia retrodens* Hilgendorf and *Platytaeniodus degeni* Boulenger, since the preorbital face is short and the supra-occipital crest deep (Greenwood, 1956). This intergeneric convergence is probably associated with the relatively massive lower jaw of all three species.

When compared with other Haplochromis (e.g. H. cronus and H. pharyngomylus) having approximately the same adult size and similar body-form, it is obvious that the mouth of H. obesus is more distensible and more protrusible. These factors may be associated with the specialized feeding habits of the species (see p. 204).

Vertebrae: 13 + 16 and 13 + 15 (type H. obesus).

Coloration in life: Adult males. Ground colour dark malachite green shading to silvery-blue ventrally; a coppery sheen on the operculum, chest and belly; a

distinct dark mid-lateral stripe. Dorsal fin dark, with an overall pinkish flush; caudal and anal fins dark, the latter with four or five orange-yellow ocelli arranged in one or, more frequently, two rows. Sexually quiescent males have a similar but less intense coloration. Adult females. Olivaceous-silver shading to silver ventrally; a distinct, dark mid-lateral stripe. All fins hyaline; in some individuals there are small yellow spots in the position of the anal ocelli in males. Some females show a typical "bicolor" black and silver (or yellow) piebald coloration. No estimate of the frequency of "bicolor" individuals can be made from the data available; such females have, so far, only been found in the Napoleon Gulf, near Jinja, Uganda.

A second atypical colour-form is also known. Fishes showing the extreme expression of this coloration are uniformly black, but lighter (sooty) ventral coloration is

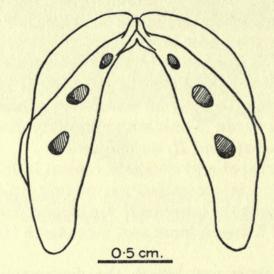


Fig. 5 (A). Haplochromis obesus; outline of dentary, ventral view.

more usual. Unlike the "bicolor" pattern, the dark form is not sex-limited and is known to occur in several different areas of the lake. Furthermore, it shows some intergradation with the usual coloration, at least in males.

Colour in preserved material: Both sexes. Ground colour golden to dark brown (adult males generally darkest); a well defined, dark, mid-lateral stripe and an ill-defined dorsal stripe following the contour of the upper lateral-line; 5–9 vertical bars on the flanks and caudal peduncle; often faint indications of a lachrymal stripe. Pelvic fins black in adult males, otherwise colourless, as are all other fins; soft dorsal and the entire caudal weakly maculate.

Distribution. Lake Victoria and Lake Kwania (Kyoga system).

Ecology: Habitat. Haplochromis obesus is apparently restricted to water less than 50 feet deep in the littoral and sublittoral zones of Lake Victoria. Most of the specimens were caught over a hard substrate (sand, shingle or rock) but two were caught over a soft mud bottom. In all probability, the distribution of H. obesus is closely linked with the spawning and brooding areas of the cichlid fishes on whose embryos and larvae it preys.

Food. Of the 73 specimens examined, 18 had food in the stomach. In every one of these fishes, only fish embryos or larvae were found; with one exception (a small cyprinid fish) the prey could be identified as Cichlidae. A hundred embryos at the same stage of development were recorded from one stomach and in many others the embryos or larvae were all at the same developmental stage; embryos at different ontogenetic stages were, however found in some individuals.

The possibility that these stomach contents did not represent food but rather the fishes' own young accidently swallowed, can be overruled by the following considerations: a mixture of early and advanced ontogenetic stages was found in one stomach; embryos and larvae were found in the stomachs of both male and female fishes and it is unknown amongst the Lake Victoria cichlids for both parents to share brooding duties; early embryos were identified in the stomach contents of



Fig. 5 (B). Haplochromis parvidens; outline of dentary, ventral view.

an immature female; and finally, personal observations show that it is unusual for a brooding female to swallow her brood when she is captured; generally, the young are jettisoned.

It is not known how *H. obesus* or the other larval fish-eating species obtain their prey. The question is complicated because the principal source of food for these species is the young of other cichlid fishes. Both species of *Tilapia* in Lake Victoria and all species of *Haplochromis* whose breeding habits are known are female mouth-brooders. Although late larval cichlids do leave the parental mouth, the earlier, non-free-swimming stages do not, except when the parent is so harrassed that it jettisons the brood. Unless a number of *Haplochromis* are not mouth-brooders, it seems that the larval and embryo fish-eating species employ some means of forcing the parent fish to abandon its brood. It may be added that there is no evidence to indicate that any Lake Victoria *Haplochromis* are not mouth-brooders.

Breeding. A single brooding female was recorded: young removed from the buccal cavity were in the germ-ring stage of development. There is no sex-correlated size difference in adult fishes and sexual maturity is reached at a standard length of about 85 mm.

Affinities. Regan (1922) suggested that H. gestri (= H. obesus) was near Astatoreochromis alluaudi Pellegrin. With the additional information now available on both species, this opinion is no longer tenable. A. alluaudi is a specialized mollusc-eater with hypertrophied pharyngeal bones and the consequent modifications to the syncranial architecture (see Greenwood, 1954). Although H. obesus has a markedly modified lower jaw and somewhat atypical upper jaw features, it is more closely related to the generalized Haplochromis species. The relationships of A. alluaudi lie, apparently, with some of the semi-specialized fluviatile Haplochromis of the Malagarasi and Congo rivers (Greenwood op. cit. and p. 167). Any resemblance between A. alluaudi and H. obesus is entirely superficial and attributable to the stout bodies and broad heads of the two species.

Perhaps the closest relatives of *H. obesus* are *H. cronus* and *H. maxillaris*, with which species it not only shows certain similarity in gross and detailed morphology, but it also shares the same food requirements.

Diagnosis. The shape of the lower jaw (in which there is usually a predominance of unicuspid outer teeth with anteriorly directed crowns) is the most trenchantly diagnostic character. The deeply embedded teeth, together with certain morphometric characters of the head, serve to distinguish *H. obesus* from other Lake Victoria *Haplochromis* species.

Study material and distribution records

Museum and Reg. No.			Locality	Collector				
Uganda								
B.M. (N.H.)	-1906.5.30.311		Bunjako		Degen.			
(Holotype	e Pelmatochromis obesu	is)						
Genoa Museur	n							
(Holotype Par	ratilapia gestri)		Jinja		Bayon.			
B.M. (N.H.)	-1958.1.16.140		Ekunu Bay		E.A.F.R.O.			
,,	1958.1.16.141		Buka Bay		,,			
,,	1958.1.16.142		Channel between Yempita and		,,			
			Busiri Isles, Buvuma Channel					
,,	1958.1.16.143-150		Beach near Nasu Point,		,,			
			Buvuma Channel					
,,	1958.1.16.154-156		SE. tip of Ramafuta Is.,		,,			
			Buvuma Channel					
,,	1958.1.16.157		Karinya, Napoleon Gulf		,,			
,,	1958.1.16.158–161		Entebbe Harbour		,,			
			Kenya					
,,	1958.1.16.151-153		Kisumu Harbour		,,			
	Lake	Vi	ctoria, Locality Unknown					
,,	1958.1.16.162-164				,,			
,,	1928.5.24.341-2				M. Graham.			
			Lake Kwania					
,,	1929.1.24.509			. E.	B. Worthington.			

Haplochromis maxillaris Trewavas, 1928 (Text-fig. 6)

Pelmatochromis microdon (part) Boulenger, 1906, Ann. Mag. nat. Hist. (7) 17, 441; Idem, 1915, Cat. Afr. Fish. 3, 412.

Haplochromis microdon (Boulenger), (part), Regan, 1922, Proc. zool. Soc. London, 173. Haplochromis maxillaris Trewavas, 1928, Ann. Mag. nat. Hist. (10) 2, 94.

Lectotype. A male 114 mm. standard length (B.M. (N.H.) Reg. No. 1928.5.24.486) from Emin Pasha Gulf, Tanganyika Territory (2° 31½′ S., 31° 43½′ E.), Michael Graham's station 227.

Description, based on 58 specimens (including the types) 90-160 mm. S.L.

Depth of body 32·0-42·8 per cent of standard length, length of head 30·0-34·8 per cent. Physiognomy variable, its shape partly dependent on the angle of the mouth

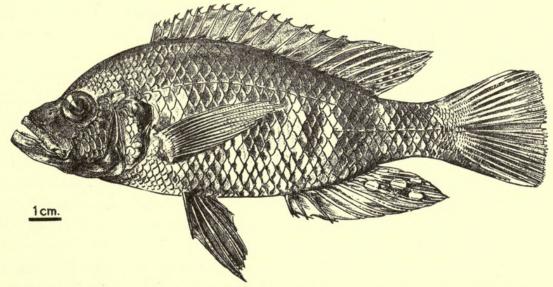


Fig. 6. Haplochromis maxillaris; holotype. Drawn by Miss M. Fasken.

and whether the lower jaw protrudes or not; dorsal head profile concave (markedly so in a few specimens) and sloping at an angle of $40^{\circ}-50^{\circ}$. A few specimens bear a superficial resemblance to H. obesus, but despite this variability in gross morphology there is a distinct modal specific facies (see Text-fig. 6).

Preorbital depth $11\cdot4-16\cdot3$ (M = $13\cdot9$) per cent of head length, least interorbital width $22\cdot6-31\cdot3$ (M = $26\cdot5$) per cent. Snout slightly broader than long, rarely as long as broad, its length $25\cdot8-34\cdot0$ (M = $30\cdot3$) per cent of head. Eye diameter shows negative allometry with standard length: in 15 fishes 60-100 mm. S.L. it is $30\cdot0-38\cdot0$ (M = $33\cdot2$) per cent of head and in 43 larger individuals it is $25\cdot0-31\cdot4$ (M = $27\cdot3$) per cent. Depth of cheek positively allometric with standard length: for the two size groups as above, $18\cdot8-24\cdot2$ (M = $20\cdot7$) and $21\cdot6-27\cdot8$ (M = $26\cdot4$) per cent head length.

Caudal peduncle 12.6–18.5 per cent of standard length, 1.1–1.7 (modal range 1.2–1.3) times as long as deep.

Mouth distensible and usually somewhat oblique when closed, but horizontal in a few specimens. Maxilla partially hidden by the preorbital, its posterior tip bullate and reaching the vertical to the anterior part of the eye or even as far as the pupil. Lips thickened. Lower jaw usually projecting, but in a few fishes the jaws are equal anteriorly. Length of lower jaw shows positive allometry with standard length, in fishes 60-100 mm. S.L. it is $39\cdot0-47\cdot5$ (M = $44\cdot8$) per cent of head length, and in larger fishes $46\cdot5-56\cdot0$ (M = $50\cdot0$) per cent. Breadth of lower jaw contained $1\cdot3-2\cdot2$ (modal range $1\cdot5-1\cdot8$) times in its length.

Gill rakers short, 10 or 11 (rarely 9 or 12) on the lower part of the first gill-arch,

the lower one or two rakers often greatly reduced.

Scales ctenoid: lateral line with 29 (f.2), 30 (f.7), 31 (f.22), 32 (f.20), 33 (f.4) or 34 (f.1) scales; cheek with 2 or 3 series; $5\frac{1}{2}$ -7 scales between the dorsal fin origin and the lateral line, 5-7 (rarely 8) between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.19), 25 (f.36) or 26 (f.3) rays, anal with II (f.18), I2 (f.37) or I3 (f.I), comprising XV-XVI (rarely XVII), 8—I0 and III, 8 or 9 (rarely I0) spinous and branched rays for the fins respectively. Pectoral shorter than the head. First soft ray of the pelvic fin produced, extending to the vent in females and to the soft part of the anal fin in adult males.

Teeth. The inner and outer rows of teeth in both jaws are deeply embedded in the thickened oral mucosa; in many specimens the inner series are invisible without dissection. Furthermore, the outer teeth of the upper jaw are covered by the thick-

ened and inwardly curved margin of the lip.

Fishes less than 80 mm. S.L. have small, weakly and unequally bicuspid outer teeth in both jaws. In larger fishes these teeth are also small, but stout and conical; those in the upper jaw are recurved, whilst those in the lower jaw generally have the crown curved anteriorly or outwardly. Similar teeth are found in *H. obesus*, but are not the predominant form in that species.

In the three skeletons examined there were 34, 36 and 40 outer teeth in the pre-

maxilla.

The inner teeth are weakly tricuspid in small fishes and unicuspid in larger individuals; arranged in one or, rarely, two series and separated from the outer row by a small interspace. Inner teeth in the upper jaw are slightly recurved and implanted so as to slope posteriorly; those of the lower jaw are vertical or directed anteriorly.

Lower pharyngeal bone triangular, the dentigerous area I·o-I·4 times as broad as long; teeth slender and cuspidate, those of the two median rows sometimes coarser.

Syncranium. The dentary of H. maxillaris departs slightly from the generalized type. As in the dentary of H. obesus there is a pronounced lateral bullation of the area surrounding the bifurcation into ascending and horizontal rami.

The premaxilla and maxilla are similar to those of *H. obesus*, except that the premaxillary teeth are restricted to the anterior and antero-lateral areas of the bone. The neurocranium is of a generalized *Haplochromis* type.

Vertebrae: 13 + 16 and 12 + 16 in two skeletons.

Coloration in life: Adult males. Ground colour dark blue-grey, lighter ventrally, with faint indications of darker transverse bars on the flanks. Dorsal fin dusky, with

maroon spots between the rays of the soft part; lappets orange-red. Caudal and anal fins smoky-grey, the latter with three to five yellow ocelli arranged in either one or two rows. Pelvic fins dusky. Coloration in life of *immature males* unknown. Females. Silver-grey ground colour. Dorsal fin greyish; anal and caudal fins similar but with a yellowish flush and, on the caudal, ill-defined, dark spots. Pelvic fins very faint yellow. Several dark, but faint, transverse bars may appear on the flanks immediately after death.

Colour of preserved material: Males. Dark, some with an underlying silvery ground colour, others almost black. Seven or more transverse bands are sometimes visible on the flanks. Dorsal and caudal fins hyaline and maculate, or dusky; anal hyaline or dusky. Pelvic fins black. Females. Ground colour yellowish-silver to brown; some with seven or more transverse bars. All fins hyaline or somewhat dusky; anal and caudal weakly maculate.

Distribution. Known only from Lake Victoria.

Ecology: Habitat. Haplochromis maxillaris is apparently restricted to water less than 30 feet deep, and particularly to the littoral and sublittoral zones of the lake. Most specimens were caught over a hard substrate (sand or shingle), but a few were recorded from mud substrates. Thus the habitat preferences of H. maxillaris are almost identical with those of H. obesus, the two species frequently being caught in the same gear.

Food. Forty of the II8 individuals examined had identifiable food in the stomach. The smallest specimen (44 mm. S.L.) proved exceptional in that the stomach was filled with Copepoda and blue-green algae. All the remaining 39 fishes had eaten cichlid embryos or larvae. In some individuals, the entire stomach contents were of prey at uniform developmental stage, whilst in other fishes two or more stages (often as widely different as early cleavage embryos and late larval fishes) were present. Both sexes were represented amongst the fishes examined, which came from numerous localities.

The remarkable similarity between the food of H. maxillaris and that of H. obesus is noteworthy. Again, it is difficult to imagine how the food is obtained if the species preys on mouth-brooding cichlids.

Breeding. There is no information on any aspect of breeding behaviour in this species. All fishes below 100 mm. S.L. were immature; it seems probable that sexual maturity is reached at a length of about 105 mm. Males and females attain the same adult size.

Affinities. The distensible mouth, stout and posteriorly bullate maxilla, and the thickened lips of H. maxillaris all suggest affinity with H. obesus. Furthermore, conical outer teeth in which the crown is directed anteriorly or laterally are known only in these two species (and H. melanopterus, see below, p. 194). Certain specimens of both species show convergence in gross morphology, but the characteristic lower jaw of H. obesus usually allows for immediate identification. Apart from these few convergent individuals, the two species differ in certain morphometric details of the head and each has a distinctive modal facies. It is difficult to assess the phyletic

significance of the resemblances and differences between *H. obesus* and *H. maxillaris*. The species could be equally well derived from a common stem or from unrelated ancestors within the Lake Victoria species flock.

Study material and distribution records

Museum and Reg. No.			Locality	Collector	
			Tanganyika		
	-1928.5.24.486 ctotype, <i>H. maxillari</i>	· s)	Emin Pasha Gulf		M. Graham.
,,	1958.1.16.182-184		Majita		E.A.F.R.O.
,,	1958.1.16.188		Mwanza, Capri Bay		,,
			Uganda		
	1958.1.16.165–171		Beach near Nasu Point,		
,,	1950.1.10.105-171		Buyuma Channel		"
,,	1958.1.16.172-179		Ramafuta Is., Buvuma Channel		,,
,,	1958.1.16.180		Njoga, Williams Bay		,,
,,	1958.1.16.181		Buka Bay		"
,,	1958.1.16.185-187		Beach near Hannington Bay		,,
,,	1958.1.16.189		Pilkington Bay		,,
,,	1958.1.16.190–193		Bukafu Bay		,,
"	1958.1.16.194–198		Entebbe Harbour		
"	1906.5.30.310		Entebbe		Degen.
"	1958.1.16.199		Ekunu Bay		E.A.F.R.O.
. ,	1958.1.16.205-214	•	Napoleon Gulf, near Jinja		,,
			Kenya		
,,	1958.1.16.200-204		Kisumu Harbour		,,
	Lake	Vi	ictoria, Locality Unknown		
(Syntypes,	1928.5.24.480–485 H. maxillaris)				M. Graham.

Haplochromis melanopterus Trewavas 1928 (Text-fig. 7)

H. melanopterus Trewavas, 1928, Ann. Mag. nat. Hist. (10) 2, 94.

Discussion. This problematical species is known from a single specimen which had suffered some post-mortem distortion before preservation. Its status is, therefore, all the more difficult to decide.

Superficially, *H. melanopterus* is most distinctive. The lower jaw (which closes entirely within the upper) is short, narrow and pointed anteriorly. The preorbital is very shallow so that the greater part of the maxilla is exposed when the mouth is shut. This latter character, together with the peculiar arrangement of the lower jaw in relation to the upper, may be an artefact of preservation and *post-mortem* distortion. The shallow preorbital and the short, pointed lower jaw cannot, however, be attributed to these causes.

The dentition closely resembles that of *H. maxillaris* both in the form of the teeth and their restricted distribution on the premaxilla (see p. 190). The immediate question raised is, are not perhaps the shallow preorbital and the lower jaw size and shape the result of some ontogenetic disturbance in the development of an individual *H. maxillaris*? The apparent distortion of the upper jaw might then be considered teratological rather than the result of *post-mortem* distortion.

In general appearance, *H. melanopterus* is unlike *H. maxillaris* but as Trewavas noted in her original description of the species, it is nearer the *H. maxillaris-obesus* complex than any other species group. Thus, it is impossible to give an adequate

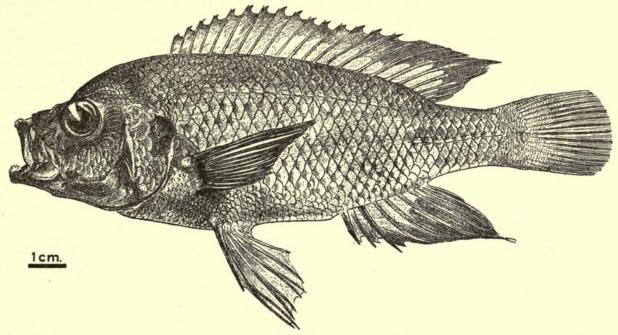


Fig. 7. Haplochromis melanopterus; holotype. Drawn by Miss M. Fasken.

answer to the question posed above. I have decided to treat *H. melanopterus* as a distinct species mainly on the grounds that it is difficult to determine whether or not the peculiar jaws are a teratological feature, and because the nuchal and pectoral squamation of the type is manifestly smaller than in either *H. obesus* or *H. maxillaris*. Also, the rounded caudal fin is a most unusual feature in a Lake Victoria *Haplochromis*.

Description, based on the holotype, an adult male 127 mm. S.L.

Dorsal head profile very concave. Mouth probably oblique; maxilla stout and bullate posteriorly, about three-quarters exposed even when the mouth is shut. In this specimen the mouth is open and the mandible lies horizontally, but the lateral limbs of the premaxilla and the maxillae are almost vertical. Lower jaw narrowing rapidly at a point almost half-way along its length; greatest width contained 1·3 times in the length; the entire lower jaw closing within the upper; lips thickened.

Dentition very similar to that of *H. maxillaris*. Outer teeth conical, those of the upper jaw recurved and restricted to the anterior and antero-lateral aspects of the premaxilla. Teeth in the lower jaw have the crown directed anteriorly or laterally; the anterior teeth of this series are somewhat stouter than the equivalent teeth in *H. maxillaris*. Teeth of the inner series small and unicuspid, arranged in two irregular rows in each jaw.

The oral mucosa appears to have shrunk; consequently the outer teeth are more exposed than those of H. obesus or H. maxillaris, but the inner teeth are deeply embedded.

Lower pharyngeal bone broken, but apparently similar to that of H. maxillaris; pharyngeal teeth slender.

Gill rakers moderately coarse; ten on the lower part of the first gill-arch.

Scales ctenoid; 33 scales in the lateral line; cheek with 3 or 4 series. Nuchal and pectoral scales small. Seven scales between the dorsal fin origin and the lateral line; 9 between the pectoral and pelvic fin bases.

Fins. Dorsal with XV, 8 rays, anal with III, 8. Pectoral very slightly shorter than the head; pelvic fins with the first and second soft rays of about equal length, not quite reaching the anal fin. Caudal rounded.

Vertebrae: 14 + 16 (from a radiograph, B.M. (N.H.) Reg. No. 955A).

Colour: Adult male. Brownish dorsally, brownish-silver on the flanks and belly. Dorsal, caudal and anal fins dusky, pelvics black.

Ecology: Habitat. Smith Sound, Tanganyika Territory (2° 33' S., 32° 50' E.) in 12 feet of water over a mud bottom (Graham, 1929).

Food. The stomach is packed with early embryos of a cichlid fish.

Affinities. Trewavas (1929) compared H. melanopterus with H. obesus (then known only from the holotype). Now that more material of H. obesus is available, the resemblance is found to be less marked. In some respects the morphology of the types is similar, but in the detailed structure of the head and dentition, H. melanopterus would seem to be more closely allied with H. maxillaris. It may yet prove to be merely a teratological specimen of that species.

Haplochromis parvidens (Boulenger) 1911 (Text-fig. 8)

Paratilapia parvidens Boulenger, 1911, Ann. Mus. Genova (3), 5, 65, pl. I, fig. 1; Idem, 1915, Cat. Afr. Fish. 3, 322 fig. 215.

Haplochromis nigrescens (Pellegrin) (part, holotype of P. parvidens only), Regan 1922, Proc. zool. Soc. London, 172.

Regan (1922) considered *H. parvidens* to be a synonym of *H. nigrescens* (Pellegrin) 1909. I have re-examined the holotypes of both species and find that, although at first sight the species do resemble one another, the dentition and form of the lower jaw in *H. parvidens* is most distinctive. Additional material now available confirms and emphasizes these differences. The two species also differ in their feeding habits; *H. nigrescens* is an insectivore and predator on small fishes, whilst *H. parvidens* is a specialized predator on embryo and larval fishes.

Haplochromis parvidens differs from the other larval and embryo fish-eating species in having a more slender and acutely pointed head, characters which typify the less specialized piscivorous predatory *Haplochromis* in Lake Victoria. The shape of the lower jaw is, however, unlike that of any predatory *Haplochromis* species (see Text-fig. 5B).

Description, based on 32 fishes (including the holotype) 63-163 mm. S.L.

Depth of body $33\cdot3-38\cdot2$ per cent of standard length, length of head $33\cdot3-37\cdot5$ per cent. Physiognomy relatively constant, the dorsal head profile straight or gently concave, sloping at an angle of $30^{\circ}-35^{\circ}$. Preorbital depth $15\cdot9-20\cdot5$ (M = $18\cdot6$) per cent of head length; least interorbital width $22\cdot2-28\cdot0$ (M = $25\cdot1$) per cent. Snout length $1\cdot2-1\cdot33$ times its breadth and $32\cdot0-41\cdot3$ (M = $37\cdot7$) per cent of the head; eye diameter $20\cdot3-27\cdot2$ (M = $23\cdot0$), depth of cheek $19\cdot7-27\cdot0$ (M = $24\cdot0$) per cent.

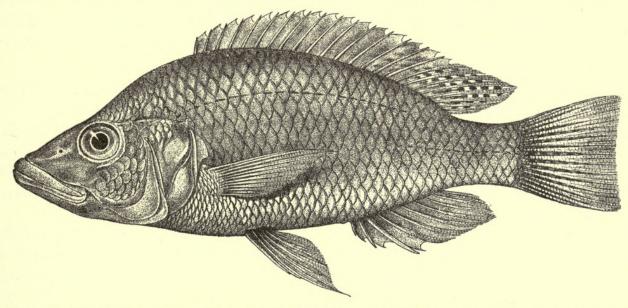


Fig. 8. Haplochromis parvidens; holotype (from Boulenger, Ann. Mus. Genova, 1911).

Caudal peduncle 13.6–16.8 per cent of standard length, 1.1–1.5 times as long as deep (modal range 1.3–1.4 times).

Mouth widely distensible and protractile, slightly oblique or horizontal when closed. Lips thickened. Lower jaw of a characteristic shape (Text-fig. 5B), somewhat rounded in cross-section and narrowing rapidly from a point about half-way along its length; consequently, the anterior part closes within the upper jaw. Length of lower jaw $43\cdot3-55\cdot5$ (M = $48\cdot0$) per cent of head length (showing a weak positive allometry with standard length) and $1\cdot5-2\cdot5$ (modal range $1\cdot9-2\cdot1$) times its width. Posterior tip of the maxilla bullate and almost completely hidden beneath the preorbital, usually not reaching the vertical to the anterior orbital margin, but extending to below the anterior part of the eye in a few specimens.

Gill rakers. Nine to II (rarely 8 or I2, mode Io) on the lower part of the first gillarch.

Scales ctenoid; lateral line with 30 (f.2), 31 (f.14), 32 (f.15) or 33 (f.1) scales. Cheek with 3 or 4 series; 6 or 7 (rarely 5) scales between the origin of the dorsal fin and the lateral line; 6 or 7 (less frequently 5) between the pectoral and pelvic fin bases.

ZOOL. 5, 7.

Fins. Dorsal with 23 (f.1), 24 (f.10), 25 (f.19) or 26 (f.2) rays, anal with 11 (f.9), 12 (f.22) or 13 (f.1), comprising XV-XVI (rarely XIV), 9 or 10 (rarely 8) and III, 8 or 9 (rarely 10) spinous and branched rays for the fins respectively. Pectoral fin shorter than the head. First soft ray of the pelvic fin produced and extending to the anal fin; proportionately longer in adult males.

Teeth. Both the inner and outer rows of teeth are deeply embedded in the oral epithelium, with the inner series often completely hidden. The outer teeth are mainly biscuspid in fishes 63—110 mm. S.L., with some unicuspids present in larger individuals. In fishes above this size, the outer teeth are predominantly unicuspid, relatively slender and recurved; laterally placed teeth point inwards. In the three skeletons available, there are 50, 54 and 62 outer teeth in the upper jaw.

Teeth in the inner series are small, slender and weakly tricuspid in fishes less than 115 mm. S.L., but are unicuspid in larger individuals. In most fishes, the inner teeth are implanted almost horizontally, so that their crowns point backwards. One or two (rarely three) series of inner teeth occur in each jaw and are separated from the outer teeth by a small but distinct interspace.

Lower pharyngeal bone with a triangular dentigerous surface, I·I-I·2 times as broad as long or, rarely, somewhat wider. Lower pharyngeal teeth fine and cuspidate.

Syncranium. The premaxilla and the dentary of H. parvidens are outstanding osteological characters. In combination they are diagnostic of the species.

In *H. parvidens*, the premaxillary pedicels are as long as, or longer than the dentigerous limb of the bone, whereas in the majority of Lake Victoria *Haplochromis* (including the large-mouthed species) the pedicels are shorter.

The mandible has been described above; its skeleton clearly shows the marked anterior narrowing and the peculiar lateral bullation of the area surrounding the bifurcation into ascending and horizontal rami (a similar swelling is also seen in *H. obesus* and *H. maxillaris*).

The maxilla is strictly comparable with that of *H. obesus* and *H. maxillaris*, but the neurocranium differs in having an elongate preorbital face. The preorbital part of the skull is about one-third of the basilar length as compared with one-fifth to one-quarter in generalized *Haplochromis*. In this respect the neurocranium of *H. parvidens* resembles that of a small predatory *Haplochromis* such as *H. nigrescens*.

Vertebrae: 13 + 16 in two skeletons examined.

Coloration in life: Adult males. Ground colour dark blue-black dorsally, silvery-blue ventrally. Dorsal fin sooty, with orange-red lappets; caudal sooty, the dorsal and ventral tips orange-red. Anal fin deep maroon, with two or three red ocelli. Pelvics black. Coloration of immature males unknown. Females. Ground colour an overall olivaceous-green, with faint indications of five to nine dark transverse bars. All fins olivaceous.

Colour in preserved material: Adult and immature males. Dark brown, some adults almost black; faint traces of five to nine transverse bars may be visible on the flanks and caudal peduncle. Dorsal fin dark, the soft part faintly maculate; pelvics black; anal and caudal fins dusky. Females. Golden-brown ground coloration, some faintly barred. All fins hyaline, the dorsal and caudal fins sometimes maculate.

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Distribution. Lake Victoria and Lake Salisbury (a single specimen in the collections of the Uganda Game and Fisheries Department, Entebbe).

Ecology: Habitat. Like H. maxillaris and H. obesus, Haplochromis parvidens is apparently confined to littoral and sublittoral zones where the water is less than 50 feet deep. Unlike the former species, however, H. parvidens is less closely restricted to a particular substrate. Although all three species have been caught in the same habitat, the available data suggest that H. parvidens may be the only member of this trophic group to occur commonly over a mud bottom.

Food. Seventeen of the 60 specimens examined had food in the stomach; of these, 15 had eaten cichlid embryos or larvae. The stomachs of the two other fishes were filled with a fatty, yellow, yolk-like substance.

Breeding. There is no information on the breeding habits of *H. parvidens*. Fishes less than 105 mm. S.L. are immature; there is no apparent correlation between sex and maximum adult size.

Affinities. Despite the deeply embedded teeth, long premaxillary pedicels and unusual lower jaw, there is an overall similarity between H. parvidens and some of the structurally less-specialized predatory Haplochromis. Haplochromis nigrescens, with which H. parvidens was previously synonymized, exemplifies this apparent relationship. There is also some similarity between H. parvidens and H. cryptodon, and more particularly with H. microdon. Haplochromis parvidens could have evolved from either an H. nigrescens-like stem or from a species resembling H. cryptodon.

Study material and distribution records

Museum	and Reg. No.		Locality		Collector
			Uganda		
Genoa Museu	m (Holotype)		Ripon Falls, Jinja		Bayon.
B.M. (N.H.)	-1911.3.3.33		,, ,,		,,
,,	1958.1.16.95		Kaianje		E.A.F.R.O.
,,	1958.1.16.96-98		Entebbe Harbour		,,
,,	1958.1.99		Busungwe Bay		,,
	1958.1.16.100		Ekunu Bay		,,
,,	1958.1.16.101		Napoleon Gulf, near Jinja		
,,	1958.1.16.108				,,
,,	1958.1.16.130–139	•	,, ,,	•	,,
,,			Mandanald Day	•	,,
"	1958.1.16.107	•	Macdonald Bay	•	,,
"	1958.1.16.109-113		Pilkington Bay	•	,,
,,	1958.1.16.114-115		Njoga, Williams Bay		,,
,,	1958.1.16.116-129		Beach near Nasu Point,		,,
			Buvuma Channel		,,
			Kenya		
,,	1958.1.16.104-106		Kisumu Harbour		,,
			Tanganyika		
,,	1958.1.16.92-94		Mwanza, Capri Bay		,,

	Museum and Reg. No.		Locality		Collector
	Lake	Victoria, Locality	Unknown		
,,	1958.1.16.102-103		_	100	,,
,,	1928.5.24.112		_		M. Graham.
,,	1928.5.24.399-400		_		,,
,,	1928.5.24.401-402		_		,,

Haplochromis cryptodon sp. nov.

Holotype. A male, 123 mm. standard length, from a beach near Nasu Point, Buvuma Channel, Uganda.

Description, based on 31 specimens (including the holotype) 92–130 mm. standard length.

Depth of body 27.5-35.6 per cent of standard length, length of head 30.3-34.9 per cent. Physiognomy relatively uniform, the dorsal head profile straight and sloping at an angle of 35°-40°.

Preorbital depth $12\cdot5-17\cdot6$ (M = $15\cdot4$) per cent of head length, least interorbital width $21\cdot2-25\cdot7$ (M = $23\cdot6$) per cent. Snout as broad as long or very slightly broader, its length $27\cdot5-34\cdot2$ (M = $31\cdot3$) per cent of head; eye $23\cdot1-29\cdot4$ (M = $25\cdot8$), depth of cheek $17\cdot7-25\cdot7$ (M = $23\cdot6$) per cent.

Caudal peduncle 14·7-17·7 per cent of standard length, 1·3-1·7 (modal range 1·3-1·5) times as long as deep.

(Four specimens [two from near Nasu Point, Buvuma Channel, Uganda, and two from Majita, Tanganyika Territory] differ in being noticeably more slender [depth 27·5–31·0 per cent S.L.] and in having less steeply sloping heads. The two Uganda specimens also have a somewhat longer lower jaw [46·0 per cent head length] than is modal. In all other characters these specimens agree with the generality of individuals. Since they are amongst the five smallest specimens available, it is possible that their divergent characters may be "juvenile").

Mouth slightly oblique and moderately distensible; lips slightly thickened. Posterior tip of the maxilla somewhat bullate and reaching or almost reaching the vertical to the anterior orbital margin. Lower jaw with a tendency to narrow rather abruptly at about its mid-point, but not narrowing so markedly as in H. parvidens; in some specimens (particularly individuals less than 100 mm. S.L.) this character is only visible after dissection. Length of lower jaw $39\cdot2-46\cdot5$ ($M=42\cdot3$) per cent of head length, $1\cdot3-1\cdot9$ (modal range $1\cdot5-1\cdot6$) times as long as broad.

Gill rakers moderately slender, 10 or 11 (less frequently 9), on the lower limb of the anterior arch.

Scales ctenoid; lateral line with 30 (f.2), 31 (f.7), 32 (f.17), 33 (f.2) or 34 (f.2) scales. Cheek with 2 or 3 (rarely 4) series; 5–7 scales between the lateral line and the origin of the dorsal fin; 6–8 (rarely 9) between the pectoral and pelvic fin insertions.

Fins. Dorsal with 23 (f.1), 24 (f.14) or 25 (f.16) rays, anal with 11 (f.7), 12 (f.23) or 13 (f.1) comprising XV-XVI, 9 or 10 (rarely 8) and III, 8 or 9 (rarely 10) spinous and soft rays for the fins respectively. Pectoral fins shorter than the head. First pelvic ray produced and extending to the spinous part of the anal.

Teeth. The inner and outer series of teeth are deeply embedded in the oral epithelium, so that only the tips of the outer teeth are visible. In specimens less

than 100 mm. S.L. the outer teeth are weakly and unequally bicuspid. In larger fishes this row is composed of small, unicuspid and slightly recurved teeth.

Teeth in the inner series are either unicuspid or weakly tricuspid, and are arranged in one or two rows. In fresh material it is usually impossible to see these teeth unless the oral mucosa is dissected away.

Lower pharyngeal bone triangular, its dentigerous area 1.0-1.5 times as broad

as long; pharyngeal teeth slender and cuspidate.

Syncranium. The syncranium of H. cryptodon resembles the generalized Haplo-chromis type, except that the maxilla is somewhat stouter and the dentary shows an incipient departure from the generalized condition towards that of H. parvidens (see p. 196 and text fig. 5B).

Vertebrae: 14 + 16 in the single specimen examined (Radiograph, B.M. (N.H.)

Reg. No. 958).

Coloration in life: Adult and immature females. Ground colour dark green-brown shading to light gold ventrally. All fins hyaline. The live coloration of males is unknown.

Colour of preserved material: Adult males. Ground colour dark gun-metal dorsally, shading to greyish-green on the flanks and ventral surfaces; chest and branchiostegal membrane dusky; faint traces of a coppery sheen on the operculum and flanks. Five to seven faint but dark transverse bars are visible on the flanks and caudal peduncle. Dorsal fin dusky; caudal and anal fins hyaline, the latter with two to four dead-white ocelli; pelvic fins black. Females. Ground colour light golden-yellow, slightly darker dorsally; in some individuals there are faint traces of about five, broad, transverse bands on the flanks. One adult is of particular interest since it displays incipient male coloration; the pelvic fins are dusky as are the chest and branchiostegal membrane. In addition there are traces of a coppery sheen on the operculum.

Distribution. Habitat. H. cryptodon has been recorded from only three localities, namely, the Napoleon Gulf near Jinja, a beach near Nasu Point (Buvuma Channel) and a beach at Majita, Tanganyika Territory. The apparent absence of H. crytodon from other localities is difficult to explain since it was one of the more abundant species at the Nasu Point station and formed a regular element of the seine-net catches there. Perhaps it is significant that the majority of H. cryptodon caught at Nasu Point were brooding or "ripe" females, thus suggesting that the area is used as a breeding ground. If this is so, the species may normally occur in some other habitat which could not be fished by conventional gear.

Food. Only one fish, a female from Nasu Point, had ingested material in the stomach and intestine. The stomach was packed with recently fertilized cichlid ova, whilst numerous small fish vertebrae were found in the posterior intestine. The stomach contents may have been the female's own brood, but the presence of larval fish

vertebrae in the faeces cannot be explained on the same grounds.

With such little positive evidence it is impossible to generalize on the feeding habits of *H. cryptodon*. But the single record of gut-contents, taken together with the jaw structure of this species, suggests a diet of embryo and larval fishes.

Breeding. H. cryptodon is a female mouth-brooder. The smallest individual caught, a female 92 mm. S.L., was sexually mature. Males and females reach the same adult size.

Affinities. With the exception of *H. cronus*, *H. cryptodon* is the most generalized of the species referred to this trophic group. In structure and proportions it shows greater affinity with *H. microdon* and *H. parvidens* than with the *H. obesus-H. maxillaris-H. cronus* section of the group. *H. cryptodon* was probably evolved from the complex of piscivorous-insectivorous species which are not markedly differentiated (except for their larger size) from the generalized *Haplochromis* stock in Lake Victoria.

Diagnosis. From the generality of Lake Victoria Haplochromis species, H. cryptodon may be distinguished by its distensible mouth and almost completely hidden dentition. From other species showing these characters, it is distinguished by the shape of the head (and particularly of the lower jaw) and an absence of teeth with anteriorly directed crowns.

Study material and distribution records

Museu	m and Reg. No.		Locality	Collector
			Uganda	
B.M. (N.H.	.).—1958.1.16.31 (Holotype, <i>H. cryptodor</i>	· i)	Beach near Nasu Point, Buvuma Channel	E.A.F.R.O.
,,	1958.1.26.32-33		,,	,,,,
,,	1958.1.16.37-62		,,	,,
,,	1958.1.16.34		Napoleon Gulf, near Jinja	,,
			Tanganyika	
,,	1958.1.16.35-36		Majita	,,

Haplochromis microdon (Boulenger) 1906 (Text-fig. 9)

Pelmatochromis microdon (part; holotype only) Blgr., 1906, Ann. Mag. nat. Hist. (7) 17, 441; Idem, 1913, Cat. Afr. Fish. 3, 412, fig. 282. Haplochromis microdon (Blgr.), (part), Regan, 1922, Proc. Zool. Soc., London, 173.

When redefining *H. microdon* Regan (1922) noted his belief that the type specimen had a malformed lower jaw (which did not bite against the upper) and that its small teeth were due to this malformation. In the light of additional specimens, I am unable to agree with Regan, and conclude that the shape of the lower jaw and its small teeth are, indeed, some of the diagnostic characters of the species. Consequently, I find that the other species which Regan referred to *H. microdon* can no longer be considered conspecific; they will be dealt with in a subsequent paper.

The peculiar lower jaw of H. microdon closely resembles that of H. parvidens but the two species differ in other osteological characters.

Description, based on eight specimens (including the holotype) 114–148 mm. S.L. Depth of body $33\cdot 1-37\cdot 6$ per cent standard length, length of head $31\cdot 2-34\cdot 8$ per cent. Physiognomy variable and dependent on whether the dorsal head profile is moderately or strongly concave. Preorbital depth $14\cdot 6-18\cdot 8$ (M = $17\cdot 1$) per cent of head length, least interorbital width $24\cdot 6-29\cdot 6$ (M = $26\cdot 6$) per cent. Snout as long as broad or very slightly longer; its length $30\cdot 8-34\cdot 5$ (M = $32\cdot 5$) per cent of head, eye diameter $24\cdot 0-28\cdot 2$ (M = $25\cdot 5$), depth of cheek $19\cdot 2-26\cdot 0$ (M = $23\cdot 8$) per cent.

Caudal peduncle 15·3-17·0 per cent of standard length, 1·3-1·5 times as long as deep.

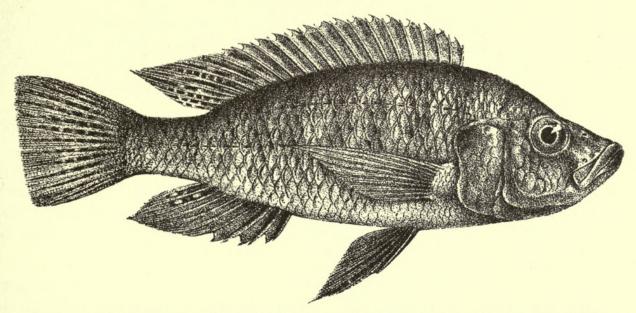


Fig. 9. Haplochromis microdon; holotype (from Boulenger, Fishes of the Nile).

Mouth oblique, distensible and moderately protractile. Jaws equal anteriorly or the lower very slightly shorter; lower jaw always closing within the upper, its length 43.5-48.0 (M = 46.2) per cent of head length, 1.6-2.3 (modal range 1.9-2.2) times as long as broad. Premaxillary pedicels shorter than the dentigerous limb. Posterior tip of the maxilla slightly bullate, partly hidden by the preorbital and extending to the vertical to the anterior orbital margin, or almost so.

[One specimen, an adult female II4·0 mm. S.L., from Pilkington Bay, is not included in the general description given above. Although it differs sufficiently from the other specimens to raise doubts as to its identity, I do not consider it to be a distinct species. The possibility of this fish being a hybrid between *H. microdon* and some other species (? *H. parvidens*) cannot, however, be excluded.

The dentition and lower jaw are of the "microdon-parvidens" type, but the

The dentition and lower jaw are of the "microdon-parvidens" type, but the dentary is narrower anteriorly and it is shorter than even the extreme specimens of either species. These characters, coupled with the large eye and short snout give this fish an unusual appearance which departs from both the "microdon" and the "parvidens" types. The mouth is oblique and the premaxillary pedicels short, so that the sum of characters places the specimen nearest H. microdon.

The principal morphometric characters are:

Po. % Io. % Eye % Cheek % L.j. % C.P.* Depth* Head* Snt. % 30.8 18.0 25.2 29.5 20.5 41.0 15.8 34.2 33.3 * Percentage S.L. % Percentage head-length.]

Gill-rakers slender, 9-II (mode II) on the lower part of the anterior arch.

Scales ctenoid; lateral line with 30 (f.2), 32 (f.4) or 33 (f.2) scales.

Fins. Dorsal fin with 24 (f.4) or 25 (f.4) rays, anal with 10 (f.1), 11 (f.3) or 12 (f.4), comprising XV-XVI, 9 or 10 and III, 7-9 spinous and branched rays for the fins respectively. Pectoral fin shorter than the head; first soft pelvic ray produced, reaching to the vent in females and to the spinous anal fin in males.

Teeth. All the teeth are so deeply embedded in the oral epithelium that they are invisible in fresh material. The teeth in the outer series of both jaws are small, unicuspid and slightly recurved. The single or rarely double row of unicuspid inner teeth is implanted at an acute angle. A distinct interspace separates the inner and outer series of teeth.

Lower pharyngeal bone triangular, the dentigerous area slightly broader than long;

lower pharyngeal teeth slender and cuspidate.

Syncranium (from a radiograph, B.M. (N.H.) Reg. No. 961, and a partial dissection). The dentary is almost identical with that of H. parvidens, but is more slender. The premaxilla is of a generalized type and does not have the elongated pedicels which characterize H. parvidens. The neurocranium is apparently intermediate between that of H. cryptodon and that of H. parvidens.

Colour of preserved specimens: Adult males. Ground colour very dark brown, the ventral abdominal region lighter in one specimen; five or six, broad and dark transverse bars visible on the flanks of some individuals. Branchiostegal membrane black. Dorsal, caudal, pelvic and anal fins dark, almost black, the anal with four, whitish ocelli.

Adult females. Ground colour greyish-brown, darker dorsally; very faint indications of five or six broad transverse bars on the flanks. Dorsal, anal, and caudal fins hyaline, the last weakly maculate especially on the upper half; pelvic fins black.

Distribution. Lake Victoria.

Ecology: Habitat. Seven of the eight fishes examined were from littoral zones of the lake, and were taken over both firm and soft substrates; two were caught at a depth of 30–36 feet and the others in water 6–12 feet deep. The habitat of the eighth specimen is not known.

Food unknown. Since the dentition and jaw structure of H. microdon so closely resemble those of H. parvidens, the feeding habits of the two species may well be

similar.

Breeding. No data are available; the eight specimens are all adults.

Affinities. The most obvious relative of H. microdon is H. parvidens; the lower jaw in both species is of a type otherwise unrepresented in the Lake Victoria Haplo-chromis species flock. The dentary of H. microdon is, however, a more extreme

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modification of the generalized type than is the dentary of *H. parvidens*. On the other hand the elongated premaxillary pedicels of *H. parvidens* do not occur in *H. microdon* which retains a premaxilla of the generalized type. Consequently the mouth is less protrusible in this species. *H. parvidens*, in its gross morphology, and particularly in the shape of its neurocranium, shows strong affinity with some of the piscivorous predators (e.g. *H. nigrescens*). In corresponding characters, *H. microdon* is near *H. cryptodon*, from which it could be derived by further specialization of the lower jaw. Thus, the resemblance between *H. microdon* and *H. parvidens* may be the result of convergent evolutionary trends.

Diagnosis. Haplochromis microdon may be distinguished from other species with deeply embedded teeth by the shape of the lower jaw, the concave dorsal head profile and the oblique mouth. It may be further distinguished from H. parvidens by its having premaxillary pedicels which are shorter than the horizontal (dentigerous) limb of this bone.

Study material and distribution records

Museum and Reg. No.			Locality	Collector
			Uganda	
B.M. (N.H.).	—1906.5.30.309		Bunjako	Degen.
(Ho	lotype Pelmatochromis	microd	on)	
,,	1958.1.16.24		Pilkington Bay	E.A.F.R.O.
"	1958.1.16.25		Entebbe Harbour	,,
"	1958.1.16.26		Ekunu Bay	,,
,,	1958.1.16.29-30		Beach near Nasu Point,	,,
			Buvuma Channel	
	Lak	e Victo	ria, Locality Unknown	
,,	1958.1.16.27-28		_	,,

DISCUSSION

The embryo-larval fish-eating habits of this species-group were briefly mentioned in the introduction. As far as I can determine from published accounts, no other African cichlids have occupied this particular niché.

That the group preys almost exclusively on the embryos and larvae of other cichlids is probably due to the fact that only the Cichlidae breed continuously; the non-cichlid fishes spawn biannually, at the periods of maximum rainfall. On the other hand, the mouth-brooding habits of most Lake Victoria *Haplochromis*, and both *Tilapia* species, would seem to provide very little opportunity for these predators unless they have evolved a method of forcing the parent to jettison its brood. Since embryos at all stages of development have been found in the stomach contents, it is clear that the species do not obtain their food solely by preying on newly fertilized eggs before these are picked up by the brooding parent. The method of attack is unknown, but from the large number of embryos or larvae taken it must be highly efficient.

Two anatomical features (a distensible and somewhat protrusible mouth, and a weak to moderately developed dentition deeply embedded in the thickened oral epithelium) characterize six of the seven species in this trophic group. It is not known if either of the characters has any functional significance in connection with the feeding habits. The seventh species, *H. cronus*, has strong and fully-exposed teeth, and the mouth is not noticeably distensible or protractile. Unfortunately, only a few specimens of *H. cronus* had food in the stomach. However, it may be significant that these fishes had fed on larger (ca. II mm.) late larvae, whilst members of the other species had fed on embryos and early larvae. That is to say, *H. cronus* had taken young of an age when they frequently leave the parent's mouth for short periods. Those species with distensible, protractile mouths and hidden teeth had taken mainly intra-oral young. Perhaps these larger mouthed species engulf the head or mouth of a brooding female and in this way force the parent to abandon its young?

As in most other trophically defined species-groups there is evidence of both phyletic and convergent relationships between the species. But, unlike most others, this group shows greater divergence and more tenuous relationships within the apparently phyletic lines.

Haplochromis cronus is the least specialized species, but it differs from the generality of Lake Victoria Haplochromis in having the caudal fin almost completely scaled (a characteristic of Lake Nyasa Haplochromis).

Haplochromis obesus and H. maxillaris seem to be much specialized derivatives of a form resembling H. cronus, but neither of these species has a scaled caudal fin. The dentition is similar in H. obesus and H. maxillaris and quite unlike that of H. cronus; in other characters (especially the shape of the lower jaw) the two species are markedly different. It is, in fact, impossible to decide whether the species are of the same lineage or the descendants of distinct but related ancestral stocks.

A similar state of affairs exists when *H. cryptodon* and *H. microdon* are considered. A further complication is introduced by the resemblance between *H. microdon* and *H. parvidens*. In this case, however, it is possible that *H. microdon* was derived from an *H. cryptodon*-like ancestor, and *H. parvidens* from one of the less-specialized piscivorous predators.

In all these species, anatomical differences between members of possible lineages are certainly greater than those encountered between species in the algal-grazing and mollusc-" shelling "groups (Greenwood, 1956b and 1957).

Two of the species described above, *H. obesus* and *H. maxillaris*, clearly demonstrate a phenomenon which is common amongst the Lake Victoria *Haplochromis*, namely, the intraspecific constancy of certain osteological and dental characters contrasting with the variability of other and often anatomically related characters. For example, the lower jaw and dentition of *H. obesus* is readily diagnostic, whilst the physiognomy is so variable that difficulty would be experienced in identifying some specimens were it not for the characteristic lower jaw. Likewise, there is marked variation in the gross morphology of *H. maxillaris*, yet the dentary and the dentition of both jaws are relatively constant. *Haplochromis parvidens*, however, shows only slight variation in its gross morphology.

In certain characters, *Haplochromis taurinus* Trewavas, of Lake Edward, resembles fishes of the *H. maxillaris-H. obesus* complex. The shape of the head approaches that of *H. maxillaris*, particularly with regard to the stout jaws and thickened lips; also, the outer teeth in the upper jaw are hidden by a fold of lip-tissue. The likeness does not extend to the dentition, which is a critical character in this group. The teeth of *H. taurinus* are large, distinct and biscuspid (at least in the holotype, a fish 164 mm. total length) and are of a form rarely encountered in any Lake Victoria *Haplochromis*. There can be little doubt therefore, that the resemblance between *H. taurinus* and *H. maxillaris* or *H. obesus* is superficial and of little phyletic significance.

Haplochromis plagiodon Regan & Trewavas 1928

(Text-fig. 10)

Haplochromis crassilabris Blgr. (part), 1906, Ann. Mag. nat. Hist. (7) 17, 445.

Paratilapia crassilabris (Blgr.), part, Blgr., 1915, Cat. Afr. Fish. 3, 345.

Haplochromis crassilabris Blgr. (part), Regan, 1922, Proc. zool. Soc. London, 167.

Hemitilapia bayoni Blgr. (part), Blgr., 1908, Ann. Mus. Genova (3), 4, 6; Idem, 1915, Cat. Afr. Fish. 3, 491.

Clinodon bayoni (Blgr.) (part), Regan, 1920, Ann. Mag. nat. Hist. (9) 5, 45 (footnote). Haplochromis obliquidens Hilgendorf (part), Regan, 1922, Proc. zool. Soc. London, 188. Haplochromis plagiodon Regan & Trewavas, 1928, Ann. Mag. nat. Hist. (10), 2, 224.

Description, based on five specimens (including the holotype), 56–85 mm. standard length.

H. plagiodon is a generalized species, except that it has teeth of an unusual form, resembling stout and somewhat modified versions of the teeth found in *H. lividus* Greenwood. Although *H. plagiodon* is represented by only five specimens, the form of the teeth is sufficiently distinctive and constant to warrant the assumption that the species is biologically valid.

The principal morphometric characters for each of the five specimens are tabulated. below. All are males.

S.L.	Depth*	Head*	Po. %	Io. %	Snt. %	Eye %	Cheek %	L.j. %	C.P.*
56.0	35.7	31.2	13.1	25.7	28.6	30.2	21.7	34.2	17.0
72.0	36.0	30.5	15.0	27.2	27.2	29.2	22.7	36.3	16.7
76.0	36.8	31.6	15.9	25.0	29.2	31.3	23.0	37.5	15.2
†81·o	32.7	29.6	16.7	28.4	29.2	28.4	20.8	34.6	18.0
85.0	36.5	30.3	15.6	26.9	26.9	30.8	23.0	34.6	16.5

* Percentage standard length. % Percentage head length.

† Holotype.

Dorsal head profile straight and steeply sloping (ca. 50°). Mouth horizontal; posterior tip of the maxilla extending to the vertical to the anterior orbital margin, or slightly beyond. Jaws equal anteriorly, the lower 1·3-1·6 times as long as broad; lips not thickened.

Teeth. Outer teeth stout, erect and bicuspid, with the major cusp obliquely truncate and somewhat compressed, the minor cusp conical. In one specimen

(72 mm. S.L.) the teeth are very worn, so that the minor cusp is indicated merely as a faint groove on the labial aspect of the tooth. There are 30–38 teeth in the outer series of the upper jaw.

In most respects, the shape of these teeth closely resembles one of the variants occurring in *H. lividus* (see Text-fig. 2B in Greenwood, 1956b), except that in *H. plagiodon* the teeth are not recurved, are stouter and do not have a distinct neck.

The inner teeth are tricuspid and arranged in two or three rows in each jaw and are separated from the outer row by a distinct interspace.

Lower pharyngeal bone triangular, fairly stout (as compared with, for example, fishes of the H. lividus-H. nuchisquamulatus group); dentigerous area 1.2-1.5

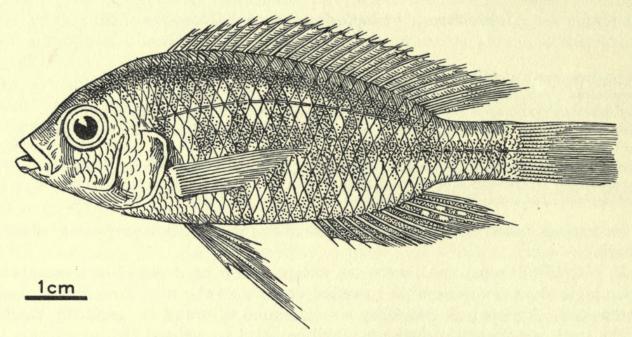


Fig. 10. Haplochromis plagiodon. Drawn by Miss D. Fitchew.

times as broad as long. Lower pharyngeal teeth cuspidate, those of the two median series enlarged; conical in three specimens but cuspidate in two others.

Gill rakers short and stout; 7 or 8 on the lower limb of the anterior arch.

Scales ctenoid; lateral line with 31 (f.1), 32 (f.3) or 33 (f.1) scales. Cheek with 3 or 4 (rarely 2) series; 6 or 7 scales between the dorsal fin origin and the lateral line, 8 or 9 between the pelvic and pectoral fin bases.

Fins. Dorsal with 24 (f.1), 25 (f.2) or 26 (f.2) rays, anal with II (f.1), I2 (f.3) or I3 (f.1) comprising XV-XVI, 9 or I0 and III, 8—10 spinous and branched rays for the fins respectively. First soft pelvic ray produced and extending to the spinous part of the anal fin. Pectoral fin slightly shorter than the head.

Coloration. Unknown in life and known only for preserved males. Ground colour silver-grey to brownish-grey; eight to ten transverse bars on the flanks and caudal peduncle, a fairly well-defined mid-lateral stripe, with indications of an interrupted band running slightly above the upper lateral line. Faint traces of two interocular bands and a lachrymal stripe. Dorsal, caudal and anal fins pale and immaculate;

six to eight small ocelli arranged in two rows on the anal fin. Pelvic fins dusky on the outer two-thirds in two specimens and entirely pale in the remainder.

Ecology. No ecological data are available for the type and one other specimen; the three other fishes were caught in a seine-net operated in shallow water over an exposed, sandy beach at Entebbe, Uganda, In two of these specimens, remains of larval Diptera and Ephemeroptera (together with many fine sand grains) were found in the intestines.

Diagnosis and affinities. Haplochromis plagiodon may be distinguished from other species in Lake Victoria by its peculiar teeth. The relatively coarse lower pharyngeal bone and the enlarged median pharyngeal teeth, together with the stout, firmly implanted and few (30–36) outer teeth, separate *H. plagiodon* from the two other species (*H. lividus* and *H. nuchisquamulatus*) with obliquely truncated, biscuspid outer teeth.

Regan & Trewavas (1928) compared the teeth of *H. plagiodon* holotype with those of the type of *Bayonia xenodonta* Blgr. (now considered a synonym of *Macropleurodus bicolor* (Blgr.), Greenwood, 1956a). They emphasized the differences existing between the two species, even though there appeared to be some resemblance in the shape of the teeth. Now that additional specimens of comparable sizes are available for both species, it is clearer than ever that *H. plagiodon* is not closely related to *Macropleurodus bicolor*. Regan & Trewavas also suggested that *H. plagiodon* might be related to *H. humilior* (Blgr.). Although both these species have somewhat enlarged lower pharyngeal bones and median pharyngeal teeth, the resemblance in gross morphology is less marked and ceases when the oral dentition is compared. Likewise, although the oral teeth of *H. plagiodon* resemble those of *H. lividus*, the latter species has a fine lower pharyngeal bone with slender, cuspidate median teeth, and finer, more numerous oral teeth.

Thus, it is only possible to suggest that *H. plagiodon* represents an independent offshoot from the generalized *Haplochromis* stem.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.).—1909.5.4.29	Sesse Isles	Bayon.
(Holotype H. plagiodon)		
,, 1906.5.30.427	Entebbe	Degen.
,, 1958.1.16.245-247	Entebbe, Bugonga Beach	E.A.F.R.O.

Haplochromis chilotes (Blgr.) 1911 (Text-fig. 11)

Paratilapia chilotes Blgr., 1911, Ann. Mus. Genova (3), 5, 68, pl. II, fig. 2; Idem, Cat. Afr. Fish. 3, 338, fig. 228.

Haplochromis chilotes (Blgr.), Regan, 1922, Proc. zool. Soc. London, 170.

As defined below, *H. chilotes* exhibits a high degree of individual variability. The species may be divided into two morphotypes: first, those individuals with hyper-

trophied and lobed lips and secondly, those in which the lips are thickened but not produced into well-defined lobes. Seventeen of the 25 specimens available fall into the first category and eight into the second. The division is not sharp, however, since the lips of some individuals in the second category do have a lobe-like, median swelling.

Certain other characters are apparently correlated with the extent of lip development. For example, in most specimens with strongly lobed lips, the upper dental arcade is narrow and acutely rounded anteriorly. Also, in these fishes, the lower jaw is usually longer. The correlation is not complete and some lobe-lipped fishes

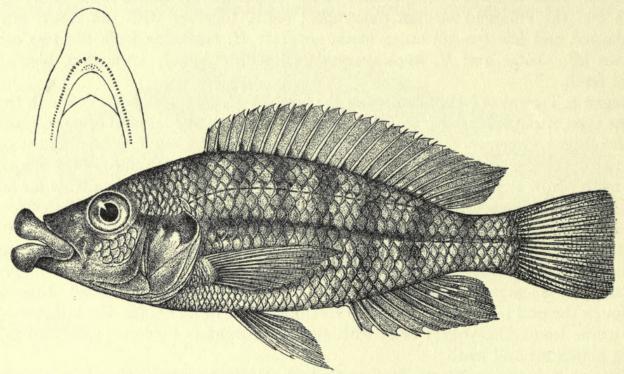


Fig. 11. Haplochromis chilotes; holotype (from Boulenger, Fishes of the Nile).

have a mixture of these characters. It is because the sample as a whole shows a complete intergradation of lip, jaw and dental characters that I consider the material to represent a single species. Furthermore, I can discover no ecological differences between the two morphotypes, nor is there any obvious difference in the breeding coloration of the males. Nevertheless, the present arrangement should probably be considered tentative until more material and further field observations are available.

Description, based on 25 specimens (including the holotype) 70–148 mm. standard length.

Depth of body 32.5-40.8 per cent of standard length; length of head (excluding the lips) apparently correlated with the degree of lip hypertrophy, 31.4-34.7 (M = 32.7) per cent of standard length in fishes without clearly lobed lips and 32.0-38.2 (M = 35.5) per cent in those with lobed lips. Dorsal head profile straight and gently sloping, or slightly decurved. Preorbital depth 15.0-18.2 (M = 16.8) per cent of head; least interorbital width 19.3-27.2 (M = 23.8); snout longer than broad in lobe-lipped fishes and as broad as long in others, its length 30.8-38.4 (M = 34.0) per

cent of head; eye 28.6-21.8 (M = 25.4), depth of cheek 18.1-25.4 (M = 20.5) per cent.

Caudal peduncle 12.5-17.2 (M = 15.3) per cent of standard length. Mouth horizontal, posterior tip of the maxilla reaching or almost reaching the vertical to the anterior orbital margin. Lips thickened, grossly so in some specimens in which each lip is produced medially into a tongue-shaped or globose lobe; in others there may be an incipient lobe or even no indication of any such development. Jaws equal anteriorly, the lower proportionately longer (36.0-49.0, M = 39.6) per cent of head) in fishes with lobed lips than in the others (30.0-36.6, M = 33.2) per

Gill-rakers short and stout, 7-9 on the lower limb of the anterior arch.

Scales ctenoid; lateral line with 31 (f.3), 32 (f.10), 33 (f.9), 34 (f.2) or 35 (f.1) scales. Cheek with 3 (rarely 2 or 4) series. Seven or 8 (rarely 6) scales between the origin of the dorsal fin and the lateral line; 8 or 9 (less commonly 6, 7 or 10) between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.3), 25 (f.18) or 26 (f.4) rays, anal with II (f.3) or I2 (f.22), comprising XV-XVI, 9 or 10 and III, 8 or 9 spinous and branched rays for the fins respectively. Pectoral fin shorter than the head; first soft pelvic ray produced, variable in its posterior extension but proportionately longer in adult males than females. Caudal subtruncate.

Teeth. In most specimens with hypertrophied and lobed lips the outer teeth in the upper jaw are arranged in an acutely rounded arcade, a pattern not found in any other Haplochromis from Lake Victoria. Specimens with thickened but non-lobed lips have more broadly rounded dental arcades, which are, nevertheless, more acutely rounded anteriorly than those of most other species. Complete intergradation exists between the various arcade shapes; the correlation between lip development and dental pattern is not complete since some fishes with lobed lips have a broad arcade.

In fishes 70–108 mm. standard length the outer tooth row is composed of unicuspid and weakly bicuspid, slender and slightly recurved teeth. In larger individuals these teeth are always unicuspid, are stouter and very slightly, if at all, curved. From 16 to 46 teeth may occur in the outer series of the upper jaw; there is apparently some correlation between lip development and the number of teeth, with a tendency for label limit of the standard length the outer tooth row is composed of unicuspid and weakly bicuspid, slender and slightly recurved teeth. In larger individuals these teeth are always unicuspid, are stouter and very slightly, if at all, curved. for lobe-lipped fishes to have more teeth.

The inner series are composed of tricuspid and weakly tricuspid teeth in fishes less than IIO mm. standard length, and of predominantly unicuspid teeth in larger individuals. These teeth are arranged in two or three rows (less commonly four or one) anteriorly in each jaw.

Lower pharyngeal bone triangular, the dentigerous area I·o-I·5 (modal range I·2-I·3) times as broad as long. With one exception, all specimens have the median teeth (particularly the posterior few pairs) enlarged but still clearly cuspidate. In the exceptional specimen, the median teeth are slender.

Coloration in life: Breeding males. Ground colour greyish-black or black; lips and branchiostegal membrane black. Dorsal fin black, lappets and margin of soft part

red, as are the maculae between the branched rays. Caudal black basally, but light yellow or hyaline distally; anal yellow or hyaline, with three or four reddish-yellow ocelli; pelvics black. *Non-breeding males*: Ground colour variable, usually greyish-black; a dark mid-lateral band and a less intense, interrupted, wavy dorsal band, are generally visible. Dorsal, caudal and anal fins greyish; pelvics black.

Females and immature males. Ground colour greyish-silver, creamy-white on the chest and ventral surface of the head. Lips grey or cream; six to nine dark transverse bars on the flanks and caudal peduncle, which are broadest at the points of intersection with the broad, mid-lateral stripe and the narrower, interrupted dorsal band. Dorsal caudal and anal fins greyish; pelvics hyaline.

One of the eight females available was a piebald, black and yellow "bicolor"

variant (p. 212); it was of the group with hypertrophied and lobed lips.

Preserved material: Sexually active males. Ground colour blackish, lower jaw, branchiostegal membrane and chest dusky; lips usually pale but dusky in a few specimens. A dark, mid-lateral stripe and a less intense dorsal band, together with six or seven broad transverse bars, are usually visible on the flanks. Dorsal fin black, with light lappets and margin to the soft part. Anal fin pale orange-yellow, with three or four white ocelli arranged in a single row. Caudal fin black on the basal third to half, orange-yellow distally. Pelvic fins black, somewhat lighter medially. Sexually inactive males have a similar coloration except that the ground colour is lighter, as is the lower jaw and the branchiostegal membrane, whilst the chest is silvery. Females and juvenile males are brownish-fawn, lightest ventrally; the banding and barring is more obvious than in adult males. All fins hyaline, with the soft part of the dorsal fin and the caudal fin maculate.

Distribution. Known from Lake Victoria and probably also from the Victoria Nile since the type locality is given as "Victoria Nile at Ripon Falls" (Boulenger, 1911).

Ecology: Habitat. H. chilotes is apparently confined to the littoral and sublittoral zones of the lake, where the depth of water is less than 50 feet and to localities with a hard substrate (sand, shingle and rocks). Only two specimens were caught over a mud bottom. Furthermore, it seems that the species may be confined to sheltered bays and gulfs; with two exceptions, no H. chilotes have been recorded from exposed habitats. The exceptional fishes were caught near islands lying some distance from the mainland.

Food. Eight of the 23 specimens contained food in the stomach and intestines; these fishes represent five different localities, four of which are geographically distant from one another.

One fish had fed almost exclusively on prawns (Caridina nilotica Roux) and the others on insect larvae. Larvae of the boring may-fly (Povilla adusta Navás) formed the main insect prey, and it was noticed that the silk case of the larva had also been ingested. Other insects eaten included Trichoptera and Diptera larvae. From the amount of plant debris and sand occurring in the stomach it would seem that H. chilotes feeds from the bottom.

Breeding habits. Females 70 mm. S.L. are sexually active, but the smallest adult

male in this sample was 97 mm. S.L.; from the available data it seems probable that males reach a greater adult size than females. One female was found with three late larvae in the buccal cavity; since the condition of this fish was clearly "spent" it is assumed that the larvae were part of a larger brood which was lost when the female was captured.

Morphology of late larval H. chilotes. The three young fishes (all ca. 10 mm. S.L.) referred to above are indistinguishable from the larvae of other and unrelated Haplochromis species. Although the female parent had hypertrophied and lobed lips, no trace of these characters was visible in the larvae.

Affinities. Haplochromis chilotes was probably derived from an H. chromogynoslike ancestor by further development of the lips, narrowing of the head and the consequent effects on the dental pattern. H. chilotes without lobed lips resemble H. chromogynos more closely than do specimens with lobed lips. But the similarity between the two species, even at its closest, is less marked than for example, that between H. sauvagei and H. prodromus (Greenwood, 1957).

There is a striking superficial resemblance between H. chilotes and Lobochilotes labiatus (Blgr.) of Lake Tanganyika. The range of lip development in L. labiatus is about equal to that of H. chilotes but with this difference; it is positively correlated with size in L. labiatus. Small fishes have weakly lobed lips whilst, in larger individuals the lobes are well developed. Tooth form in Lobochilotes is quite unlike that of H. chilotes, but there is a tendency for the dental arcade to be acutely rounded anteriorly.

Lobed lips are also developed in *Haplochromis lobochilotes* of Lake Nyasa and thus there is some resemblance between this species and *H. chilotes*. In this instance, however, the similarity is less marked because the general proportions of the two species are somewhat different; again, the form of the teeth is dissimilar.

Of the lobe-lipped species occurring outside Lake Victoria, *Melanochromis labrosus* Trewavas, of Lake Nyasa shows the greatest overall and detailed likeness with *H. chilotes*. The dentition of *M. labrosus* and *H. chilotes* of a comparable size is similar, as is the gross and finer morphology of the head. The nuchal and pectoral squamation of *M. labrosus* is, however, markedly smaller than that of *H. chilotes*. Unfortunately, *M. labrosus* is known only from one specimen so a detailed comparison of the two species cannot be made.

Diagnosis. H. chilotes with hypertrophied and lobed lips are immediately distinguishable from other Lake Victoria species on this character alone; from H. lobochilotes of Lake Nyasa and Lobochilotes labiatus of Lake Tanganyika, it is distinguished by differences in the shape of the teeth and by various morphometric characters Haplochromis chilotes with moderately developed and weakly or non-lobed lips may be confused with H. chromogynos or with species of the H. sauvagei complex. They are immediately distinguishable from the latter group in having fewer rows of inner teeth and by the shape of the outer teeth, which do not have strongly recurved tips. From H. chromogynos, H. chilotes is distinguished by its narrower interorbital region and longer snout.

ZOOL. 5, 7.

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Study material and distribution records

Museum and Reg. No.			Locality	Collector
			Uganda	
Genoa Museu	m		Jinja, Ripon Falls	Bayon.
	e Paratilapia chilotes)			
	—1911.3.3.33 atype <i>P. chilotes</i>)		,,	,,
,,	1958.1.16.3		Ramafuta Is.	 E.A.F.R.O.
,,	1958.1.16.4		Pilkington Bay	,,
,,	1958.1.16.5		Lukula Is.	,,
,,	1958.1.16.6	•	Channel between Dagusi Is. and mainland	,,
,,	1958.1.16.9		Ekunu Bay	"
,,	1958.1.16.10–16		Off south tip of Buvuma Is.	,,
"	1958.1.16.17–23		Napoleon Gulf, near Jinja	"
			Tanganyika	
,,,	1958.1.16.1		Kaseiraji Is.	,,
,,	1958.1.16.8	•	Godziba Is.	,,
			Kenya	
,,	1958.1.16.2		Kisumu Harbour	"
	Lake	e Vic	toria, Locality Unknown	
,,	1958.1.16.7			,,

Haplochromis chromogynos sp. nov.

Haplochromis bicolor Blgr. (part), 1906, Ann. Mag. nat. Hist. (7) 17, 444.

Paratilapia bicolor (Blgr.) (part), Blgr., 1915, Cat. Afr. Fish. 3, 346.

Haplochromis sauvagei (Pfeff.), (part), Regan, 1922, Proc. zool. Soc. London, 167.

Haplochromis chromogynos is unique amongst the Haplochromis of Lake Victoria (and probably the other lakes as well) since a high percentage, if not all, of the females have a piebald, black and yellow "bicolor" coloration. "Bicolor" female variants are known to occur in several Haplochromis species, but in none does the frequency of the variants exceed about 30 per cent. All 22 specimens of female H. chromogynos are "bicolor". These fishes were collected from several different parts of the lake and include fishes at various stages of sexual development.

Holotype. A female, 79 mm. standard length, from the Napoleon Gulf, near Jinja, Uganda.

Description, based on 29 specimens (including the holotype) 50-110 mm. standard length.

Depth of body $32\cdot5-42\cdot3$ (M = $35\cdot0$) per cent of standard length; length of head $30\cdot4-37\cdot3$ (M = $33\cdot2$) per cent. Dorsal head profile curved and moderately declivous. Preorbital depth $13\cdot2-17\cdot0$ (M = $15\cdot4$) per cent of head length, least interorbital width $22\cdot6-31\cdot4$ (M = $27\cdot5$) per cent. Snout slightly longer than broad, or less commonly, broader than long, its length $26\cdot3-33\cdot3$ (M = $30\cdot7$) per cent of head; eye $25\cdot7-32\cdot7$ (M = $28\cdot6$); depth of cheek $17\cdot9-24\cdot6$ (M = $21\cdot6$) per cent of head.

Caudal peduncle 13.6-18.5 per cent of standard length, 1.1-1.6 times as long as deep.

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Mouth horizontal; jaws equal anteriorly, the lower $i \cdot i - i \cdot 5$ (mode $i \cdot 3$) times as long as broad, its length $30 \cdot 0 - 34 \cdot 4$ ($M = 32 \cdot 5$) per cent of head length. Lips thickened; posterior tip of the maxilla extending to the vertical through the anterior orbital margin or slightly beyond.

Gill rakers short, 8 (less frequently 9 and rarely 6 or 7) on the lower limb of the anterior arch.

Scales ctenoid; lateral line with 31 (f.3), 32 (f.10), 33 (f.13) or 34 (f.3) scales. Cheek with 3 (less frequently 2 or 4) series. Six to 8 scales between the origin of the dorsal fin and the lateral line; 8 or 9 between the pectoral and pelvic fin bases; chest scales small.

Fins. Dorsal with 24 (f.3), 25 (f.24) or 26 (f.2) rays, anal with 11 or 12, comprising XV–XVI, 8–10 and III, 8 or 9 spinous and branched rays for the fins respectively. Pectoral fin slightly shorter than the head; first pelvic ray produced, variable in its posterior extension but usually reaching the spinous part of the anal fin.

Teeth. In the outer row of both jaws, the teeth are slender and gently recurved. Fishes less than 65 mm. S.L., have only unequally bicuspid teeth; individuals 65–95 mm. S.L. have an admixture of bi- and unicuspid teeth in which either type may predominate. Fishes more than 95 mm. S.L. have only unicuspid teeth. There are 24–42 (modal range 30–32) outer teeth in the upper jaw.

The inner teeth are tricuspid in fishes less than 95 mm. S.L. and unicuspid in larger individuals; an admixture of both types may occur. These teeth are arranged in three rows (less frequently two or four) in both jaws.

Lower pharyngeal bone triangular, the dentigerous area I·I-I·4 (mode I·2) times as broad as long. Occasionally the median series of teeth are enlarged and submolariform; more frequently, only the posterior few pairs are markedly enlarged. In a few specimens, no median teeth are enlarged.

Coloration. As mentioned above, *H. chromogynos* is unique in apparently having only "bicolor" females. The colour patterns of these fishes are variable, but are within the range known for other species with "bicolor" females. In preserved material, the yellowish-silver ground colour appears yellowish-white, silver or brown. The colours of live males are unknown.

Coloration of preserved males. Ground colour greyish-brown to grey; lips, lower jaw and the anterior part of the branchiostegal membrane, lighter; six or seven faint transverse bars visible on the flanks and caudal peduncle; a faint lachrymal stripe is often present. Dorsal fin with the spinous part dusky, lappets lighter; soft part orange-yellow. Anal dusky on the basal half, orange-yellow distally, with one to three white ocelli arranged in a single row. Caudal fin dark, but with a broad, orange-yellow margin. Pelvic fins black on the outer half, orange mesially.

Ecology: Habitat. H. chromogynos is probably confined to the littoral zone and to water less than 20 feet deep; it has only been caught over a firm substrate (rock, sand or shingle).

Food. One record of stomach and intestinal contents is available; the main contents were the remains of Trichoptera larvae and sand-grain cases, but a few larval chironomids and baétids were also identified.

Breeding. One female carrying embryos in the buccal cavity was recorded. Sexual maturity is reached at a standard length of 90–100 mm. in both sexes.

Affinities. H. chromogynos may be related to H. chilotes (see p. 211). The similarity between these species is most pronounced when the non-lobed lip forms of H. chilotes are compared with H. chromogynos. Superficially, H. chromogynos resembles H. crassilabris (Blgr.) but the dentition of the two species is markedly different.

The available specimens of H. paucidens Regan, from Lake Kivu, indicate a very close relationship between the two species; the most marked difference is the shallower cheek of H. chromogynos (mean depth 21.6, cf. 27.6 per cent for H. paucidens). Unfortunately there is no information on the coloration of female H. paucidens or on the breeding colours of male fishes of either species.

Study material and distribution records

Street meeter	the with wistribution,	000	,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,		
Museum and Reg. No.			Locality		Collector
			Uganda		
B.M. (N.H.).	—1958.1.16.83		Napoleon Gulf, near Jinja		E.A.F.R.O.
(Ho	olotype)				
,,	1958.1.16.71-75		Napoleon Gulf,		,,
			near Jinja golf course		
,,	1958.1.16.76-81		Napoleon Gulf, Jinja pier		"
,,	1958.1.16.82		Napoleon Gulf,		,,
			bay opposite Jinja pier		
,,	1958.1.16.84		Entebbe Harbour		,,
,,	1958.1.16.69		Grant Bay		,,
,,	1958.1.16.67-68		Ramafuta Is., Buvuma Channel		,,
,,	1906.5.30.415-416		Bugangu		Degen.
	1906.5.30.407-412		Bunjako		, , , , , , , , , , , , , , , , , , ,
			Tanganyika		
,,	1958.1.16.63-66		Mwanza, Capri Bay		E.A.F.R.O.
			Kenya		
,,	1958.1.16.70		Kisumu Harbour	•	"

Haplochromis aelocephalus sp. nov.

(Text-fig. 12)

Holotype. A male 96 mm. S.L., from Igwe Island.

An interesting feature of this species is its wide range of variation in head shape; the more extreme individuals might well be considered distinct species were it not for the presence of annectent forms (Text-fig. 13). This variation is not correlated with sex or size. The most constant specific characters are the multiseriate dentition, the small scales on the pectoral region, and the thickened lips.

Description. Based on the holotype and 21 other specimens, 63-120 mm. standard length.

Depth of body $31\cdot3-38\cdot4$ per cent of standard length; length of head $33\cdot0-38\cdot6$ per cent. Dorsal head profile straight or very slightly concave, sloping gently; physiognomy variable. Preorbital depth $14\cdot7-19\cdot4$ (M = $17\cdot2$) per cent of head length,

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least interorbital width $21\cdot9-26\cdot4$ (M = $24\cdot8$) per cent. Snout $1\cdot1-1\cdot2$ times as long as broad, except in a few extreme individuals where it is $1\cdot25-1\cdot30$ times as long as broad; snout length $32\cdot0-39\cdot0$ (M = $35\cdot3$) per cent of head. Diameter of eye shows fairly clear-cut negative allometry with standard length, $25\cdot0-30\cdot8$ (M = $27\cdot8$) per cent of head in fishes 62-100 mm. S.L. and $23\cdot2-25\cdot7$ (M = $24\cdot5$) per cent in larger individuals; depth of cheek $17\cdot3-24\cdot7$ (M = $20\cdot5$) per cent.

Caudal peduncle 12.8-18.5 (M = 16.2) per cent of standard length, 1.1-1.6 (modal

range 1.4-1.5) times as long as deep.

Mouth horizontal, lower jaw projecting slightly; posterior tip of the maxilla not quite reaching the vertical through the anterior margin of the orbit, except in one specimen. Lips thickened and variable; in a few fishes there are faint indications of a lobe-like swelling on the lower lip. In all specimens there is a pronounced sub-

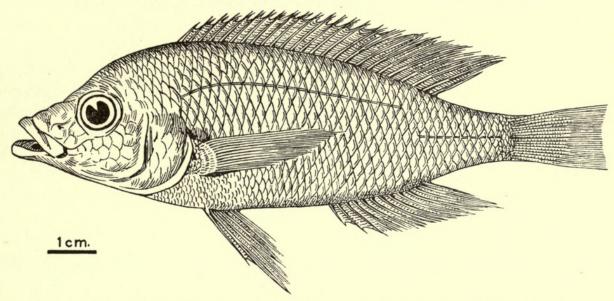


Fig. 12. Haplochromis aelocephalus; holotype. Drawn by Miss D. Fitchew.

mental thickening which extends posteriorly for a short distance. Lower jaw length apparently correlated with head shape, being greatest in the more extreme individuals; namely, in seven "extreme" specimens (Text-fig. 13) $42 \cdot 5 - 48 \cdot 5$ (M = $45 \cdot I$) per cent of head and in the remaining specimens $37 \cdot 0 - 46 \cdot 9$ (M = $41 \cdot 3$) per cent. The length/breadth ratio of the lower jaw $1 \cdot 6 - 2 \cdot 6$ (modal range $1 \cdot 8 - 2 \cdot 0$).

Gill rakers short, 7-9 on the lower limb of the anterior arch.

Scales ctenoid; lateral line with 31 (f.1), 32 (f.5), 33 (f.10) or 34 (f.6) scales. Cheek with 3 or 4 (rarely 2) series. Six to 8 scales between the origin of the dorsal fin and the lateral line; 8 or 9 (rarely 7 or 10) scales between the pectoral and pelvic fin bases; chest scales small.

Fins. Dorsal with 24 (f.3), 25 (f.17) or 26 (f.2) rays, anal with II (f.1), I2 (f.16) or 13 (f.5), comprising XV or XVI, 9 or 10 and III, 8—10 spinous and branched rays for the fins respectively. Pelvic fins with the first ray produced. Pectoral fin shorter than the head. Caudal truncate or subtruncate.

Teeth. The outer row in both jaws of fishes less than 65 mm. S.L. is composed of slender and slightly recurved bicuspid teeth; specimens 65-95 mm. S.L. have an

admixture of bi- and unicuspids in which either form may predominate, whilst in larger fishes, all the outer teeth are unicuspid. There are 24-42 (mode 32) teeth in the outer row of the upper jaw. The dental arcade in the lower jaw is narrow anteriorly; in a few specimens it is rather acutely pointed and resembles that of lobe-lipped H. chilotes (see p. 209).

Teeth in the inner series of both jaws are generally tricuspid in fishes less than 95 mm. S. L. and unicuspid in larger individuals; a mixture of both types is found in specimens of an intermediate size. There are three to five, rarely two (mode five), series of inner teeth anteriorly in the lower jaw and three to six (mode five) in the upper. The innermost series of the lower jaw is usually implanted so as to lie almost horizontally.

Lower pharyngeal bone triangular, the dentigerous area 1.0-1.4 (mode 1.2) times as broad as long. Teeth in the median series are variable in form. In most specimens

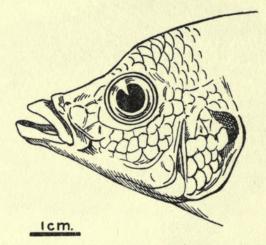


Fig. 13. Haplochromis aelocephalus; individual variant of head profile (extreme form).

these teeth (especially the upper three or four pairs) are somewhat enlarged and weakly cuspidate; the next most common variant has these teeth slightly enlarged and clearly cuspidate. Finally, in a few fishes the median teeth are unmodified and resemble the other teeth. Two exceptional fishes had the entire median series enlarged and molariform and the pharyngeal bone noticeably stouter.

Coloration. The colours of living fishes are unknown.

Preserved material: Sexually active males. Ground colour grey-black, chest and branchiostegal membrane black; faint indications of a coppery sheen on the operculum and flanks. Dorsal fin black except for the light lappets and a colourless band outlining the soft part of the fin; caudal black basally, light (? orange) distally; anal fin dark on the basal half and light (? orange) distally, with three or four hyaline ocelli arranged in a single row. Pelvics black. Females, quiescent and juvenile males. Ground colour greyish-silver (in sexually quiescent males there is a faint trace of coppery sheen on the operculum and the chest is dusky) with, in some, an interrupted or continuous, dark, mid-lateral stripe and five or six transverse bars on the flanks. Dorsal and anal fins yellowish, slightly dusky on the proximal half in quiet males, but hyaline and faintly maculate in females and immature males. Pelvic fins yellowish or hyaline in females and immature males, dusky in quiet males.

Distribution. Known only from Lake Victoria.

Ecology: Habitat. The species has been found in relatively few localities and only in the Uganda waters of the lake. However, the available data suggest that H. aelocephalus is restricted to water less than 40 feet deep and to areas where the substrate is firm (sand and rock).

Food. Sixteen of the 20 specimens examined had food in the stomach or intestines; from these it would seem that H. aelocephalus preys on a variety of invertebrate animals, and possibly even small fishes.

In ten specimens the predominant food organisms were insects (particularly dipterous larvae, but also Ephemeroptera [Povilla adusta] and Trichoptera larvae). The non-insect food identified was: in two fishes, oligochaet worms; in one, the remains of a prawn (Caridina nilotica Roux); in another, fragments of plant-tissue and a few Ostracoda; and in two others, numerous fragments of lamellibranch and gastropod shells. One exceptional individual contained the remains of a small cichlid fish.

The presence of sand grains in the stomach and intestines of many individuals suggests that the species may be a bottom feeder.

Breeding. No data are available.

Affinities. Haplochromis aelocephalus shows no special affinity with any other Haplochromis species in Lake Victoria; the less extreme individuals resemble members of the H. nigrescens species-complex of piscivorous-insectivorous predators. The multiseriate dentition, however, disqualifies H. aelocephalus from a place in this complex, but suggests relationship with species of the H. sauvagei-H. prodromus group, and particularly H. xenognathus. In shape, the teeth of H. aelocephalus are unlike those of H. xenognathus which have characteristically recurved tips (Greenwood, 1957). In certain cephalic characters, especially the shape of the lower jaw, the narrow lower dental arcade and the semi-lobate lips, H. aelocephalus approaches H. chilotes but in all other characters there is no obviously close relationship between the two species.

Diagnosis. H. aelocephalus may be distinguished by the following combination of characters: proportions of the head; a multiseriate dentition with the outer teeth slender and gently recurved; lips somewhat thickened.

Study material and distribution records

Museum and Reg. No.			Locality	Collector
		3	Uganda	
B.M. (N.H.).—1958.1.16.244			Igwe Isl.	E.A.F.R.O.
(Holoty	ype)			
,,	1958.1.16.215		Ekunu Bay	,,
,,	1958.1.16.216		Entebbe, Bugonga Beach	,,
,,	1958.1.16.217		Beach near Nasu Point,	,,
			Buvuma Channel	
,,	1958.1.16.218-224		Igwe Isl.	,,
,,	1958.1.16.225-228		Bay opposite Jinja,	,,
			Napoleon Gulf	
,,	1958.1.16.232-233		Pilkington Bay	,,
,,	1958.1.16.234-235		Buka Bay	"
,,	1958.1.16.236-242		Napoleon Gulf, near Jinja	,,
,,	1958.1.16.243		Unknown	,,

SUMMARY

- I. Seven species, which feed almost exclusively on the embryos and larvae of other Cichlidae, are discussed. *Haplochromis obesus* (Blgr.), *H. maxillaris* Trewavas, *H. melanopterus* Trewavas, *H. parvidens* (Blgr.) and *H. microdon* (Blgr.) are redescribed on the basis of new and more extensive collections. Two new species, *H. cronus* and *H. cryptodon* are described.
 - 2. Notes on the ecology and feeding habits of these species are given.

3. The relationships of these species are discussed and it is concluded that the group has a polyphyletic origin.

- 4. Four other species are considered. These are all insectivorous and do not appear to be closely related to the other species of *Haplochromis* in Lake Victoria. *Haplochromis plagiodon* Regan & Trewavas and *H. chilotes* (Blgr.) are redescribed, and two new species, *H. chromogynos* and *H. aelocephalus* are described.
- 5. H. chromogynos is of particular interest since the normal female coloration is apparently the "bicolor" piebald which occurs as an infrequent and sex-limited mutant amongst the females of other and unrelated species.
- 6. Both *H. chilotes* and *H. aelocephalus* are noteworthy for the wide range of individual variability which they show.

ACKNOWLEDGMENTS

I wish to acknowledge my gratitude and thanks to the Trustees of the British Museum (Natural History) for the facilities afforded me; to the authorities of the Muséum National d'Histoire naturelle, Paris and of the Museo Civico di Storia Naturale, Genoa, who graciously allowed me to study type-material in their collections; and to Mr. A. C. Wheeler of the Zoology Department, British Museum (Natural History) who was responsible for making several radiographs used in this study. I am especially indebted to Dr. Ethelwynn Trewavas for her most helpful advice and criticism.

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