

# THE MONOTYPIC GENERA OF CICHLID FISHES IN LAKE VICTORIA

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By P. H. GREENWOOD, B.Sc.

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## INTRODUCTION

IN his revision of the Lake Victoria Cichlidae, Regan (1922) recognized four endemic monotypic genera, the species being *Astatoreochromis alluaudi* Pellegrin, 1904, *Hoplotilapia retrodens* Hilgendorf, 1888, *Platytaeniodus degeni* Boulenger, 1906, and *Macropleurodus bicolor* (Boulenger), 1906. Subsequent collections made by the Cambridge Expedition (1930–1931) extended the range of *A. alluaudi* to include the Lake Edward system and Lakes Kachira and Nakavali (Trewavas, 1933), but provided no further distributional data for the other three genera. Since *Astatoreochromis alluaudi* occurs beyond the Victoria system, it is preferable to delay revision of this species until numerous specimens from the different localities can be examined. Some notes on the osteology and possible phyletic relationships of *Astatoreochromis* have been published already (Greenwood, 1954).

A fifth genus which, but for its geographical separation, would not have been distinguished from *Labidochromis* of Lake Nyasa, is recorded for the first time.

The present study is based on specimens collected by and for the East African Fisheries Research Organization during a field study of the Lake Victoria Cichlidae, and on material in the collections of the British Museum (Nat. Hist.), Muséum National d'Histoire naturelle, Paris, and the Museo Civico di Storia Naturale, Genoa. It forms the first part of a revision of the Lake Victoria *Haplochromis* species flock.

*Notes on counts and measurements*

The counts and measurements used are as defined by Trewavas (1935), except that "length of head" is measured directly from the posterior margin of the operculum to the premaxillary symphysis. This method has been found to yield more consistent results than measurements taken between verticals through the posterior tip of the operculum and the level of the tip of the snout, along a line parallel to the longitudinal axis of the body. Likewise, length of snout is measured directly.

Other measurements and counts are :

Depth of preorbital : measured from about the middle of the orbital rim of the preorbital bone along a line which continues the radius of the eye at this point ; the line approximately bisects the bone.

Interorbital width : the least width of the roofing part of the frontal bones, between the eyes.

Lower jaw : measured directly from the angle to the symphysis.

Lateral line scale series : After last upper lateral line scale, proceed to the scale of the lower lateral line next behind the transverse row that includes the last scale of the upper lateral line and slopes downwards and forwards from it.

In addition to those defined by Trewavas. Depth of cheek : the greatest depth measured vertically from the lower orbital margin to the lower edge of the *adductor mandibulae* muscles. In most specimens this is virtually a measurement of the depth of the scaled portion of the cheek.



Post-ocular part of the head : measured directly from the posterior orbital margin to the posterior tip of the operculum.

# SYNOPSIS OF GENERA OF THE HAPLOCHROMIS GROUP OCCURRING IN LAKE VICTORIA

1. Anal spines three . . . . . 2.  
Anal spines four or more . . . . . *Astatoreochromis*
2. Teeth of upper jaw in two or more series anteriorly, but only in a single (rarely double) series laterally . . . . . 3.  
Teeth of upper jaw in 2-5 series both anteriorly and laterally . . . . . 4.
3. Anterior outer teeth disproportionately longer than the adjacent lateral teeth, slender, unicuspid and procurent. . . . . *Paralabidochromis* gen. nov., p. 327  
Anterior outer teeth forming a graded series with the lateral teeth, not forwardly directed . . . . . *Haplochromis*
4. Outer teeth enlarged and stout, with obliquely truncated and inwardly directed crowns . . . . . *Macropleurodus*, p. 299  
Outer teeth of both jaws small, bi- or unicuspid ; inner teeth in broad bands anteriorly and laterally . . . . . 5.
5. Lower jaw broad and flat, tooth bands in both jaws of uniform breadth antero-posteriorly ; those of lower jaw continued posteriorly on to the ascending part of the dentary . . . . . *Hoplotilapia*, p. 319  
Lower jaw stout, rounded anteriorly ; teeth aggregated anteriorly into two pyriform bands, contiguous at the symphysis . . . . . *Platytaeniodus*, p. 312

## Genus *MACROPLEURODUS* Regan, 1922

*Bayonia* Boulenger, 1911 (*nec.* Bocage 1865), type species *Bayonia xenodonta* Blgr.

*Macropleurodus* Regan, 1922, Proc. zool. Soc., Lond. 189 ; type species : *Haplochromis bicolor*

Boulenger, 1906, Ann. Mag. nat. Hist. (7) 17, 444.

*Haplochromis* (part)

*Paratilapia* (part)

*Hemitilapia* (part)

} For references see synonymy under species.

## Generic characters and synonymy

Prior to Regan's revision of the Lake Victoria Cichlidae (Regan, 1922) specimens of the genus here recognized as *Macropleurodus* had been described as belonging to several genera and species. When Regan (*op. cit.*) defined the apparently new genus, *Macropleurodus* he did not have at his disposal specimens covering the wide range necessary to determine ontogenetic changes in certain characters. Consequently he failed to recognize that his genus was identical with Boulenger's *Bayonia* (Boulenger, 1911), and incorrectly assigned the type specimens of this and one other synonymous "species" to *Haplochromis*.

Regan's diagnosis of *Macropleurodus* gave particular emphasis to the posterior premaxillary teeth :

" . . . several inner series of small teeth anteriorly and three or four series of enlarged teeth laterally, which are exposed when the mouth is shut " (Regan, 1922).



The two specimens on which this description was based have the posterolateral inner teeth not only enlarged, but also similar in form to adjacent outer teeth. It is now known, however, that in small individuals these inner teeth are only slightly enlarged, if at all, and do not closely resemble the outer teeth. Specimens available indicate that most fish between 80 and 90 mm. standard length have a dentition intermediate between juvenile and adult types. In these, many of the typically juvenile, stoutly bi- and unicuspid inner teeth are replaced laterally by teeth differing only slightly in size and form from those of the outer series. Individuals below 80 mm. lack enlarged inner teeth.

Thus, although Regan's diagnosis is incisive for fishes over 90 mm. S.L., it is not sufficiently comprehensive to include smaller individuals.

On the other hand, the present collection shows that the morphology of the outer teeth is equally diagnostic and, moreover, is little affected by the size of the individual. Basically, the outer series is composed of stout teeth, having enlarged and obliquely truncated anterior cusps and disproportionately smaller posterior cusps. In the upper jaw these teeth are implanted obliquely to the long axis of the premaxilla, so that their crowns lie at an angle to it and the anterior cusp points inwards. Teeth of this type are present in all the specimens examined and are not known to occur in any *Haplochromis* or related species.

The peculiar form of the outer teeth in *Macropleuroodus* at once suggests affinity with *Bayonia xenodonta* Boulenger (1911), in which the outer teeth are described as having " . . . very large compressed crowns, with long anterior cusp directed inwards and very short or indistinct posterior cusp . . . ". In this respect, the published figure of *B. xenodonta* (Boulenger, 1911 and 1914) is somewhat misleading since the teeth are stouter than depicted.

Through the courtesy of Dr. D. Guiglia, re-examination of the type specimen of *B. xenodonta* has been possible and has confirmed that the outer teeth are alike in *Bayonia* and *Macropleuroodus*. Further, as Regan and Trewavas (1928) first observed, Boulenger's description of the inner teeth is inaccurate. Posteriorly these teeth form a double series, with six teeth on either side nearly as large as the outer, and in this respect conform to the dental pattern of young *Macropleuroodus*. Also, the more anterior teeth of the two inner series are not " minute and conical " but are in fact tricuspid. Thickening of the buccal mucosa (probably a fixation artefact) has buried the inner teeth so that only their major cusps protrude. Two types of tricuspid teeth are present: one, the usual small tricuspid tooth found in many species of *Haplochromis*; the other, stout and with the minor cusps displaced so as to form a triangular crown having the major cusp at its apex. Similar trigonid teeth are also found in *Macropleuroodus*, both young and adult, but have not been observed in *Haplochromis*.

There is also agreement in morphometric characters and, although *Bayonia xenodonta* has only twenty-four outer teeth in the upper jaw, this number is within the known lower range for *Macropleuroodus* (see below).

There seems little doubt, therefore, that in all salient features the type and unique specimen of *Bayonia xenodonta* is identical with small specimens of *Macropleuroodus bicolor*, and that the two are conspecific.



One other name has been given to cichlid fishes from Lake Victoria with teeth of the *Macropleurodus* type, namely *Hemitilapia materfamilias* Pellegrin, 1913. I have examined the holotype (no. 12.278 in the collection of the Muséum d'Histoire naturelle, Paris) and found it to agree closely with *Macropleurodus* of similar size. The teeth and dental pattern of the type and three other specimens represent an advanced stage in the transition from juvenile to adult condition; that is, the postero-lateral premaxillary teeth of the first inner series are nearly comparable in size and form with the adjacent outer teeth. The remaining inner teeth are small and unequally bicuspid.

Regan (1922) tentatively synonymized *H. materfamilias* with *Haplochromis obliquidens* Hilgendorf; apparently he did not examine the type of *H. materfamilias* (*op. cit.*, pp. 157 and 158) and was misled by Pellegrin's description. Comparison of the holotype with specimens of *H. obliquidens* at once reveals the existence of fundamental differences in the dentition of the two species. In *H. obliquidens* the movably implanted outer teeth are fine and numerous (50–70 in upper jaw); the posterior cusp is wanting, except very occasionally in small fish, whilst the anterior cusp, although obliquely truncate, is compressed and slender. In contradistinction, the immovable outer teeth of *H. materfamilias* are coarse and less numerous (24–40); with few exceptions a posterior cusp is present and the stout anterior cusp is circular in cross section.

### Diagnosis

Cichlid fishes of the *Haplochromis* group as defined by Regan (1920, 1922) but differing from *Haplochromis* in having stout outer teeth with inwardly directed and obliquely truncated crowns; anterior cusp long, slightly decurved and not compressed, the posterior cusp small and indistinct. Fishes over 90 mm. S.L. have one or more inner premaxillary tooth-series composed laterally of enlarged teeth similar in form to the adjacent outer teeth. Consequent upon the enlargement of the lateral teeth, the dentigerous surface of the premaxilla is broader laterally than anteriorly. In small individuals, where the inner teeth are small and bi- or unicuspid throughout the series, the outer teeth are already characteristic. Teeth usually exposed laterally, even when the mouth is shut.

### *Macropleurodus bicolor* (Boulenger) 1906

(Fig. 1)

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

*Paratilapia bicolor* (part) Blgr. 1907, Fish. Nile 479, pl. lxxxix, fig. 1; *Idem*, 1911, Ann. Mus. Genova (3) 5, 68; *Idem*, 1915, Cat. Afr. Fish. 3, 346, fig. 234.

*Bayonia xenodonta* Blgr. 1911, Ann. Mus. Genova (3) 5, 70; *Idem*, 1915, *op. cit.*, 488, fig. 338.

*Hemitilapia materfamilias* Pellegrin, 1913, Bull. Soc. zool. France, 37, 313; Boulenger, 1915, *op. cit.*, 492.

*Haplochromis obliquidens* (part), Regan 1922, Proc. zool. Soc., London, 188.

*Macropleurodus bicolor*, Regan, 1922, *op. cit.*, 189.



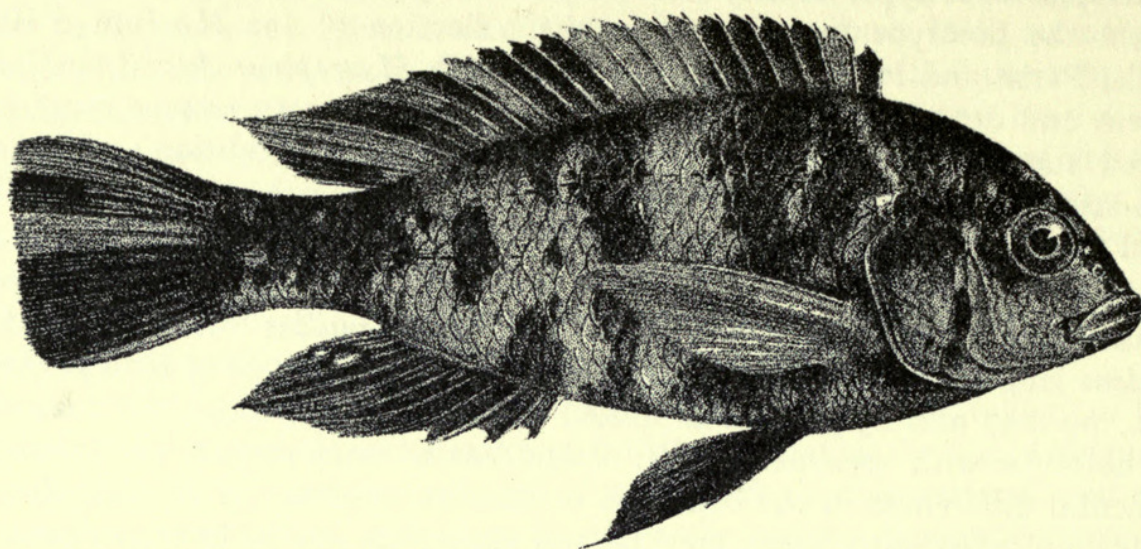
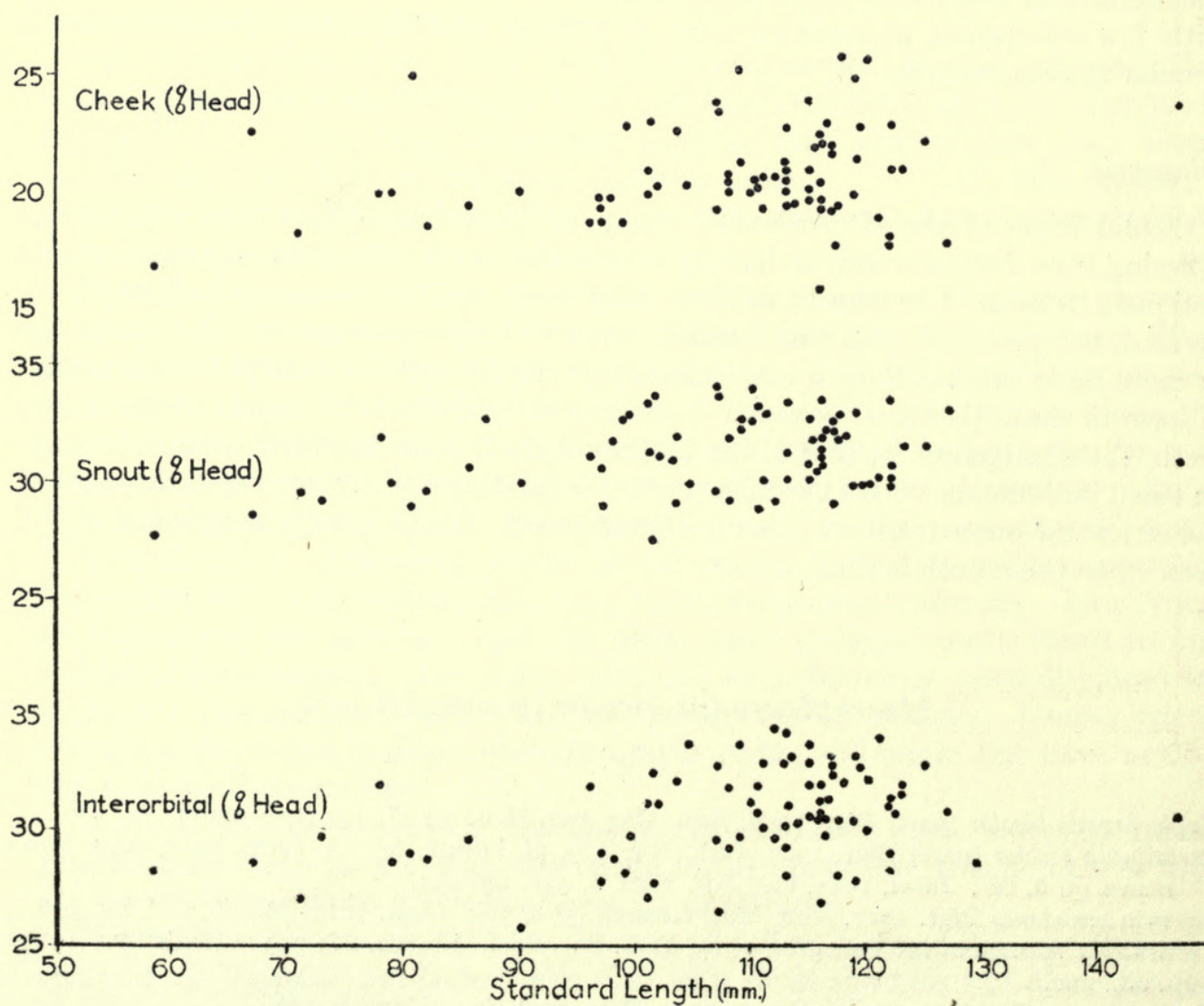


FIG. 1.—*Macropodus bicolor*, holotype. 7/8 N.S. (From Boulenger, *Fishes of the Nile*.)





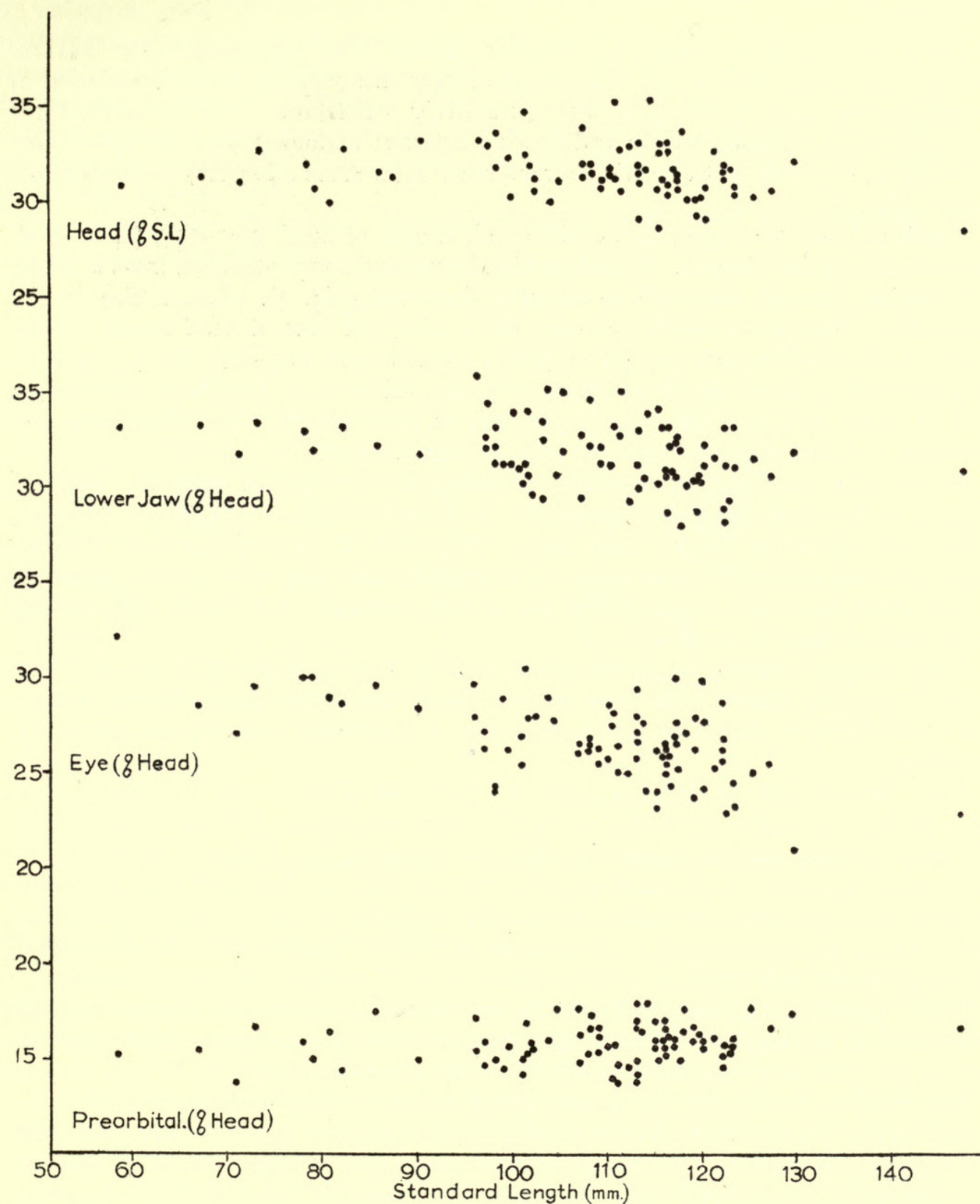


FIG. 2.—Scatter-diagram to show individual variation and allometry of the characters indicated. The isometric relationship of head length and standard length is usual, as is the allometry of head length and the inter-related snout, eye and preorbital measurements. The negative allometry between length of lower jaw and head length is unusual and seems to be related to the stronger jaws and enlarged teeth of larger specimens. These diagrams show scatter but not frequency. Within the size-range 100 to 125 mm. S.L., each dot in the denser aggregates represents at least two specimens.



*Description*

The selectivity of sampling gear used has resulted in a very unequal size distribution of specimens, with a bias towards the larger size groups. Thus subdivision of morphometric data by size groups is not entirely satisfactory; furthermore, there is considerable variation within and overlap between various groups. Despite these limitations, however, most metric characters do show some allometry with standard length (Fig. 2).

Depth of body 34.4–40.8, mean (M)=37.6, length of head 29.0–35.3 (M = 31.7) per cent of standard length. Dorsal profile of head and snout variable, from straight but sloping through decurved to strongly decurved (Fig. 3), without size or sex correlation. Preorbital depth 13.6–18.3 (M = 16.0) per cent of head length; least width of interorbital 25.8–34.5 (M = 30.8); snout length 26.5–34.2 (M = 31.5), eye 21.4–32.0 (M = 27.0), depth of cheek 16.7–26.0 (M = 21.3), length of post-ocular part of head 41.0–50.0 (M = 47.8) per cent of head length. Described from one hundred and one specimens, 60–150 mm. standard length.

Mouth short and broad; maxilla extending to the vertical from the anterior margin of the orbit, or, more frequently, to anterior third of eye. Jaws unequal, lower jaw somewhat shorter than upper, 28.0–36.0 (M = 31.9) per cent of head length, its length/breadth ratio from 1.3 to broader than long, with a mode at unity.

*Gill rakers* short and stout, lowest one or two reduced; 7–8 (rarely 9 or 10) on lower limb of anterior arch.

*Scales* ctenoid; lateral line interrupted, with 31 (f.7), 32 (f.36), 33 (f.29), 34 (f.26), or 35 (f.3) scales. Cheek with three or four (rarely two) rows of imbricating scales; 6–8 scales between dorsal fin and lateral line, 7–9 between pectoral and pelvic fin insertions.

*Fins.* Dorsal with 23 (f.1), 24 (f.13), 25 (f.67), 26 (f.18), or 27 (f.2) rays; anal with 11 (f.7), 12 (f.82), 13 (f.11), or 14 (f.1) rays comprising XIV–XVII 8–11 and III 8–11 spinous and soft rays for the fins respectively. Pectoral fin 25.2–32.0 (M = 28.8) per cent of standard length. Pelvics with the first soft ray produced, variable in its posterior extension, but usually reaching to vent in immature fishes, and as far as the spinous part of the anal fin in adults. Caudal sub-truncate, scaled on the proximal half only.

*Teeth.* Little remains to be added to the description given above. There are 24–40 outer teeth in the upper jaw (mode 34); the number of teeth shows a weak positive correlation with size, especially in fish less than 100 mm. S.L.

Two variants of the outer teeth are known, neither of which affects their characteristic shape. In one there is developed a double posterior cusp; in the other, the posterior cusp is wanting. As this latter type occurs only in large fishes, it is possible that loss of the smaller cusp may be due to attrition.

Inner tooth bands with 2–4 series anteriorly and laterally, narrowing to 1 or 2 series posteriorly. In contrast to the outer series, inner teeth show considerable variation in form, being tricuspid, or variously bicuspid. Tricuspid teeth with the cusps arranged in triangular outline, occur at all sizes; the type of *Bayonia xenodonta* is exceptional in possessing inner teeth mainly of this type.

There is noticeable asymmetry in the degree to which lateral teeth of all series



are enlarged. Most specimens examined show a distinct tendency for the dextral tooth band to be wider and its teeth larger than on the left side. Only a few specimens show symmetrical or sinistral hypertrophy. In both fresh and preserved material the outermost premaxillary teeth are usually exposed laterally even when the mouth is closed, although there is marked variation in the symmetry and degree of exposure. Hypertrophy of lateral teeth on one side is usually associated with a greater exposure of the teeth on that side.

*Pharyngeal bone.* Triangular, short and broad; teeth small and cuspidate, the median series often enlarged.

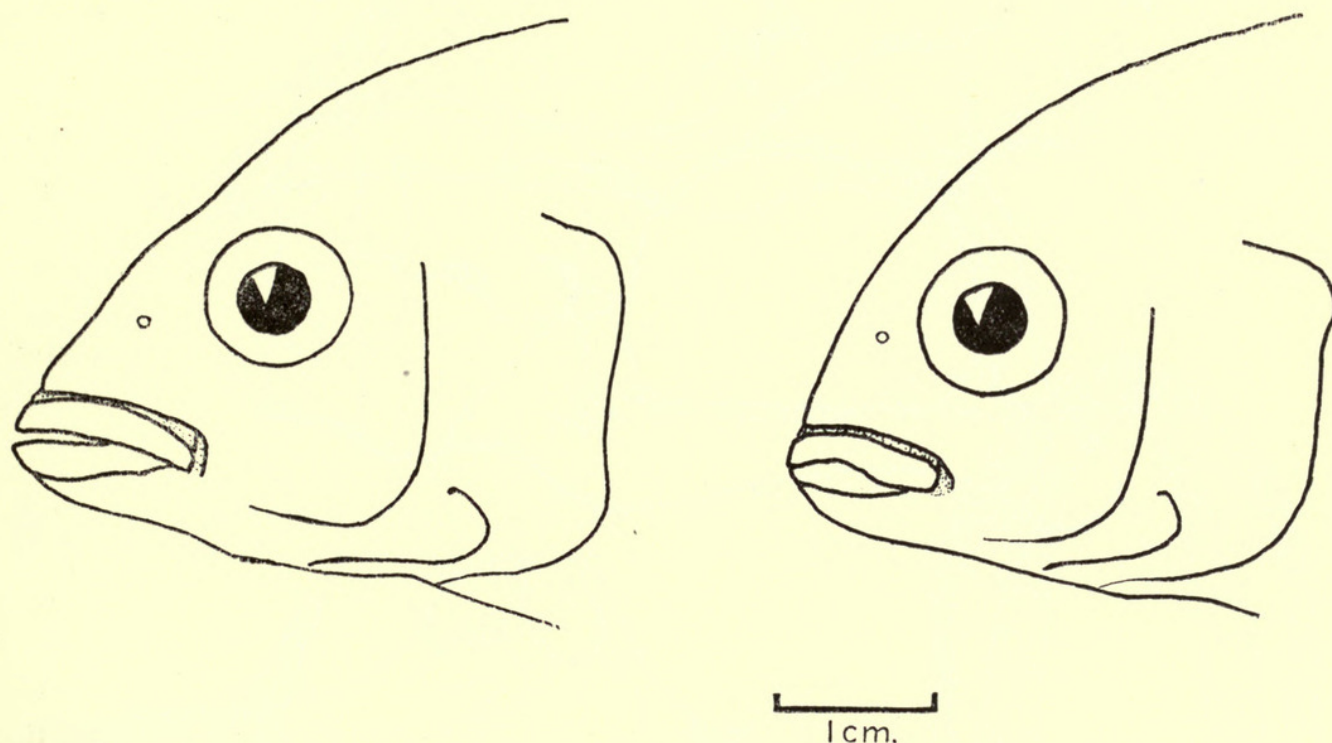


FIG. 3.—*Macropleuroodus bicolor*. Individual variability of head profile.

#### *Syncranium and associated musculature*

A general impression gained from the syncranium of *Macropleuroodus* is one of antero-posterior compression. This is due to the short lower jaw, steeply aligned ethmo-vomerine complex and deep concavity in the entopterygoid, which accommodates part of the short and broad *adductor-mandibulae* muscles.

Both the neurocranium and premaxilla warrant description (Fig. 4). Unpublished observations on skulls of Lake Victoria *Haplochromis* show clearly that the neurocranium of *Macropleuroodus* is atypical, although closely paralleled by that of *Haplochromis prodromus* Trewavas, 1935 (= *H. annectens* Regan, 1922, *nec Cyrtocara annectens* Regan, 1921). From the generalised, but common *Haplochromis* skull-type, it differs principally in having a shortened and strongly curved preorbital face, with the anterior profile ascending almost vertically. In generalized *Haplochromis* skulls (Fig. 5) and more particularly in skulls of elongate species, this part of the neurocranium lies parallel to a straight and gently sloping line connecting the foremost part of the ethmoid with the anterior extremity of the supra-occipital (Fig.



5, A). Posteriorly, the neurocranium does not differ significantly from the generalized type, except that the pharyngeal apophysis is not greatly depressed below the parasphenoid, and its pro-otic buttress is broad and bullate.

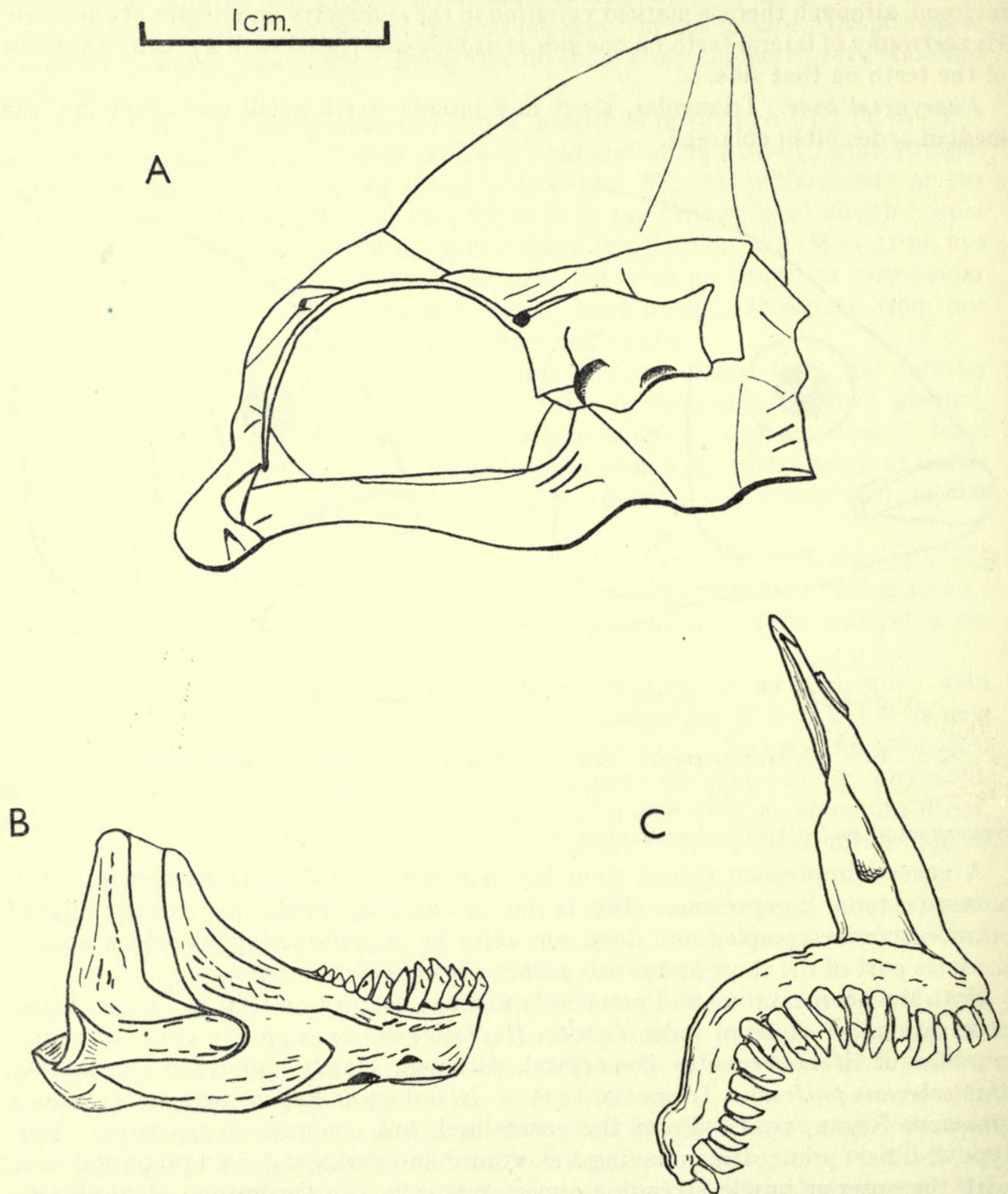


FIG. 4.—*Macropleuroodus bicolor*. (A) Neurocranium in left lateral view; (B) dentary, (C) premaxilla, both in right lateral view. Skeleton prepared from a specimen of 115 mm. S.L.



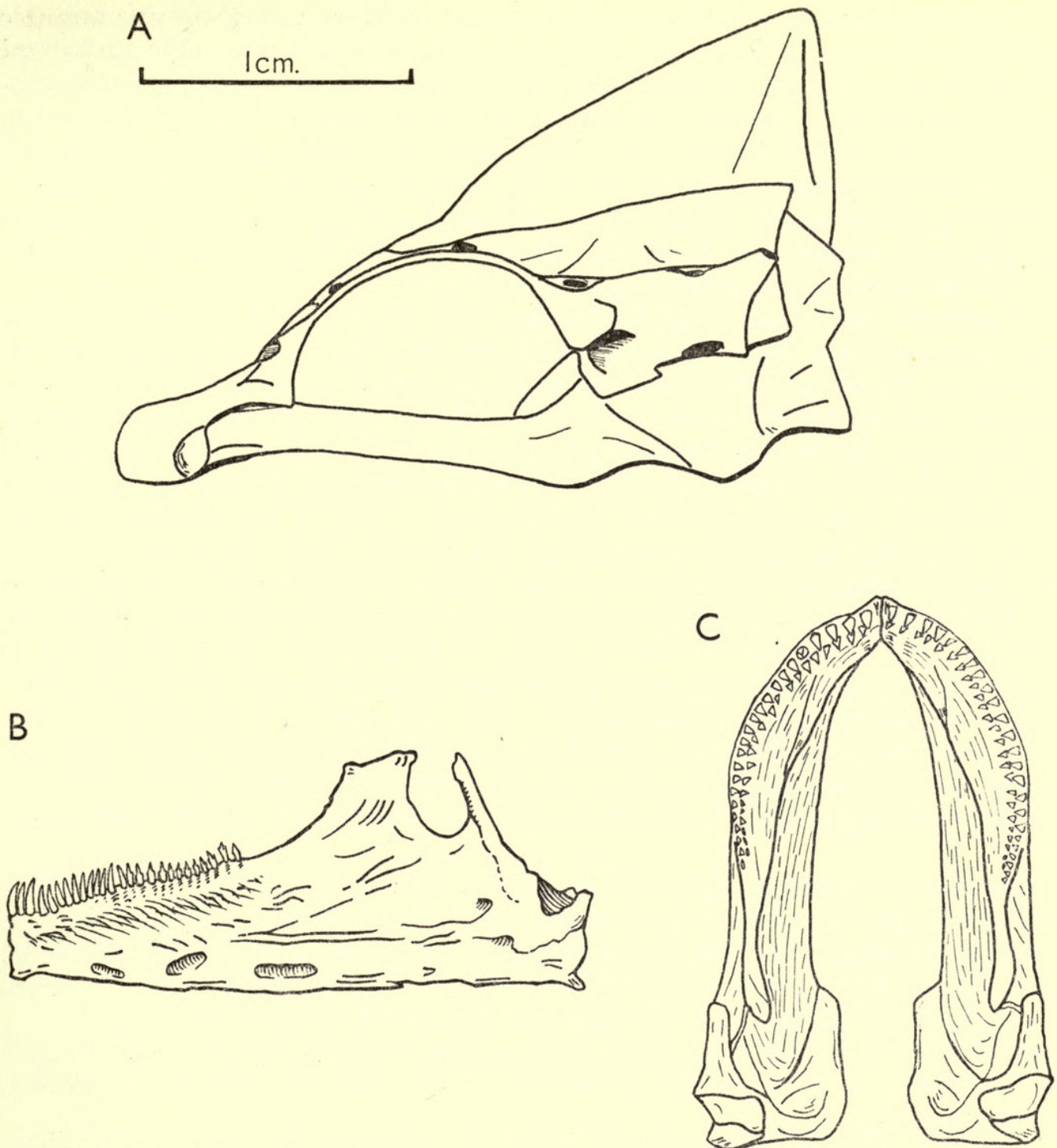


FIG. 5.—*Haplochromis michaeli*. (A) Neurocranium, (B) dentary, left lateral view ; (C) dentary, occlusal view ; to show the skull and jaws of a generalized *Haplochromis* from Lake Victoria. Skeleton prepared from a specimen of 115 mm. S.L.

The premaxilla shows considerable departure from the basic type found in most *Haplochromis* species. Whereas in *Haplochromis* there is slight ventral arching of the horizontal limb of this bone, in *Macropleurodus* the arch is greatly exaggerated, with its point of maximum curvature at the broadest part of the tooth band (Fig. 4, B). Individuals with a marked dextrally developed tooth pattern have a corresponding degree of asymmetry in the two halves of the premaxilla, which is then more acutely arched on the right side.



A comparative study of jaw musculature was made with *Haplochromis sauvagei* and *H. prodromus*, species in which the jaws show some deviation from the generalized *Haplochromis* condition towards that of *Macropleurodus*. Negligible differences were observed in the musculature of the three species, except that in *M. bicolor* the *adductor mandibulae* I measures only 28% of the head length, whilst in *H. sauvagei* and *H. prodromus* this muscle is 33% of head length. *Adductor mandibulae* II is also relatively shorter in *M. bicolor* (21.0% compared with 33.6% in *H. sauvagei* and 26.9% in *H. prodromus*). In all other respects the cranial musculature of *Macropleurodus* is typical for a generalized *Haplochromis* species.

Functional significance of the skull form, together with that of the well developed teeth, jaws and muscles, is best considered in relation to the predominantly molluscan diet of *M. bicolor*, and the manner in which its prey is secured. Whereas in most *Haplochromis* species the lower jaw is somewhat obliquely inclined when the mouth is shut, in *M. bicolor* it is almost horizontal. The position of the lower jaw at rest directly affects the manner in which the whole mouth is protruded; in typical *Haplochromis*, maximal protrusion is achieved as a result of the mandible moving from an inclined to a horizontal position. On the other hand, when the mouth of *M. bicolor* is opened, mandibular movement is from the horizontal to a point below it. Premaxillary movement is also directed downwards by the near vertical ethmoid complex over which the premaxilla slides. In consequence, the whole mouth is protruded ventrally, with the upper jaw slightly in advance of the lower. The short and broad *adductor mandibulae* muscles allow the mouth to be retracted with remarkable rapidity, thereafter mounting a powerful and sustained pressure on any object held between the teeth. The crushing power of the jaws is further enhanced by the stout outer teeth and well developed bands of lateral and postero-lateral inner teeth.

Aquarium observations show that *M. bicolor*, when feeding, usually approaches a snail from above, rapidly protruding the mouth in an attempt to snatch its prey from the substrate. Once the snail is firmly held and suitably orientated—generally with the foot directly orally—there follows a series of short biting movements which crush the shell and thus free the soft parts, which alone are ingested.

Attention has already been drawn to the similar skull structure in *M. bicolor* and *H. prodromus*; it is not surprising therefore to find that both species have similar feeding habits.

*Ontogeny.* Alizarin preparations of larval *M. bicolor*, *H. macrops* (a generalized species), and *H. prodromus* have been compared. These specimens reveal no fundamental differences in osteology or dentition of the three species when compared at morphologically equivalent developmental stages. For example, at the latest stage examined (9.0 mm. total length; yolk sac almost completely resorbed) the small conical outer teeth are morphologically and numerically identical in all three species.

From these admittedly few observations it would seem that characteristic adult skull form and outer teeth must develop during post-larval ontogeny.

#### *Coloration and polychromatism*

*Coloration in life.* Adult females with greenish-yellow ground colour, becoming



lighter or silver ventrally. Dorsal and anal fins yellow-green, the former with or without two irregular, dark, longitudinal stripes, the latter with two to four ill-defined yellow spots on the posterior part. Caudal and ventral fins generally colourless, though the latter may sometimes be slightly dusky. Young of both sexes and sexually inactive males have similar coloration.

*Adult males* (breeding coloration). Dark slate-blue ground colour, lighter, sometimes silver, ventrally. Chest, branchiostegal membrane, lower jaw and ventral aspects of the cheek, black. Operculum and flank sometimes with a faint scarlet flush. Dorsal fin dusky, with deep red spots and streaks between the rays, especially intense on the soft part. Anal dusky, with well marked scarlet ocelli. Ventral fins black. Intensity of male coloration is correlated with sexual state; inter-grades are known between the coloration described above and that of typical female or juvenile coloration.

Besides normal sexually dimorphic coloration, certain fish exhibit a third colour pattern, in the form of an individually variable piebald, black on a yellow-green ground. The holotype is such a specimen (Fig. 1). The *bicolor* pattern is clearly composed of vertically arranged irregular and often interrupted dark bands, which are generally continued across the body on to the vertical and paired fins. Although some are more intensely blotched than others, no intergrades are known between normal female coloration and *bicolor* variants.

With two exceptions all *bicolor* individuals examined were females. The colour-pattern and degree of pigmentation differ in the two exceptional male fishes. Since protandry might be suspected, the gonads were sectioned and examined microscopically. In both fishes, however, there was evidence only of testicular tissue. In one fish the pattern is typical; in the other the pattern is less intense and occurs on a darker ground than is typical for female fishes.

Accurate frequency-estimates for *bicolor* individuals are difficult to obtain, since collectors show marked sampling bias in favour of these strikingly coloured fishes. However, in more rigorously controlled collections from one area, *bicolor* frequency amongst female fish in the 105 mm. to 125 mm. size class is approximately 30%, an incidence sufficiently high to justify regarding the phenomenon as being due to polymorphism and not to the maintenance of an atypical phenotype by recurrent mutation.

If the two female colour patterns are accepted as an example of polymorphism, it is necessary, *ex hypothesi*, to consider the selective balance which must exist between the two forms. This question is further complicated by the apparently almost completely sex-limited polymorphism in *M. bicolor*.

Since the genetical basis of polymorphism and sex determination is unknown for *Macropodus*, some hypothesis at least is desirable before considering the question of selective values for the two colour patterns.

If, as in many fishes, the female is the heterogametic sex, then a possible (and doubtless oversimplified) explanation for this sex-limited polymorphism is that the gene or gene complex underlying development of a *bicolor* pattern may lie in a sex chromosome, be recessive to the gene or genes for normal colour, and be linked with a recessive lethal gene. Thus full expression of *bicolor* pattern could only be manifest



in the heterogametic sex. Males carrying the double complement of recessive *bicolor* genes necessary for phenotypic expression in that sex, would, on the linkage supposition, die as a result of simultaneously receiving the two recessive lethal genes. Since linkage is sometimes broken, a small percentage of male *bicolor* individuals might well be expected and the two *bicolor* male fishes in this collection are possibly such individuals.

By this reasoning, either selection in favour of polymorph genes must be sufficient to compensate for loss of males and consequent unbalance of the sex-ratio or, alternatively, the unbalanced sex ratio may be the factor preventing spread of *bicolor* genes throughout the species, should these have a selective value slightly higher than "normal".

Two possible advantages associated with *bicolor* patterns, or genotypes, present themselves. Firstly, a *bicolor* pattern is, in effect, a disruptive one and may thus provide some protection against the attacks of predators. Studies on fish-eating birds (Cott, 1952) and on piscivorous fishes such as *Bagrus* and *Clarias* (personal observation) neither support nor negate this possibility, since *M. bicolor* has not been found among the prey of these animals. Secondly, there is the possibility, also unproven, that a female *bicolor* genotype, or a male heterozygous for *bicolor*, may possess some physiological advantage over other genotypes.

Regrettably, then, insufficient positive evidence is available at present to warrant further discussion on the evolutionary aspects of polymorphism in *Macropleuroodus*.

### Ecology

*Habitat.* *M. bicolor* is widely distributed within Lake Victoria, occurring most frequently in littoral and sublittoral regions, especially where the bottom is hard (sand, rock or shingle), but only rarely over mud. Depth distribution is fairly restricted, with a maximum of between 30 and 40 feet (see also Graham, 1929).

*Food.* From gut analyses of numerous specimens (throughout the size range 60–150 mm.) it is apparent that snails and insect larvae are the predominant food organisms (see also Graham, 1929). Shell fragments are rarely found in the stomach or intestine although opercula are usually present. Aquarium observations confirm that almost the entire body of the snail is removed from its shell before ingestion takes place (*vide* p. 325), although small snails and, on occasion, thin-shelled species, may be crushed intra-orally before being swallowed. As a result of this feeding mechanism snail remains are so fragmentary as to preclude accurate identification; remains of *Gabbia* sp. have, however, been positively identified on several occasions.

The insects most commonly recorded from the pabulum of *M. bicolor* are larvae of the boring may-fly, *Povilla adusta* Navás, with other larval Ephemeroptera, and larval Chironomidae occurring less frequently. The proportion of insect to molluscan food eaten is difficult to determine and is probably related to local and cyclic abundance of these organisms.

In the light of numerous gut analyses which are now available for this species, Graham's record (1929) of fish and cichlid eggs from the stomach of *M. bicolor* requires some comment. Apart from this record no other instances of piscivorous habits are known for *M. bicolor*. Unfortunately, Graham does not give a detailed analysis of



the gut contents, particularly of the number of specimens from which his data are derived. Bearing in mind this limitation, it is suggested that the fish-remains and eggs were from the stomachs of different individuals and consequent upon brooding female fishes swallowing their own young, a relatively common occurrence when the fishes are caught in gill-nets.

*Breeding.* The exact spawning grounds of *M. bicolor* are unknown: eggs and larvae at all stages of development have been found in the mouths of various female fishes and it is presumed that the species is a mouth-brooder. Brooding females have been caught in all parts of the species range. The smallest sexually active fish examined was a female 96 mm. long (*ex* Kisumu). The habitat of post-larval fishes is unknown.

### *Affinities*

Unlike the other monotypic genera *M. bicolor* can apparently be related to an extant species of *Haplochromis*. Similarity in skull architecture of *M. bicolor* and *H. prodromus* has already been noted. There are additional similarities in the short and stoutly constructed jaws of both species, besides a marked resemblance in general facies. Against these resemblances must be set the very different tooth form and dental pattern of *H. prodromus*, although in this species the teeth are stout and the inner series well developed. The structure of the head and dental patterns suggest that, at a functional level, the condition represented by *H. prodromus* might well be considered pre-adaptive to the development of a relatively massive dentition, such as that of *M. bicolor*.

### *Study material and distribution records*

Museum and Reg. No.	S.L. (mm.).	Locality.	Collector.
British Museum (N.H.) :			
1906.5.30.414 (type of <i>H. bicolor</i> )	125	Bunjako (Uganda)	Degen
1906.5.30.378 . . . . .	115	Ditto	"
1928.5.24.493-503 . . . . .	115-125	See below	M. Graham
1928.5.24.1-3 . . . . .	120-125	Ditto	Ditto
Paris Museum :			
12.278 (holotype of <i>H. materfamilias</i> . . . . .)	109	Port Florence, Kenya	Alluaud and Jeannel
12.279-281 (paratypes of <i>H. materfamilias</i> ; proportions not included in description above) . . . . .	91-97	Ditto	Ditto
Genoa Museum :			
(Type of <i>Bayonia xenodonta</i> Blgr.) . . . . .	73	Jinja	Bayon
B.M.(N.H.) :			
1955.2.10.5-11 . . . . .	78-110	Kisumu	E.A.F.R.O.
1955.2.10.50-57 . . . . .	101-123	Jinja, Napoleon Gulf	Ditto
1955.2.10.43-46 . . . . .	79-104	Beach nr. Nasu Point, Buvuma Channel	"



Museum and Reg. No.	S.L. (mm.).	Locality.	Collector.
B.M.(N.H.) :— <i>cont.</i>			
1955.2.10.22-23 . . .	82 and 97	Grant Bay (Uganda)	E.A.F.R.O.
1955.2.10.21 . . .	102	Dagusi Island	Ditto
1955.2.10.65-73 . . .	105-120	Off southern tip of Buvuma Is.	„
1955.2.10.24-42 and 74-83 . . .	90-122	Harbour at Entebbe	„
1955.2.10.58-62 . . .	58-67	Bugonga Beach	„
1955.2.10.12, 16-20 and 48 . . .	112-130	Busongwe Bay (Kagera River mouth)	„
1955.2.10.63-64 . . .	110 and 147	Majita Beach (Tanganyika Terr.)	„
1955.2.10.4, 49 and 84 . . .	115-119	Mwanza	„

Graham (1929) records the occurrence of *M. bicolor* as follows :

Kenya : Kavirondo Gulf : Off Sukuri Island.  
Off Ulambwi bay.  
Mbita Passage.

Near Nzoia River.

Kadimu Bay.

Tanganyika Territory : Mwanza.  
Smith Sound.

#### Genus *PLATYTAENIODUS* Boulenger, 1906

*Platytaeniodus* Boulenger, 1906, Ann. Mag. nat. Hist. (7) **17**, 451 ; *Idem*, 1907, Fish. Nile, 493 ;  
*Idem*, 1915, Cat. Afr. Fish. **3**, 426, fig. 292 ; Regan, 1922, Proc. zool. Soc., Lond. 190. Type  
species : *Platytaeniodus degeni* Blgr. 1906.

Generic synonyms :

*Astatotilapia* (part) }  
*Haplochromis* (part) } For references see synonymy under species.

#### Generic characters and synonymy

Both Boulenger and Regan considered the premaxilla and its tooth pattern diagnostic. Boulenger (1914) states :

“ . . . the alveolar surface of the premaxilla widening towards the pharynx, the band of teeth in the upper jaw horseshoe shaped . . . ”

Additional material shows, however that in fishes below 100 mm. standard length the posterior premaxillary dentigerous (alveolar) surfaces are not always expanded medially. Nevertheless, even in small specimens the premaxilla is stouter and its dentigerous surface wider than in *Haplochromis* ; posteriorly the teeth are arranged in several rows, so that the premaxillary tooth band is always clearly U-shaped, with the arms at least as broad as the medial part. Broadening of the posterior alveolar surfaces is gradual and shows positive allometry with standard length ; in some large individuals the left and right surfaces are closely apposed in the mid-line (Fig. 6, c).



Tooth bands in the lower jaw are more readily diagnostic and less subject to variation with absolute size than those of the premaxilla. In *Platytaeniodus* the mandibular teeth are confined to the anterior and antero-lateral portions of the dentary and are grouped into two broad and roughly pyriform patches, contiguous at the symphysis; posteriorly there is a short, single row of four to seven teeth

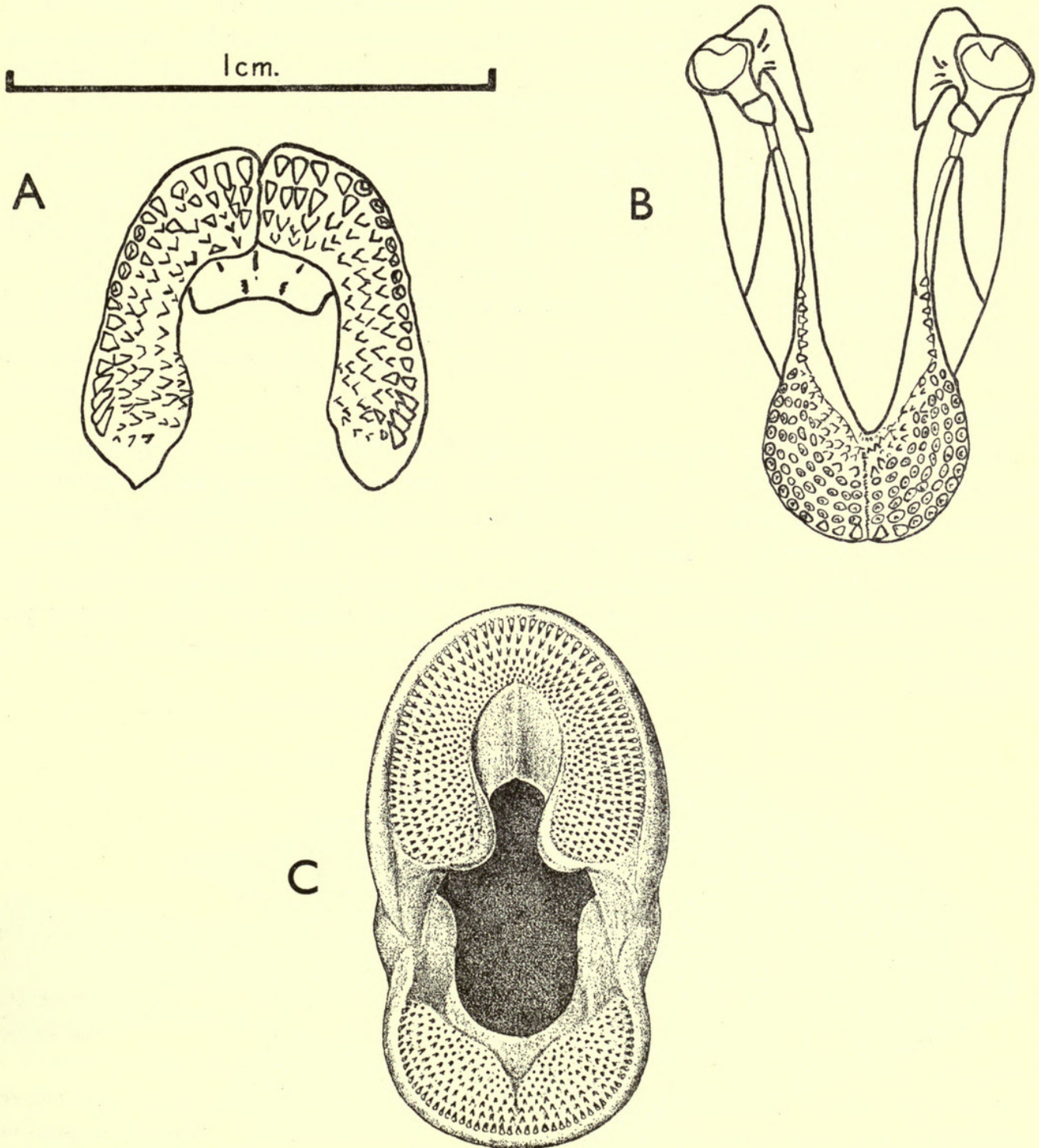


FIG. 6.—*Platytaeniodus degeni*. (A) Premaxilla, (B) dentary, both in occlusal view. Skeleton prepared from a specimen 80 mm. S.L. (c) Mouth of the holotype, ca.  $\times 4$ . [(c) from Boulenger, *Fishes of the Nile*.]



lying between the ascending part of the ramus and the anterior tooth bands (Fig. 6, B and C).

When provisionally referring *Astatotilapia jeanneli* Pellegrin to *Haplochromis macrops* Blgr., Regan (1922) was apparently misled by the large eye and shallow preorbital of *A. jeanneli*. There is undoubtedly some resemblance between *H. macrops* and *P. degeni*, but this is confined to superficial characters, and is belied by their fundamentally different dentition. Re-examination of the types of *A. jeanneli* reveals that the premaxillary teeth are arranged in four or five series of equal breadth both laterally and posteriorly, a condition never observed in *H. macrops*. Furthermore *A. jeanneli* has the mandibular teeth grouped anteriorly and laterally in five series, with only a short, single series posteriorly. That is to say, both type specimens have a dentition typical for small *P. degeni*. In other characters too, notably the mouth with its broad lower jaw, shorter than the upper, and the almost completely hidden maxilla, *A. jeanneli* agrees more closely with *P. degeni* than does *H. macrops* or any other *Haplochromis* species.

On these grounds, therefore, I consider *A. jeanneli* to be synonymous with *P. degeni*.

### Diagnosis

Cichlid fishes of the *Haplochromis* group, but differing from *Haplochromis* in having broad bands of teeth on the posterior part of the premaxillary dentigerous surface, which is expanded medially in large specimens but is of almost equal breadth anteriorly and laterally in fishes of less than 100 mm. S.L. Teeth on the dentary grouped into two, broad, pyriform, curved and contiguous bands anteriorly and antero-laterally, but continued posteriorly as a short single row only. Lower jaw usually shorter than the upper; maxilla almost completely hidden below the preorbital.

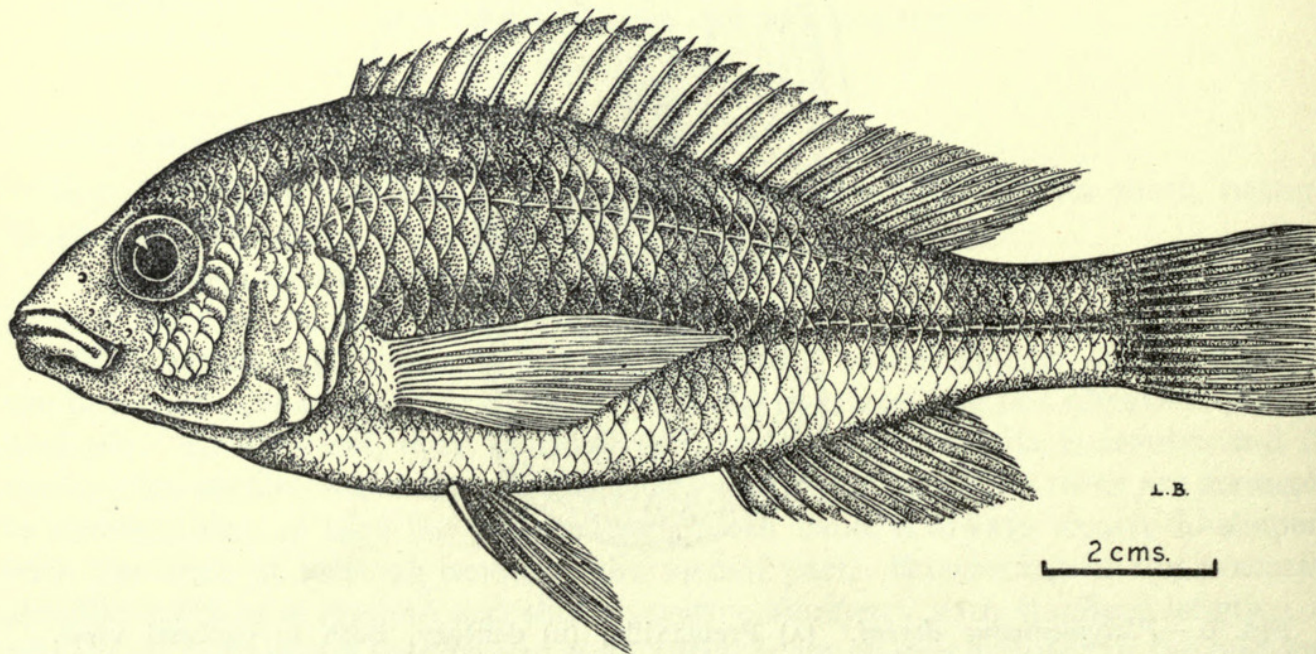


FIG. 7.—*Platytaeniodus degeni*, ♀. Drawn by Miss L. Buswell.



*Platytaeniodus degeni* Boulenger, 1906

(FIG. 7)

*Platytaeniodus degeni* Boulenger, 1906, *l.c.*; 1907, *l.c.* and pl. xci, fig. 1; 1915, *l.c.* and fig. 292; Regan, 1922, 190, fig. 14.

*Astatotilapia jeanneli* Pellegrin, 1913, Bull. Soc. zool. France, **37**, 313.

*Haplochromis jeanneli* (Pellegrin), Blgr. 1915, Cat. Afr. Fish. **3**, 291.

*Haplochromis macrops* (part) Regan, 1922, Proc. zool. Soc. London, 166.

*Description*

Thirty-six specimens (size range 67 to 154 mm.) comprising the type and other specimens in the British Museum (Nat. Hist.) (including material newly collected by E.A.F.R.O.), as well as the types of *A. jeanneli* are considered in this description.

Since most characters tabulated below show some allometry with standard length these data are grouped into two size classes. In some characters intra-group variability is high, but further subdivision into smaller groups is impracticable.

In the table of proportions, head length, depth of body and length of caudal peduncle are expressed as percentages of standard length; all other characters are expressed as percentages of head length. Range and mean are given for each character.

TABLE I.

Standard Length.	67-93 mm. (23 specimens).	98-154 mm. (13 specimens).
Depth of body . . .	32.5-40.5 M = 35.6	34.78-43.0 M = 38.4
Length of head . . .	30.0-36.5 M = 32.4	31.5-34.7 M = 32.7
Depth of preorbital . . .	12.0-16.0 M = 14.2	13.7-17.4 M = 15.2
Least interorbital width . . .	25.0-30.8 M = 27.1	28.2-34.8 M = 31.2
Length of snout . . .	25.0-32.0 M = 30.0	31.75-37.4 M = 34.8
Diameter of eye . . .	27.4-33.4 M = 30.8	22.1-26.0 M = 24.8
Depth of cheek . . .	18.5-26.1 M = 19.7	20.0-26.6 M = 23.4
Length of lower jaw . . .	32.1-39.6 M = 37.0	35.0-38.1 M = 36.0
Caudal peduncle . . .	13.9-21.5 M = 16.5	14.0-18.5 M = 16.7

Dorsal profile of head and snout gently (in a single specimen somewhat strongly) decurved; mouth horizontal; lower jaw equal to or more usually shorter than upper, its length/breadth ratio 1.16-1.68: in some specimens the lower jaw, including lips, is slightly broader than the upper. Lips well developed and somewhat thickened; maxilla almost completely hidden beneath the preorbital, with only its postero-ventral tip exposed and extending to below the anterior orbital margin, or slightly beyond.



The holotype, a male of 115.0 mm. S.L., is figured by Boulenger (1907 and 1915). This fish is both somewhat atypical and slightly distorted in preservation and the impression given of a deep ventral profile and a slightly oblique mouth is not characteristic.

*Gill rakers.* Short and stout, 7–8 on lower limb of the anterior arch, the lowest one or two usually reduced.

*Dentition.* Premaxilla with 4–8 rows of teeth; dentary with 4–6 rows.

With few exceptions, specimens over 100 mm. S.L. have the posterior part of the premaxillary dentigerous surface expanded medially, so that the upper tooth bands are broader posteriorly than anteriorly. In small individuals, although there are several series of teeth posteriorly, the tooth band is either of equal width at all points, or medial expansion of the premaxilla may have begun, causing the band to be very slightly wider posteriorly (Fig. 6, A). Expansion of the posterior surface is not correlated with an increase in the number of tooth rows borne on it, which are, in fact, equal to or slightly fewer than those on the anterior part of the premaxilla.

Mandibular dental pattern as described for the genus; pyriform band from half to two thirds as broad as long.

Teeth are variable in form, those of the outer series slenderly conical, with or without an admixture of unequally bicuspid teeth. Teeth of the inner series all unicuspid in most specimens above 100 mm. S.L. and in some below that size; otherwise the outermost teeth unicuspid and the remainder tricuspid or exceptionally, bicuspid.

*Scales* ctenoid; lateral line interrupted, with 31 (f.2), 32 (f.5), 33 (f.14), 34 (f.10), 35 (f.2), or 36 (f.3) scales. Cheek with 3–4 series of imbricating scales; 7–9 scales between lateral line and origin of dorsal fin; 7–9 (rarely 10) between the pectoral and pelvic fins.

*Fins.* Dorsal with 24 (f.3), 25 (f.23) or 26 (f.10) rays, anal with 11 (f.6), 12 (f.23) or 13 (f.7) rays, comprising XV–XVII 8–10 and III 8–10 spinous and soft rays. Pectoral fin 22.6–31.8 ( $M = 28.0$ ) per cent of standard length. Caudal truncate, scaled on its proximal half only. Pelvics with the first ray produced, extending to the vent in a few specimens and to the spinous part of the anal in most.

*Syncranium.* Since the form of premaxilla and dentary in *P. degeni* is correlated with the well-developed tooth pattern, both these bones depart very strikingly from the typical *Haplochromis* condition.

In small individuals of *P. degeni*, the premaxilla bears a superficial resemblance to that of *Hoplotilapia*, particularly with regard to the dental pattern, but in large fishes it is unique. On the other hand, the dental pattern and morphology of the dentary are comparable in both large and small individuals. The dentary is characterized by its broad and laterally expanded anterior tooth-bearing portion, which imparts to this bone an appearance unique amongst the Lake Victoria cichlids.

The neurocranium of *P. degeni* is intermediate between the generalized *Haplochromis* type and that of *M. bicolor*. It is strictly comparable with the neurocrania of species of the *H. crassilabris* group. Here the skull is characterized by a somewhat shortened and steeply inclined ethmo-vomer complex; in consequence, the anterior skull profile is also steep. In a typical *Haplochromis* skull the ethmo-vomer is longer



and rises less steeply, meeting the downward sloping frontals at a wide angle. As a result, the anterior profile is shallower and also more acute than in the "*crassilabris*" type skull (Fig. 5).

Jaw musculature in *P. degeni* does not differ greatly from that of a generalized *Haplochromis* species.

*Coloration. Preserved material. Males:* dusky to dark grey; dorsal and anal fins dark; pelvics black, caudal colourless. *Females and immature individuals:* silver-grey or light brown; fins colourless.

Transverse and longitudinal banding sometimes occurs, being most clearly marked in females and young individuals; when present, there is a well marked median longitudinal stripe, a fainter and interrupted band running slightly below the dorsal fin, and eight or nine narrow transverse stripes on the flank and caudal peduncle. Faint lachrymal and interocular stripes may also be present. The presence and intensity of these markings is apparently related to the emotional state of the fish or may only appear after death.

*Coloration in life. Sexually active males:* ground colour light blue-grey, lips iridescent blue. Chest and branchiostegal membrane black. Fins; dorsal sooty, lappets and spots on soft part red; caudal with red flush, most intense along margin; anal with dusky pink flush and several yellow ocelli. *Females:* ground colour golden fawn; all fins neutral, dorsal with orange lappets and spots, especially on the soft part; caudal with orange margin and maculae; anal with faint or well marked yellow ocelli.

### *Ecology*

*P. degeni* is recorded from several areas in Lake Victoria (see below), but as so few specimens are known it is not possible to generalize on habitat preferences. From the scanty data available it appears that the species is probably restricted to littoral and sub-littoral regions where the water is less than fifty feet deep. Specimens have been caught in nets set over both hard and soft substrates, but the greater number came from stations having a sand or shingle bottom.

*Food.* The distinctive dentition of this species suggests a highly specialized diet. Tantalizingly few fish, however, have yielded ingested material. Twelve specimens have been examined, all of which were caught in nets set overnight or in seines operated during varied daylight hours. According to the substrate over which they were living, ten fishes had either sand grains or organic mud in the stomach and intestines, together with fairly dense aggregations of mucus. Two fishes, caught on different occasions at a station near the southern tip of Ramafuta Island (Buvuma Channel), had the entire alimentary tract filled with the diatom *Melosira*. Diatoms from the stomachs of these fishes showed only slight signs of digestion, but samples taken from the mid-intestines and recta were almost completely digested. Animal remains, occurring sporadically, included insect larvae, Hydracarina, fragments of Copepoda, Ostracoda, and in two specimens shell fragments of Pelecypoda (Sphaeriidae).

Most guts also contained some diatoms and blue-green algae, the former apparently digested, the latter intact. The very small quantity of ingested material in any one



individual is striking and no particular organism, or group of organisms, occurs with sufficient frequency to indicate what the food of *P. degeni* may be. Since sand and bottom debris is significant in the majority of specimens, it is possible that the species may feed on the micro-fauna and flora living on and within the substrate. Thus, broad bands of jaw teeth may serve to rasp and loosen food from the surrounding sand.

*Breeding.* Spawning sites are unknown; only two females, both from beaches in the Mwanza area, have been found with eggs in the mouth. The smallest individual with demonstrably active gonads was a female, 71.0 mm. long.

### *Affinities*

There is no obvious relationship between *P. degeni* and any known Lake Victoria species or species-group of *Haplochromis*, with which genus the species shows fundamental affinities. The peculiar premaxillary and mandibular tooth patterns serve to set *P. degeni* apart from even those *Haplochromis* with several series of inner teeth. Regan (1922) considered *P. degeni* as being "very near" to *H. prodromus*, which species he believed "shows a slight departure from the normal *Haplochromis* dentition towards the *Platytaeniodus* type". His opinion was based on the holotype and then unique specimen of *H. prodromus*. Summarizing unpublished data on *H. prodromus*, it is clear that the type specimen has an aberrant dental pattern and that its resemblance to *P. degeni* is purely superficial. Whereas in large *Platytaeniodus* there is an actual expansion of tooth-bearing surfaces, in *H. prodromus* only the tooth-band is apparently expanded; its increased breadth is actually due to the posterior teeth being more widely separated from one another than are the anterior teeth. In no specimen of *H. prodromus* is the upper tooth band as broad posteriorly as anteriorly, yet this is the usual condition in *P. degeni*. Further, the dentary of *P. degeni* differs considerably from that of *H. prodromus*. The evolution of a wholly multi-seriate dentition has probably occurred more than once within the Lake Victoria species-flock, as for instance in the *H. sauvagei* group and again in the monotypic genera. Thus any apparent relationship between *P. degeni* and *H. prodromus* should be considered as consequent upon convergent evolutionary trends, the ultimate expressions of which are achieved by manifestly dissimilar means.

### *Study material and distribution records*

Museum and Reg. No.	S.L. (mm.).	Locality.	Collector.
British Museum (Nat. Hist.):			
1906.5.30.511 (holotype)	114	Bunjako (Uganda)	Degen
1909.3.29.10	98	Sesse Is. (Uganda)	
1928.5.24	93	Mbita Passage (Kenya)	M. Graham
Paris Museum:			
12.262 (holotype of <i>A. jeanneli</i> )	72	Port Florence (Kenya)	Alluaud and Jeannel
12.262 (paratype of <i>A. jeanneli</i> )	67	Ditto	Ditto



Museum and Reg. No.	S.L. (mm.).	Locality.	Collector.
B.M. (N.H.) :			
1955.2.10.91-94 . . . .	73-79	Kisumu (Kenya)	E.A.F.R.O.
1955.2.10.105-106 . . . .	78-90	Kamarenga (Kenya)	Ditto
1955.2.10.115 . . . .	74	Kendu (Kenya)	„
1955.2.10.88 . . . .	74	Likungu (Kenya)	„

### Genus *HOPLOTILAPIA* Hilgendorf, 1888

*Hoplotilapia* Hilgendorf, 1888, S.B. Ges. naturf. Fr. Berlin, 76-77 (type species (*Paratilapia*?) *retrodens* Hilgendorf, l.c.) ; Regan, 1922, Proc. zool. Soc., Lond. 190.

*Cnestrostoma* Regan, 1920, Ann. Mag. nat. Hist. (9) 5, footnote p. 45 (type species *Paratilapia polyodon*, Blgr.).

*Haplochromis* (part) }  
*Paratilapia* (part) } For references see synonymy under species below.  
*Hemichromis* (part) }

### Generic characters and synonymy

The holotype of *Hoplotilapia retrodens* (in the collections of the Zoologisches Museum der Humboldt-Universität, Berlin) has not been examined by me, nor can it be definitely established whether this specimen is still in existence. Dr. Kurt Deckert of the Zoologisches Museum has, on two occasions, kindly attempted to locate several specimens, including the type of *H. retrodens*. Of these he writes: "Ich muss Ihnen leider mittheilen, dass unser Suchen nach den verlangten Typen ohne Erfolg geblieben ist, obwohl ich mit grosser Sicherheit annehme, dass sie nicht verloren-gegangen sind."

Hilgendorf's original description of (*Paratilapia*?) *retrodens* (1888), although brief and lacking detail, nevertheless stresses characters which clearly separate this species from others of the *Haplochromis* group: viz. a multi-seriate dental pattern with stout and enlarged posterior teeth. Pfeffer's redescription (1896) of the same specimen confirms and extends this account. In the material at my disposal, however, the posterior teeth are clearly enlarged only in the upper jaw, and not in both, as stated for the type. Specimens described below agree closely with the type in the other characters described by Hilgendorf and Pfeffer; slight differences in scale numbers can probably be attributed to different methods of making these counts.

In addition to the four specimens of *H. retrodens* in the British Museum (Nat. Hist.) it has been possible, through the kindness of Dr. Delfa Guiglia, to examine the type of *Paratilapia polyodon* Blgr. and one other specimen (Museo Civico di Storia Naturale, Genoa, reg. no. G.E. 12.994) determined by Boulenger as *P. polyodon*, and to confirm Regan's view (1922) that these are conspecific with *H. retrodens*.

### Diagnosis

Differing from *Haplochromis* as defined by Regan (1920 and 1922b) in having broad bands of teeth in both jaws, well developed and usually of almost uniform breadth throughout or very slightly narrower posteriorly. Posterior teeth of the upper jaw enlarged and stout, those of the lower jaw slightly, if at all, enlarged, but



the tooth-band continued posteriorly on to the steep ascending contour of the dentary. Lower jaw wide and flat, almost square in anterior outline, slightly shorter than the upper.

Since only three of the collected specimens of this genus are small it is not possible to generalize on differences which apparently exist between the dentition of adult

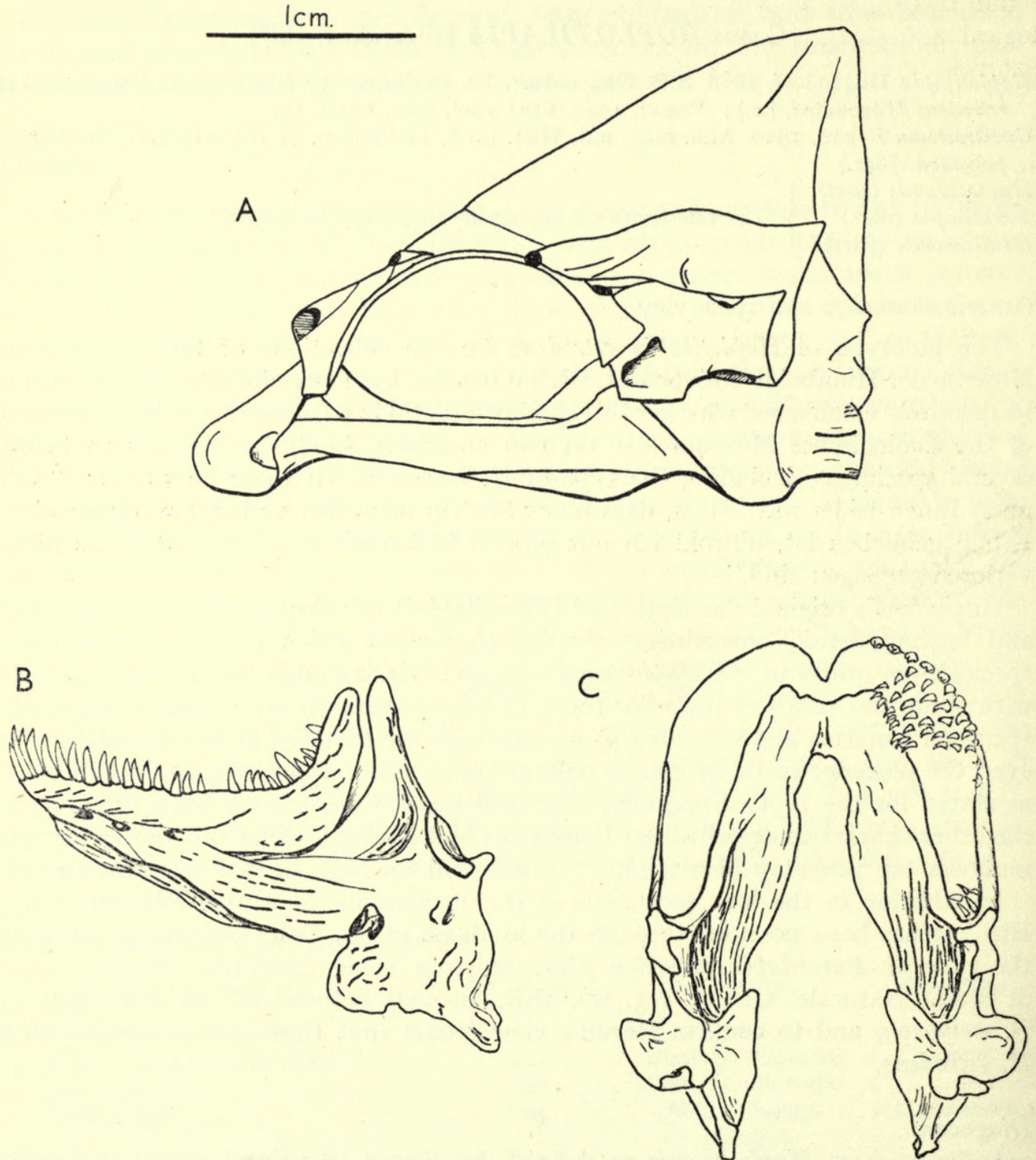


FIG. 8.—*Hoplotilapia retrodens*. (A) Neurocranium, (B) dentary in lateral view, (C) dentary, occlusal view. Dentition only part indicated. From a specimen of 125 mm. S.L.



and juvenile fishes. In these three specimens (74.0, 76.0 and 55.0 mm. S.L.) the tooth bands are broad anteriorly, being composed of 5, 3, and 3 series respectively. Laterally, however, they are reduced to two series, whilst postero-laterally only the outer series persists. In none is the dentition continued onto the ascending part of the dentary, although the shape of the lower jaw is as in the adult.

Two adults of 96 and 110 mm. S.L., collected in a single seine haul at Bukakata, retain these presumed juvenile dental characters. They form a graded morphological series with a third specimen (134.0 mm. S.L., from the same station) which exhibits only slight departure from the "typical" condition.

The broad and shallow lower jaw (Fig. 8, B and C) of typical individuals is unique amongst Lake Victoria Cichlidae. A few specimens of *H. retrodens* have the dentary, at least in external appearance, similar to that of *Haplochromis*, although in every case the dental pattern is typical for *Hoplotilapia*.

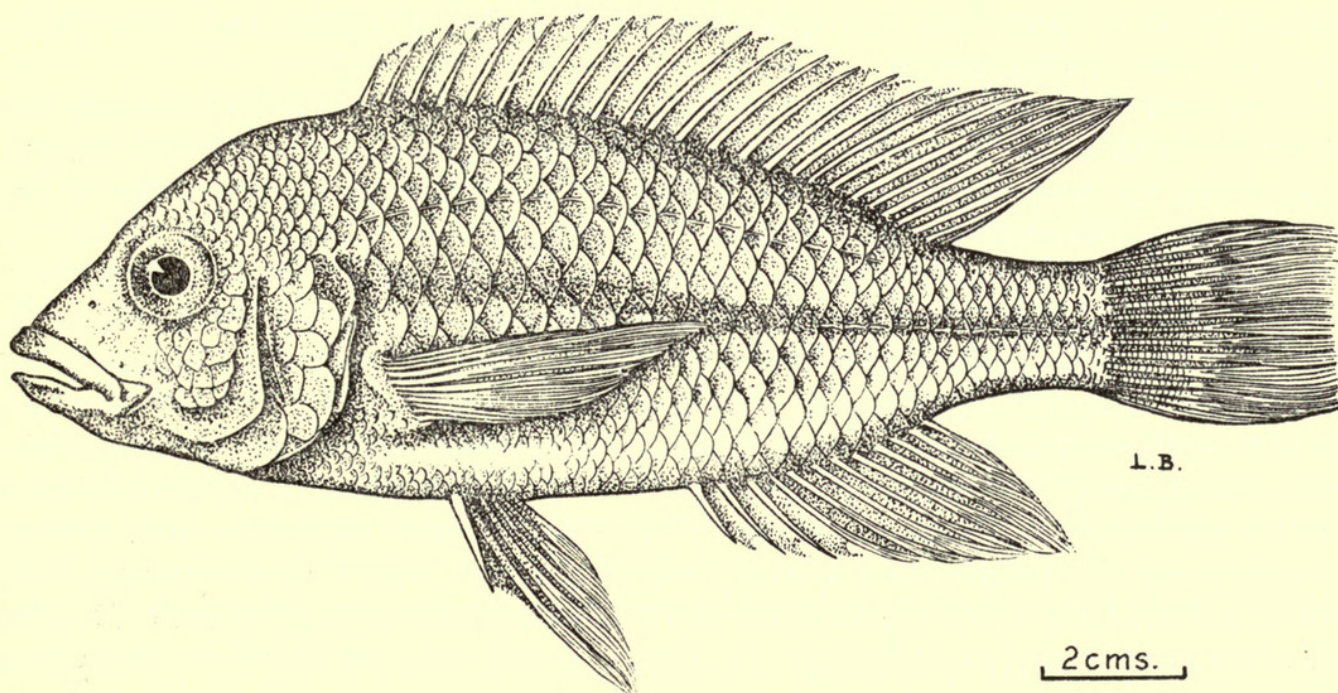


FIG. 9.—*Hoplotilapia retrodens*, ♀. Drawn by Miss L. Buswell.

### *Hoplotilapia retrodens* Hilgendorf, 1888

FIG. 9.

(*Paratilapia* ?) *retrodens* Hilgendorf, 1888, S.B. Ges. naturf. Fr. Berlin, 76.

*Hoplotilapia retrodens* Hilgendorf, t.c., 77.

*Hemichromis retrodens*, Pfeffer, 1896, Thierw. O. Afr. Fische, 19.

*Haplochromis bicolor* (part) Boulenger, 1906, Ann. Mag. nat. Hist. (7) 17, 444; two specimens B.M. no. 1906.5.30.417 and 418.

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

*Paratilapia polyodon* Boulenger, 1909, Ann. Mus. Genova (3) 4, 306, fig.; *Idem*, 1911, *ibid.* 5, 68; *Idem* 1915, Cat. Afr. Fish. 3, 349, fig. 236.

*Cnestrostoma polyodon* (Boulenger), Regan, 1920, Ann. Mag. nat. Hist. (9) 5, footnote p. 45.



*Description*

From available material it would appear that only the interorbital width shows marked allometry with standard length. It must, however, be borne in mind that paucity of specimens within the smaller and larger size groups may obscure such relationships, especially since, in those size-groups which are well represented, individual variability is high. With the exception therefore of interorbital width, ranges and means are given for the sample as a whole. For interorbital width the range and mean are given for three size groups, 74–115 mm. ( $N = 21$ ), 116–130 mm. ( $N = 32$ ), and 131–144 mm. ( $N = 11$ ).

Depth of body 31.6–41.6 ( $M = 38.3$ ), length of head 30.1–34.8 ( $M = 32.0$ ) per cent of standard length. Dorsal profile of head and snout straight or slightly concave, steeply sloping. Preorbital depth 12.5–18.8 ( $M = 16.4$ ) per cent of head length; least width of interorbital 24.2–33.8 ( $M = 28.7$ ), 28.6–35.1 ( $M = 31.5$ ) and 31.1–33.4 ( $M = 31.6$ ) per cent for the three size groups respectively; length of snout 29.0–36.8 ( $M = 32.5$ ), eye 23.8–29.6 ( $M = 26.9$ ), depth of cheek 19.5–28.2 ( $M = 23.9$ ) per cent of head length.

Lower jaw slightly shorter than upper 33.7–40.8 ( $M = 38.2$ ) per cent of head, the length/breadth ratio from broader than long to 1.33 times as long as broad. Mouth horizontal, lips somewhat thickened. Posterior tip of the maxilla extending to the vertical from the anterior margin of the orbit or as far as the pupil.

Described from 64 specimens, 55–144 mm. standard length.

With few exceptions, there is remarkable uniformity in the general facies of *H. retrodens*. In this respect the figure of *Paratilapia polyodon* type specimen in Boulenger (1909 and 1915) can be considered fairly representative. The lower jaw in this specimen has, however, been broken and subsequently distorted in preservation, consequently the ventral head profile of the figured specimen is inclined upward and is not horizontal, as it would be in life. The greatest departure from typical physiognomy and body form is seen in a single specimen from Bukoba (Tanganyika) which has the body relatively elongate and the head profile strongly curved. Despite this aberrance in gross morphology, the dentition and other fundamental characters of this specimen are typical.

*Teeth and dental pattern.* Fishes above 90 mm. S.L. have 5 to 8 series of teeth anteriorly and 4 to 5 series posteriorly in the upper jaw; 5 to 8 (rarely 9 or 10) series anteriorly and 3 to 5 series posteriorly in the lower jaw. From 40 to 68 teeth in outer series of the upper jaw. Teeth small, those of the outermost series largest, variable in form, but usually unicuspid; some bi- and tricuspid teeth occur in the inner series. Two specimens from Majita and Mwanza (Tanganyika Territory) have markedly aberrant, stoutly conical or nearly molariform teeth in all series of both jaws. In both specimens the dental pattern is otherwise typical.

*Syncranium.* The premaxilla is comparable in form with that of *Haplochromis*, except that it is stouter, especially posteriorly, and its dentigerous surface broader.

As noted above, the broad and greatly flattened dentary is unique amongst Lake Victoria cichlids (Fig. 8).

The neurocranium agrees closely with that of *Platytaeniodus* and with *Haplochromis* of the “*crassilabris*” species-group (see p. 316).



Pharyngeal bone with a triangular and approximately equilateral dentigerous surface; pharyngeal teeth cuspidate, the median series often enlarged.

*Scales* ctenoid, lateral line interrupted, with 31 (f.1), 32 (f.10), 33 (f.38), 34 (f.14) or 35 (f.1) scales. (Hilgendorf (1888) gives L.S. 30 [probably on a mid-lateral series] for the holotype.) Cheek with three or four series of imbricating scales. (Hilgendorf [*loc. cit.*] gives 4–5 rows); 7–8 scales—rarely 6—between lateral line and origin of dorsal fin; 8–9, less commonly 7, between pectoral and pelvic fin bases.

*Fins.* Dorsal with 24 (f.4), 25 (f.45) or 26 (f.13) rays, comprising XV–XVII 8–10 spinous and soft rays. Two specimens have the formulae XIV 8 and XVII 6, but there are indications that these are the results of wounding and subsequent irregular healing. Anal with 11 (f.6), 12 (f.54) or 13 (f.4) rays, i.e. III, 8–10. Caudal fin truncate, scaled on proximal half only. Pectoral fin 23.9–33.0 ( $M = 28.4$ ) per cent of standard length. Pelvics with first ray produced in both sexes but proportionately longer in adult males.

*Coloration.* Colours of preserved specimens are variable. *Adult males*: dark grey to black, median fins dark, caudal colourless or maculate; pelvics black. *Females and immature males*: light olive brown to silver, all fins yellow or colourless. Sometimes faint traces of transverse bars, an interrupted band below insertion of dorsal fin and a well-marked mid-lateral stripe.

*Colours in life.* *Adult males*: ground colour dark grey-green (darkening to deep slate-grey immediately after death), chest and branchiostegal membrane black. Dorsal fin dark grey-green, lappets red; red spots, often coalescing into streaks, between the rays. Caudal with proximal third to half black, distal part red. Anal with dark base, remainder red; ocelli yellow. Pectoral colourless; pelvics black, with faint red flush along median rays. *Adult females*: ground colour light olivaceous dorsally, shading through sulphur-yellow to pearly-white ventrally; usually two longitudinal bands as described above, of variable intensity. Lips yellow. Dorsal and caudal fins olivaceous; anal colourless or with slight yellow flush; small and ill-defined orange spots sometimes occur in the position of the male ocelli. Pelvics and pectoral fins yellow.

Three specimens (2 ♀, 1 ♂) from Bukakata, which were noted when discussing atypical dental patterns (p. 321), also exhibit aberrant coloration. This is known only from preserved material, in which it has the form of three large and elongate black spots, arranged mid-laterally, on a light ground colour.

Almost completely sex-limited polychromatism occurs in this species and, as in *M. bicolor*, it is the female which usually exhibits atypical coloration. Besides the black and yellow piebald, as described for *M. bicolor*, there is a second and more colourful, if less distinctive, pattern. Any attempt to describe this pattern must perforce be imprecise, since intensity and detail show a remarkable range of individual variability. The ground colour is invariably a light sandy-yellow, with a superimposed orange flush, usually most intense on the head. Dorsally there are a number of irregular and ill-defined dark blotches, separate or confluent, which occasionally extend on to the flank. In some individuals this dorsal pigmentation is comparable with the clearly defined blotches of a typical *bicolor* pattern; in others it is more diffuse and individual elements are only faintly discernible. The whole



body, including the fins, is also peppered with small melanophores, particularly on the head and opercula. Fin coloration is extremely variable, but the caudal and anal are usually flushed with bright orange.

Sampling bias in favour of atypically-coloured individuals undoubtedly occurs and precludes the accurate estimation of frequency. Of thirty-five females examined, thirteen were "*bicolor*" and eleven of the other pattern. Polychromatism is known in populations from most areas in which the species has been collected.

A single male (119.0 mm. S.L., Busongwe, Kagera River area) had an incipient *bicolor* pattern, resembling in appearance and degree of pigmentation one of the "*bicolor*" males of *M. bicolor* (p. 309).

The genetical basis of, and selection factors maintaining polychromatism in *H. retrodens* remain undetermined, as previously explained in the case of *M. bicolor*.

### Ecology

*H. retrodens* is widespread throughout Lake Victoria (see below). Sampling in many habitats shows the species to be restricted to littoral and sub-littoral areas, especially where the substrate is hard, and usually where there is submerged vegetation. The majority of specimens was caught in water from twelve to twenty feet deep, with a few from slightly deeper water.

*Food.* The gut contents of sixty-five individuals (size-range 75.0–144.0 mm. S.L.) have been examined; of these, only seven were empty. Mollusca (particularly Lamellibranchiata) are the predominating food, being recorded from thirty-six fishes. The majority of Mollusca is represented by finely broken shells. Insecta (f.8)—especially Ephemeroptera, Trichoptera and Chironomidae—together with Crustacea (f.3) and Hydracarina (f.2) occur less frequently. In fifteen fishes the ingested material consisted almost entirely of fragmented plant epidermis, whilst eleven others contained only sand grains or organic mud.

Observations made on fishes living in aquaria show that *H. retrodens*, when feeding, repeatedly makes short, darting movements into or over the substrate, the broad and horizontal mouth serving as a scoop or shovel. Much bottom material is spilled from the mouth or with the exhalent current. Snails were retained and apparently crushed within the jaws before being passed back to the pharynx. The presence of macerated plant epidermis in several fishes may be explained either as ingested bottom debris, or as the result of the fish actively scraping the leaves and stems of submerged plants, for which purpose the multi-seriate dentition would seem adapted. It may be significant to note that the frustules of epiphytic diatoms found in the stomachs of these fishes were empty, as were the epidermal cells which had been ruptured.

*Breeding.* No information is available on the breeding habits of *H. retrodens*. The smallest sexually mature individual was a female of 96 mm. S.L. (Bukakata, Uganda).

### Affinities

Morphologically, *Hoplotilapia retrodens*, like *P. degeni* is relatively far removed from any Lake Victoria *Haplochromis* species or species group. Neither is it closely



related to the other monotypic genera of that lake. Regan's remark (1922, p. 159) that "A remarkable group of three species includes *Haplochromis sauvagei* and the monotypic genera *Macropleuroodus* and *Hoplotilapia*, which scarcely differ from each other except for the considerable differences in dentition, . . . " is difficult to endorse, unless the various structures whose forms are modified in association with the dentition and feeding habits are included in the term "dentition". *Macropleuroodus* and *Hoplotilapia* have manifestly dissimilar jaw morphology and also differ in the form of the neurocranium. These structural differences impart a characteristic physiognomy to the species, which allows them to be recognized without reference to the dental form and pattern. The occurrence of "bicolor" patterns in both *M. bicolor* and *H. retrodens* is suggestive, but at present little importance can be attached to this character since it occurs in at least three widely divergent species of *Haplochromis* as well as in *M. bicolor*. If neurocranial form can be considered as being of phylogenetic value, then the affinities of *Hoplotilapia* lie with the *H. crassilabris* species group, although *H. retrodens* has departed considerably from this complex in the form of its jaws and dental pattern.

*Hoplotilapia* and *Macropleuroodus* show interesting trophic parallels, both between the two genera and in relation to the three mollusc-eating cichlids of Lake Victoria, viz. *Astatoreochromis alluaudi*, *Haplochromis pharyngomylus* and *H. ishmaeli*. Ecologically, *Hoplotilapia* and *Macropleuroodus* occur together with *A. alluaudi* and *H. pharyngomylus*, but the diet of *Hoplotilapia* and especially of *Macropleuroodus*, unlike that of the two last-named species, includes a substantial number of insects.

The parallelism between *Hoplotilapia* and *Macropleuroodus* extends to the method of feeding, and particularly the manner in which the hard-shelled prey is crushed. It is this characteristic which most clearly emphasizes the morphological disparity between the two genera under discussion on the one hand and the three mollusc-eating species on the other; these latter species, although including a monotypic genus, have deviated less markedly from the generalized *Haplochromis* anatomy. Whereas in *Astatoreochromis alluaudi*, *H. ishmaeli* and *H. pharyngomylus* the food is crushed entirely by means of the hypertrophied pharyngeal bones and teeth, in *Hoplotilapia* and *Macropleuroodus* the food is broken mainly by the peculiarly developed jaws and oral dentition, although the relatively poorly-developed pharyngeal mill doubtless continues the process.

Despite functional similarity in the jaws and dentition of *Hoplotilapia* and *Macropleuroodus*, there is considerable divergence in the detailed morphology of these elements. On the one hand, in *Macropleuroodus* the jaws are short and stout, with a narrow gape; associated with the stout supporting skeleton, the teeth are strong. On the other hand, the dentary and premaxilla of *Hoplotilapia*, although broad and encompassing a wide gape, appear relatively fragile. The dentition of *Hoplotilapia*, when compared with *Macropleuroodus*, is seen to be composed of small and slender teeth which are arranged in bands broader both anteriorly and posteriorly than the corresponding teeth of *Macropleuroodus*. Since the shells of Gastropoda in Lake Victoria are stouter than those of Lamellibranchiata, it would not be unreasonable to suppose that the strong, laterally concentrated and enlarged teeth of *Macropleuroodus*, and the uniformly multi-seriate, finely-pointed teeth of *Hoplotilapia*, are



associated with the predominantly gastropod diet of the former species, and the predominantly lamellibranch diet of the latter.

*Study material and distribution records*

Museum and Reg. No.	S.L. (mm.)	Locality.	Collector.
British Museum (Nat. Hist.) :			
1906.5.30.417-418 . . .	90 and 106 .	Buganga (Uganda) .	Degen
1909.5.4.16 . . .	112 .	Sesse Is. (Uganda) .	Bayon
1911.3.3.34 . . .	144 .	Jinja, Ripon falls (Uganda) .	"
1928.5.24.489-492 . . .	125-132 .	Lake Victoria .	Graham
Genoa Museum :			
C.E.12.995 (holotype of <i>P. polyodon</i> ) . . .	135 .	— .	—
C.E.12.994 . . .	112 .	— .	—
B.M. (N.H.) :			
1955.2.10.141, 147-149. . .	128-142 .	Rusinga Is. (Kenya) .	E.A.F.R.O.
1955.2.10.145 . . .	129 .	Homa Bay (Kenya) .	Ditto
1955.2.10.142-144, 146. . .	105-135 .	Kamaringa (Kenya) .	"
1955.2.10.137-140 . . .	104-117 .	Kisumu (Kenya) .	"
1955.2.10.116-123, 180 . . .	76-138 .	Jinja (Uganda) .	"
1955.2.10.177-178 . . .	55 .	Beach nr. Nasu Point. (Buvuma Channel, Uganda)	"
1955.2.10.170-171 . . .	105 and 107 .	Pilkington Bay (Uganda) .	"
1955.2.10.176 . . .	114 .	Ramafuta Is. (Uganda) .	"
1955.2.10.168-169 . . .	155 .	Yempita Is. (Rosebery Channel, Uganda) .	"
1955.2.10.124-132 . . .	117-124 .	Harbour, Entebbe .	"
1955.2.10.133 . . .	109 .	Bugonga beach, Entebbe .	"
1955.2.10.172-175 . . .	96-142 .	Old Bukakata (Uganda) .	"
1955.2.10.150-163 . . .	104-132 .	Busongwe (Kagera R. mouth, Uganda) .	"
1955.2.10.179 . . .	127 .	Beach south of Bukoba (Tanganyika) .	"
1955.2.10.164-167 . . .	106-117 .	Majita beach (Tanganyika) .	"
1955.2.10.134 . . .	86 .	Harbour, Mwanza (Tanganyika) .	"
1955.2.10.135-136 . . .	74 and 139 .	Capri Bay, Mwanza (Tanganyika) .	"

Graham (1929) lists the distribution of *H. retrodens* as follows :

Kenya Colony : Mbita passage ; Kavirondo Gulf ; Kadimu Bay.

Tanganyika Territory : Mussonya Bay (Ukerewe Is.); trawl near Bukoba.



**PARALABIDOCROMIS** gen. nov.*Diagnosis*

Cichlid fishes of the *Haplochromis* group, but differing from that genus in having the anterior teeth in both jaws procurent and disproportionately longer than the adjacent lateral teeth. Jaws narrowing at the symphysis; lips thickened. Known only from Lake Victoria.

Type species: *Paralabidochromis victoriae* sp. nov.

The single specimen of *Paralabidochromis* available provides an interesting taxonomic and phylogenetic problem. No characters have been found which will distinguish this fish generically from specimens of the genus *Labidochromis* Trewavas; a genus otherwise known only from Lake Nyasa. Unfortunately comparisons must be limited to characters apparent in preserved material and then only to the few specimens available. Nothing is known of the coloration in life of adult males in either genus. This is regrettable since coloration might well provide a reliable indication of the affinities of the two genera, both in relation to one another, and to the species flocks of Victoria and Nyasa (*vide* Regan, 1921, 686). The presence of a dark sub-marginal band on the dorsal fin of *Labidochromis vellicans*, in contradistinction to its absence in *Paralabidochromis* is probably of some importance. A sub-marginal band is not known in any Lake Victoria *Haplochromis* species, but is present in most species of the group of Nyasa genera to which *L. vellicans* is apparently related (*vide* Trewavas, 1935, p. 71).

Although on purely morphological grounds it might seem advisable to include the Lake Victoria species within the genus *Labidochromis*, such a decision would imply phyletic relationships between the Victoria and Nyasa species closer than those between either species and others of its own lake. To avoid this I have given greater weight to the difference in colour-pattern than would perhaps have been justified if both inhabited the same lake.

Apart from the presence of the pan-African genera *Tilapia* and *Haplochromis*, there is no obvious relationship between the Cichlidae of Lakes Nyasa and Victoria. Superficial resemblances between individual species, or genera, in the two lakes have been associated with differences which point to their being examples of convergent evolution (Regan, 1922, p. 159), although it would perhaps be preferable to consider this convergence of morphological characters as parallel evolution since the phenomenon occurs between species within a group of related genera.

It would seem most probable, therefore, that *Paralabidochromis* represents a remarkable example of exact and detailed parallel evolution with *Labidochromis*. Apart from the enlarged anterior teeth, neither *Labidochromis* nor *Paralabidochromis* departs greatly from the generalized *Haplochromis* type, as represented in the rivers of East and Central Africa. Thus, it is possible that the two genera were independently evolved from different parental *Haplochromis* species, which, however, shared the generalized facies of fluviatile species.



*Paralabidochromis victoriae* sp. nov.

FIG. 10.

*Description*

Depth of body 33.0; length of head 31.6 per cent of standard length. Dorsal profile of head and snout slightly curved and sloping moderately steeply. Preorbital depth 16.7 per cent of head length; interorbital width 25.0, snout length 33.4, diameter of eye 29.2 and depth of cheek 20.8 per cent of head length. Caudal peduncle 1.33 times as long as deep, its length 15.8 per cent of standard length.

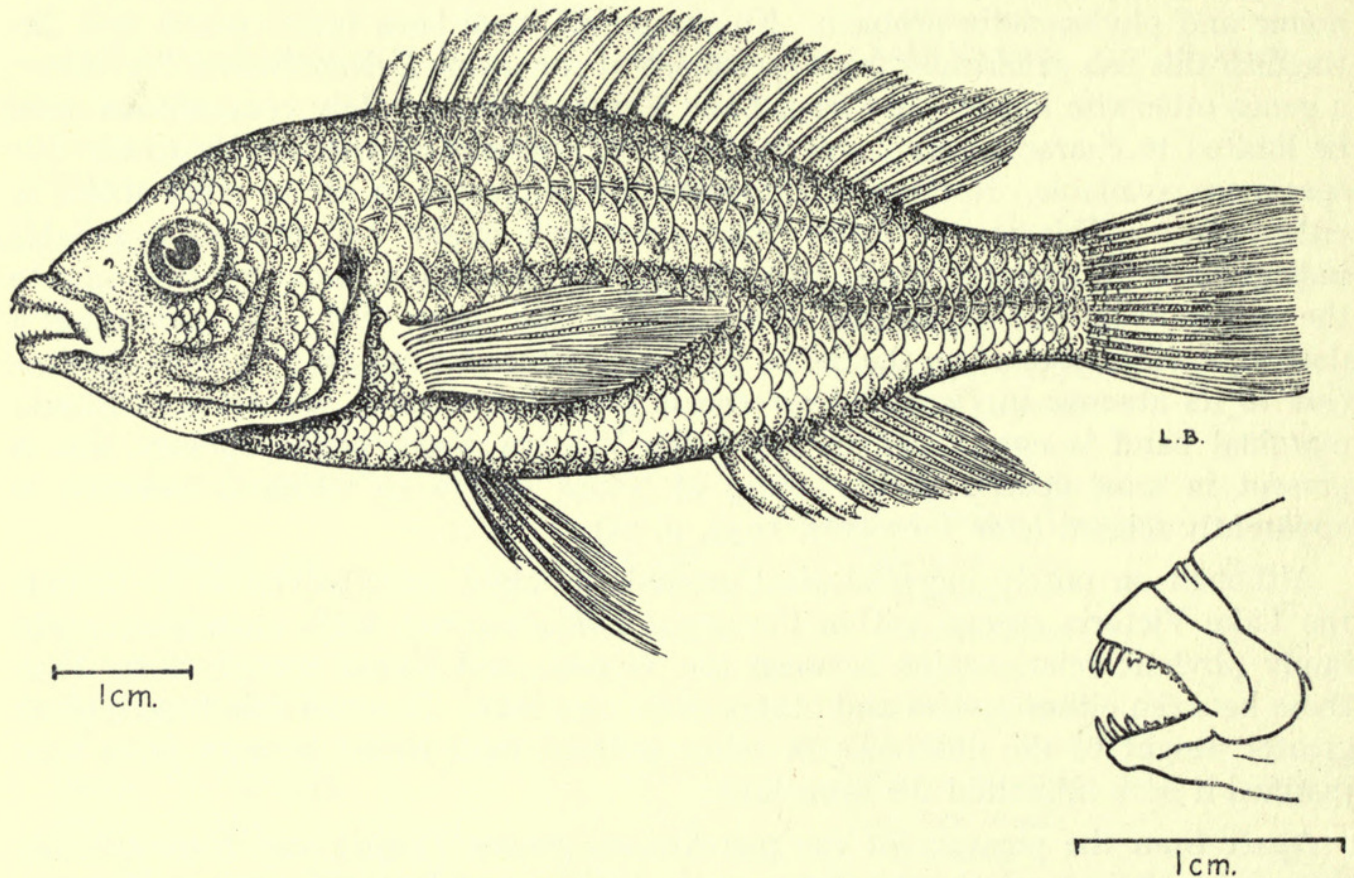


FIG. 10.—*Paralabidochromis victoriae*, ♂, holotype. Drawn by Miss L. Buswell.

Mouth almost horizontal, lips well developed. Posterior tip of the premaxilla extending to a point nearer the nostril than the anterior orbital margin. The angle between the rami of each jaw is acute giving a beak-like appearance, which is enhanced by the peculiar dentition.

*Dentition.* Thirty-eight teeth in the outer series of the premaxilla; the six anterior teeth in both jaws procurent, greatly elongate, slender, slightly recurved and dagger-like; movable (Fig. 10). Postero-lateral outer teeth small and unicuspid, becoming progressively larger and weakly bicuspid laterally. Inner series in both jaws composed of tricuspid and compressed teeth, of which there are three rows in the upper and four in the lower jaw; outermost row of inner teeth in both jaws, somewhat enlarged and standing slightly apart from the remaining rows.

*Lower pharyngeal bone* triangular, the teeth small and cuspidate, with only the median series slightly enlarged.



*Gill rakers* short ; seven on lower limb of first arch.

*Scales* ctenoid ; lateral line interrupted, with 32 scales. Cheek with 2 series of imbricating scales ; 6 scales between origin of the dorsal fin and the upper lateral line ; 7 between pectoral and pelvic fins. Nuchal scales not exceptionally small.

*Fins*. Dorsal, XV 8 ; anal, III 9. Pectoral fin 25.0% of standard length ; pelvics with the first soft ray produced and extending posteriorly to the third anal spine. Caudal truncate, scaled on proximal half only.

*Coloration*. Preserved specimen light brown, with indications of seven faint transverse bands on the flanks, and a dark lachrymal stripe. Pelvic fins black, all other fins colourless.

*Type locality*. Sandy littoral, near Nasu Point, Buvuma Channel.

Described from a single specimen, a male 76.0 mm. S.L. (91.0 mm. T.L.), collected by the author whilst seine-netting at night, 29th May, 1951.

### *Affinities*

*Paralabidochromis victoriae* is closely related morphologically, to *Labidochromis vellicans* of Lake Nyasa, from which it differs principally in possessing large scales on the chest, cheek and nape. The dorsal profile of the head and snout in *L. vellicans* apparently differs from that of *P. victoriae*, in being straighter and more steeply sloping.

Amongst the *Haplochromis* species of Lake Victoria, *P. victoriae*, has some structural affinity with *Haplochromis chilotes*. Both species have short and narrow jaws, thickened lips and a certain similarity of dentition. For example, the teeth of *H. chilotes* are slender and elongate anteriorly, few in number and arranged in an acute dental arch. However, the disproportionately long and procurent anterior teeth of *P. victoriae*, and the hypertrophied lips of *H. chilotes*, immediately serve as diagnostic characters. The phylogeny of *H. chilotes*, is at present, obscure, but the species would seem more closely related to the *H. crassilabris* species group in Lake Victoria, than to *Paralabidochromis*.

### DISCUSSION

It is clear from Regan's analysis of the Lake Victoria Cichlidae, that he did not consider the monotypic genera far removed phylogenetically from certain *Haplochromis* species, a view which is strengthened by the additional data now available. Although the monotypic genera are readily defined by trenchant characters they retain fundamental affinities with the *Haplochromis* species of Lake Victoria. But the morphological differentiation which these genera have undergone creates an impression of greater divergence than is shown by other adaptive groups within the Lake Victoria species flock. Analysis of the diagnostic characters of the genera described here, shows that, in any one genus, the anatomical characters of the head are functionally related to the dentition. Further, the ontogenetic basis for most of these characters is probably attributable to differential growth and not to any large-scale qualitative change. Thus the first evolutionary steps involved may well have been relatively simple and similar, in the earliest stages, to those which initiated the often slight differences characterizing the greater number of *Haplochromis* species.



Despite fundamental inter-relationship, three of the four monotypic genera exhibit considerable inter-generic divergence in the characters affected by the peculiar development of their dentition. The degree of divergence and the means by which it has been effected in *Macropodus*, *Platytaeniodus* and *Hoplotilapia* are such that the genera cannot be related *inter se*. That is to say, these genera represent three independent evolutionary offshoots from the basic *Haplochromis* stock. The fourth genus, *Paralabidochromis*, shows least departure from the generalized *Haplochromis* condition, but must also be looked upon as having evolved independently.

A broad outline of the probable phyletic relationships within the *Haplochromis* species flock is perhaps necessary before attempting further discussion of the monotypic genera.

There are some Lake Victoria *Haplochromis* species which, when seen in isolation or when known only from a few specimens, might seem almost as distinctive as the monotypic genera. It is possible, however, to relate these outstanding species to others more typical of their particular adaptive group (mollusc eaters, piscivores, epiphytic-algal grazers, etc.). Furthermore, when larger series of specimens are examined, intra-specific variation is sufficiently high to reduce considerably any apparent inter-specific gap.

With few exceptions, specific differences amongst the *Haplochromis* are quantitative and generally consequent upon the differential growth of various syncranial parts. Qualitative differences, on the other hand, are usually those which can be related to, and are used in defining, adaptational groups. At both inter- and intra-group levels, qualitative and quantitative differences tend to be small and intergrading.

It is in both qualitative and quantitative characters that the monotypic genera depart most markedly from *Haplochromis* but, unlike the inter-group differences within the *Haplochromis* flock, the morphological gap is clear cut, and remains so even when large series of specimens are examined.

On this interpretation, *Hoplotilapia* and *Platytaeniodus* probably exemplify the phenomenon of "quantum evolution" as described by Simpson (1944 and 1953). It is difficult to suggest any ancestry for these genera nearer than a present-day species group, *viz.* the *H. crassilabris* complex. Even at this level relationship is extremely tenuous, and based only on similarity of skull form, in itself probably an adaptational character and therefore of doubtful phylogenetic significance. The jaws and dental pattern are so dissimilar in *Hoplotilapia* and *Platytaeniodus* that one must consider the genera separately and not as elements of a single lineage.

*Macropodus* is less readily regarded as being a product of quantum evolution, and will be discussed later.

Simpson (1944) has noted that quantum evolution is usually associated with a shift from one adaptive zone to another, and that the interzonal populations or species would be relatively ill-adapted, unstable and short-lived. Thus, morphological discontinuity is generally observed between the parental and divergent lineages.

The morphological discontinuity existing between *Platytaeniodus* and *Hoplotilapia*, and between these two genera and *Haplochromis* has been demonstrated; it is the more regrettable then that pertinent ecological data for *P. degeni* are both inadequate



and confusing, so that it is difficult to equate the apparent morphological specialization of this species with any particular ecological niche. The food of *P. degeni* is virtually unknown, although inorganic material and scant but varied organic remains suggest bottom-feeding habits. A multi-serial and concentrated dentition, such as that of *P. degeni* may possibly have adaptive value, particularly if food must be freed from the substrate or if it requires trituration before digestion can be effected. (It should be noted that no *Haplochromis* has consistently yielded such baffling residua in the gut.)

*Hoplotilapia retrodens* is somewhat better understood. In this species food is predominantly Molluscan. The functional significance of the jaw structure and dental pattern in *Hoplotilapia*, particularly with regard to its observed diet of thin-shelled bivalves, has been discussed above (p. 325). From these characters and the predominance of Mollusca over the other food organisms it would seem that the essential elements of quantum evolution are fairly well defined in *H. retrodens*. That is to say, the species shows both morphological discontinuity and entry into an adaptive niche different from that of the presumed parental stock.

There is, of course, the possibility that *Platytaeniodus* and *Hoplotilapia* represent an early stage in quantum evolution and that these species may be relatively ill-adapted to existing ecological conditions. Their further evolutionary development or, alternatively, extinction, will therefore depend upon environment change effecting, or failing to effect, the realization of characters which at present could only be considered prospective adaptations (*sensu* Simpson, 1953, p. 188).

The slight and often indeterminable adaptive differences between *Haplochromis* species occupying the same ecological zone, together with numerous instances of inter-specific overlap in feeding habits, would seem to suggest that there is, and has been, only slight selection-pressure acting through competition for food. Thus the continued existence of *Platytaeniodus* and *Hoplotilapia*, like that of many closely related *Haplochromis* species, could be attributed to a period of decreased selection pressure.

Although *Macropleurodus*, like *Platytaeniodus* and *Hoplotilapia*, is separated from *Haplochromis* by a clearly defined morphological gap, the gap is of lesser degree. Whereas *P. degeni* and *H. retrodens* exhibit unique jaw morphology and dental patterns without departure from *Haplochromis* in tooth form, the basic dental pattern of *M. bicolor* is foreshadowed in two *Haplochromis* species, as is the form of the dentary. Only in tooth form and shape of the premaxilla does *M. bicolor* show great differentiation from *H. prodromus*. The latter species is morphologically closely related to *H. sauvagei*, a smaller species, which in turn shows departure from the basic *Haplochromis* type towards *H. prodromus*. In *H. sauvagei* and *H. prodromus* the outer teeth are relatively stout and, anteriorly, there are several rows of inner teeth; the neurocranium and dentary of these species also approach the *M. bicolor* condition. Both species feed on Mollusca and Insecta, the very slight differences in the feeding habits of *H. prodromus* and *H. sauvagei* being attributable to the smaller size of *H. sauvagei*.

It is tempting, therefore, to consider the members of the series *H. sauvagei*-*H. prodromus*-*M. bicolor* as representing stages of a lineage, although the possibility



of independent evolution of the same adaptive characters, cannot be ignored. Until more critical evidence is available for the phyletic relationship of these species, they may be regarded either as separate end points of different lineages, or as a "stufenreihe", or single phyletic line. The three species do illustrate the gross anatomical and functional stages through which *Macropleuroodus* could have evolved, although the transition in shape of teeth from a typical *Haplochromis* to *Macropleuroodus* is not represented in any living species.

The isolated position of *Paralabidochromis* in relation to the *Haplochromis* species of Lake Victoria was commented upon above.

Little information is available on the evolutionary relationships of *Paralabidochromis*. Although taxonomically isolated from *Haplochromis* the genus is nearer the *Haplochromis* stem than either *Hoplotilapia*, *Platytaeniodus* or *Macropleuroodus*. In Lake Nyasa, Trewavas (1935 and 1949) considers *Labidochromis vellicans* as belonging to a group of nine genera (which group excludes *Haplochromis*), that, although lacking an absolute character to distinguish them, are more closely related to each other than to any other genus. Such grouping is impossible for the monotypic genera of Lake Victoria. Within this lake the divergent genera of the *Haplochromis* group must be considered as being distinct from one another, as well as from the parental stock.

#### SUMMARY

(1) The genera *Macropleuroodus* Regan, 1922, *Platytaeniodus* Boulenger, 1906, and *Hoplotilapia* Hilgendorf, 1888, are redefined on the basis of new and fairly extensive collections. Similarly, the species *M. bicolor* (Blgr.) 1906, *P. degeni* Boulenger, 1906, and *H. retrodens* Hilgendorf, 1888, are redescribed.

(2) Generic and specific characters are discussed, with particular regard to ontogenetic changes. Information gained from small specimens shows that three species previously considered as *Haplochromis* must be added to the synonymies of *M. bicolor* and *P. degeni*.

(3) Comparative anatomical and osteological studies of the head indicate that *Hoplotilapia* and *Platytaeniodus* are not closely related to any extant *Haplochromis* species in Lake Victoria. Morphological stages leading to the syncranial type found in *Macropleuroodus* are, however, represented by two endemic *Haplochromis* species. On the basis of syncranial morphology, it is clear that the monotypic genera are not closely related *inter se*.

(4) Apparently sex-limited polychromatism occurring in *Macropleuroodus* and *Hoplotilapia* is described and discussed.

(5) A fifth monotypic genus, *Paralabidochromis victoriae* is described. This genus exhibits remarkably close morphological parallelism with *Labidochromis vellicans* from Lake Nyasa.

(6) Locality lists and notes on the ecology of the genera are given, together with observations on the feeding habits of *Macropleuroodus* and *Hoplotilapia*.

(7) The evolutionary relationships of the four genera are discussed. It is suggested that *Hoplotilapia* and *Platytaeniodus* may represent the products of low-level quantum evolution.



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