

Towards a phyletic classification of the 'genus' *Haplochromis* (Pisces, Cichlidae) and related taxa.

Part II; the species from Lakes Victoria, Nabugabo, Edward, George and Kivu.

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Introduction

In the first part of this paper (Greenwood, 1979) I dealt at length with the philosophical and taxonomic problems posed by the polyspecific 'genus' *Haplochromis*. Applying a basically Hennigian approach to the problem (Hennig, 1966), I attempted to sort the fluviatile species of Africa and Israel into a number of monophyletic lineages. Since the interrelationships of these lineages could not be resolved cladistically, each was treated as having equal rank and classified as a genus (see Nelson, 1972).

The nominate genus, *Haplochromis*, was restricted to five species sharing a particular and highly derived form of dentition. All five are essentially lacustrine in habitat, and are confined to Lakes Victoria, Kioga, Edward, George, Nabugabo and Kivu (see Greenwood, 1979 : 278–281).

As in the first section of this review, the second part is concerned with an attempted arrangement of haplochromine taxa into presumed monophyletic lineages. Each lineage, as before, is recognized by its member species possessing uniquely derived features (synapomorphies). Where possible, the sister-groups of these lineages were determined but are not, at this stage of the revision, given any formal taxonomic status (save that of subgenus when that rank seemed the most appropriate one to indicate apparent relationship).

The taxa considered here are from the east African Lakes Victoria, Kioga, Edward, George, Nabugabo and Kivu. These lakes are well-known for the high levels of endemism exhibited by their haplochromine species, and are interrelated through their hydrographical and geographical histories (see Greenwood, 1965, 1973 & 1974; and Fryer & Iles, 1972 for discussions and relevant literature).

A close taxonomic relationship between the '*Haplochromis*' species of these lakes, despite the high level of intralake endemism, has long been acknowledged. But, this factor was, perhaps, overshadowed by the size and ecological complexity of the so-called *Haplochromis* 'species-flocks' in Lakes Victoria and Edward-George. Either explicitly, or implicitly, the flocks were assumed to be of mono- or at most oligophyletic origin (see Greenwood, 1974 : 19–20). In Lake Victoria it was thought that '... The existing species are certainly more closely related to one another than to any species outside the lake, and it seems justifiable to refer to the assemblage as a species flock' (Greenwood, 1974).

Research embodied in this paper readily falsifies that statement. Many lineages described below (*ie* groups of taxa sharing a recent common ancestry and therefore more closely related to one another than to members of another lineage) are composed of species from at least four of the lakes. Furthermore, it is rarely possible to establish, within a lineage, that the species from one lake are in fact each other's closest relatives. There are, of course, a few lineages known only from one lake (eg *Macroplocheilichthys* and *Hoplotilapia* in Lake Victoria, and *Schubotzia* in Lake Edward-George), but the overall picture is one of a super-flock comprised of several lineages whose members cut across the boundaries imposed by the present-day lake shores.

Is it correct then, to continue using the term 'species flock' (= species swarm of Mayr, 1963) if the component species cannot be shown to stem from a single and fairly recent ancestor? Strictly the answer is 'no'; in future the term should be used sparingly and informally (whether to describe the haplochromines of one lake or of the lakes combined) and it should be employed more in an ecological than a taxonomic context.

Regrettably, no new data have emerged which might establish a monophyletic origin for the haplochromine species of Victoria-Edward-Kivu¹ (see also Greenwood, 1979 : 269). In

¹ Since Lake Kioga is an extension of Lake Victoria, albeit one now isolated by the Owen Falls Dam at Jinja, Lake Nabugabo a cut-off bay of Lake Victoria (Greenwood, 1965 & 1974), and because Lakes Edward and George are in direct contact with one another (see Greenwood, 1973), the entire system can be referred to by the shorthand name Victoria-Edward-Kivu.

other words, no uniquely derived character (or characters) has been found amongst all or the majority of haplochromines in these lakes.

Anatomically, and particularly in their squamation patterns, the Victoria–Edward–Kivu species are of a basically *Astatotilapia* type, as they are in the occurrence of true ocelli on the anal fin of adult male fishes (see Greenwood, 1979 : 274–5 & 281–3). They far exceed *Astatotilapia*, however, in their range of body form, dental morphology, gill-raker shapes and number, and syncranial architecture (see Greenwood, 1973 & 1974). They also differ from fluvial *Astatotilapia* in having a higher modal range of lateral line pore scales (31–33 cf. 28–30), the range extending to 36 (cf. 30, rarely 33 in riverine *Astatotilapia*), and in having a higher modal number of caudal vertebrae (16 cf. 15) and thus a higher count for the total number of vertebrae.

The ranges for both these counts, it should be noted, do overlap, although the lower values seen in fluvial *Astatotilapia* species are rarely encountered in the Victoria–Edward–Kivu lineages (including species referred to *Astatotilapia* itself; see p. 8).

The significance of these differences is difficult to assess. A shift in modal values and in the end points of a range could, for such meristic characters, be genetically determined or might be the result of environmental factors acting during ontogeny. For the moment there are insufficient data on which to develop either argument further. This is, however, a problem that could have bearings on the possible monophyletic origin of the lake's super-flock (see above).

An earlier attempt to resolve phyletic relationships within the Lake Victoria *Haplochromis* flock (Greenwood, 1974) is now seen to be quite inadequate, and in many respects misleading when taxa from the historically related lakes Edward and Kivu are taken into account. The new arrangement, apart from suggesting a different grouping for certain taxa, also indicates that fewer species and lineages can be interrelated on a sister-group basis.

Outside lakes Victoria–Edward–Kivu, too, no sister-group relationships can be established for the lineages from those lakes. This situation may, however, change when the Lake Malawi haplochromines are studied more critically and within a cladistic framework.

At present, the former genus *Haplochromis* can be resolved into a number of apparently monophyletic lineages; the search for characters uniting these lineages through various levels of common ancestry must continue. More discriminating anatomical studies may reveal linkages so far undiscovered, and there would seem to be great scope for developing biochemical techniques directed towards that end.

In some respects it might seem that the application of a cladistic approach to the *Haplochromis* problem has failed, particularly when it appears impossible to construct dichotomously branching phylogenies at either the inter- or the intral lineage levels (cf. for example, Vari's (1978) work on the teraponids which did achieve these goals).

It must be accepted that within any such polyspecific assemblage as the former taxon *Haplochromis*, some species will, through descent from a shared common ancestor, be more closely related to one another than to other species or groups of species. So far it has been possible only to make a first step towards discovering these relationships.

Yet, I believe that even this step could not have been made without the application of a basically Hennigian philosophy to the problem. In that way any morphological gaps (*ie* apomorph characters) have been used as positive characters to construct testable hypotheses (*ie* lineages) rather than as a means of ranking lineages through the subjectively estimated 'size' of the gap.

The creation of over twenty-five 'genera' where there was previously only one, has, I know, upset some of my colleagues who look upon my actions as those of a splitter run wild. But that indeed may have been the way in which the haplochromines (particularly the lacustrine species) evolved. To lump these lineages in a single genus (even as subgenera), whose monophyletic origin has not been established (and whose artificial and polyphyletic nature is strongly hinted at), is to hide the phylogenetic element of a classification. Regrettably, the constraints imposed by the Linnaean system of classification oblige one to

use the formal rank of genus for the different lineages if one is not to be forced into implying a relationship that may not exist.

Part of the difficulty encountered in classifying the Victoria–Edward–Kivu haplochromines at both the inter- and intragroup level may be a consequence of their recent and explosive speciation (see Greenwood, 1974). Take, for example, the large number of *Astatotilapia* species in these lakes (page 8 below). All are remarkably similar, differing only in male coloration and minor (at any rate to the taxonomist) morphometric features. Any one of these anatomically and ecologically unspecialized species could be the nearest living relative of the ancestor to a lineage recognized by its one or, at most, its few derived features. In other words, one is dealing with a situation where the first phenotypically manifest 'marker' apomorphies have evolved only recently. It is thus impossible to recognize the plesiomorph sister group (or species) since the characters it shares with the derived sister species are primitive ones (*ie* symplesiomorphies).

Methods and materials

Methods

Little more need be added to the points discussed in the 'methods' section in the first part of this paper (see Greenwood, 1979 : 269–276), except to define certain characters not employed in that paper. These are concerned either with describing neurocranial shape or with the morphology of the jaw skeleton.

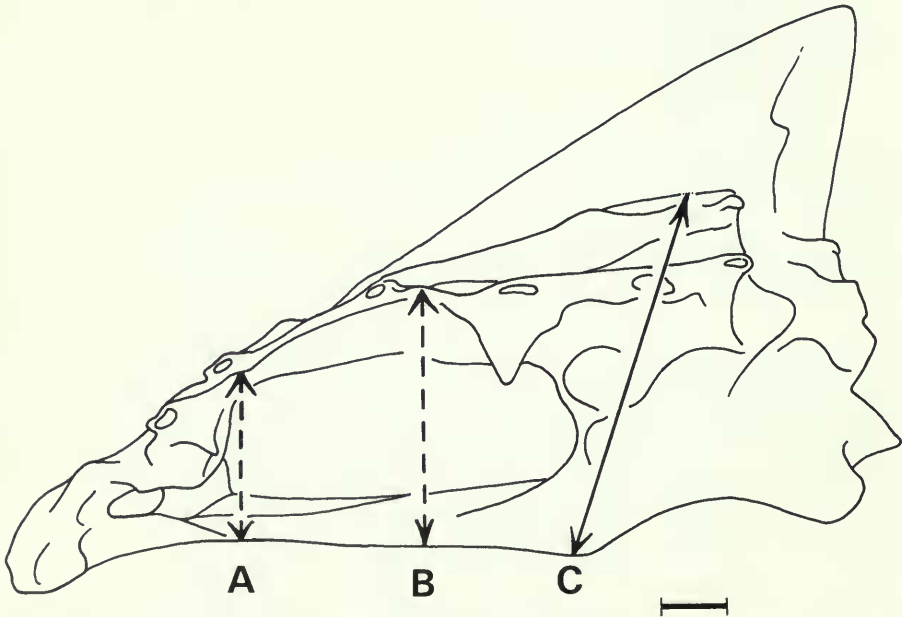


Fig. 1 Diagram to show reference points for various neurocranial measurements. A. Preorbital depth. B. Depth of orbit. C. Depth of otic region. (Solid line = direct measurement. Dashed line = to horizontal from parasphenoid margin.) Neurocranial outline from a skull of *Prognathochromis argenteus*. Scale = 3 mm.

Neurocranial length. The length of the skull measured directly¹ from the anterior tip of the vomer to the posterior point on the rim of the basioccipital facet for articulation with the first vertebra.

¹ That is, with the tips of the dividers actually contacting the points concerned, and the measurement then made between these points.

Preorbital depth. The depth of the skull through the anterior part of the orbit; measured in the vertical from the highest point on the horizontal surface of the frontal (*ie* disregarding the frontal wing which rises to meet the anterior tip of the supraoccipital) immediately above the point where the posterior margin of the lateral ethmoid meets the frontal, to the level of a horizontal line extended from the ventral face of the parasphenoid (see Fig. 1).

Depth of the otic region. The greatest depth measured directly¹ from the highest point on the supraoccipital base (*ie* excluding the crest), downwards and somewhat forwards to the lowest point on the parasphenoid posterior to the orbit (usually situated below the lateral commissure); see Fig. 1. It was necessary to choose the latter reference point as the ventral one because of considerable intra- and interspecific variability in the depth of curvature between that part of the parasphenoid and the articular surface of the pharyngeal apophysis.

Greatest width across the otic region. The maximum width of the skull as measured directly¹ across the pterotics.

Preotic skull length. Measured directly¹ from the anterior point of the vomer to the junction between the prootic and the ascending wing of the parasphenoid (*ie* near the base of the lateral commissure).

Depth of orbit. Measured vertically from the highest point on the curve of the frontal margin forming the dorsal rim of the orbit (ignoring the lateral line tubule if that should coincide) to a horizontal line extended from the ventral margin of the parasphenoid in that vertical (Fig. 1).

Height of premaxillary ascending processes. Measured directly¹ from the bony distal tip of the processes to a point on the anterior face of the dentigerous arm (*ie* the beak or peak) level with the upper margin of its horizontal posterior prolongation (Fig. 2).

Length of premaxillary dentigerous arm. Measured directly¹ from the premaxillary symphysis to the posterior point on the horizontal arm.

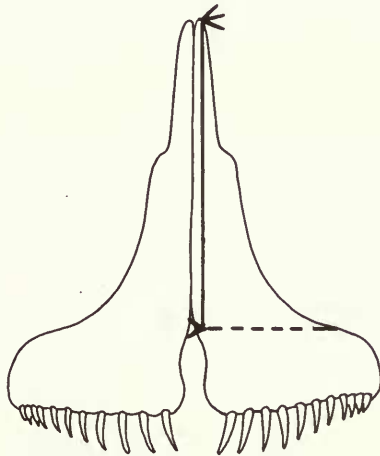


Fig. 2 Diagram showing reference points for measuring height of premaxillary ascending processes.

Length of lower jaw. Measured directly¹ from the symphysis to the posterior face of the anguloarticular bone immediately below the articular facet for the quadrate. All lower jaw measurements quoted were taken from whole specimens and, since some soft tissue is interposed between bone and divider point, these are fractionally greater than measurements taken from a skeleton.

The shape and proportions of jaw elements (dentary, anguloarticular bone, premaxilla and maxilla) in *Astatotilapia* species are taken to represent the plesiomorph (*ie* primitive) condition amongst haplochromines. This conclusion is based on the principle of

commonality (see discussion in Greenwood, 1979 : 270). Departure from the *Astatotilapia* condition is, therefore, interpreted as being a derived (*ie* apomorph) state.

Such departures include bullation of the dentary in the region where it divides into ascending (coronoid) and horizontal arms; a change in various of its proportions so that the dentary no longer appears to be a slender, elongate bone but is relatively deeper and stronger, thereby assuming a stout, foreshortened appearance; and, finally, extensive lateral development of the dentigerous region so that its alveolar surface projects outwards as a distinct shelf overhanging the lateral wall of the dentary. Primitively, the symphyseal region of the dentary is vertically aligned and narrow, and there is no distinct mental protuberance developed at its anteroventral angle.

Derived conditions in the anguloarticular are usually associated with a stout and foreshortened dentary; they include a general thickening of the bone, a reduction in its relative height (*ie* of the coronoid arm, the so-called primordial process of Barel *et al.*, 1976), and a change in the shape of its anteroventral projection (*ie* the arm which underlies the dentary), especially its anterior angle (which, primitively is produced and acute, but deepened and rounded or rectangular in its derived form).

Derived characteristics in the premaxilla include a lengthening of its ascending processes relative to the dentigerous arms, inflation of the dentigerous arms which thus become nearly cylindrical or distinctly ovoid in cross-section, and an increase in the width of their alveolar surfaces (a change generally but not invariably correlated with inflation of the arm itself). An expansion of the dentigerous arms anteriorly and anterolaterally, in the region below, and in front of the ascending processes, is also considered to be a derived condition. This gives the bone a 'beaked' or 'peaked' appearance.

The maxilla shows fewer changes in its morphology; chief amongst the derived conditions recognized are those in which the posterior part is relatively deepened, or is bullate, or when the articulatory head is turned medially at a marked angle (sometimes almost to form a right angle with the shaft of the bone). These apomorph conditions may occur together, in various combinations, or singly.

Materials

In addition to the specimens noted in Part I of this paper, all the BM(NH) haplochromine material from the five lakes has been involved in this review. It includes spirit specimens, dry skeletons (many prepared for this paper) alizarin transparencies, and radiographs.

Descriptions and comments are generally based on adult or subadult specimens. This is partly because the specific identity of juvenile and post-larval fishes cannot always be determined, and partly because some morphological features change during ontogeny (the dentition and some syncranial features are particularly liable to be affected in this way). However, where ontogenetic modifications appear to throw some light on problems of phylogeny, these have been taken into account.

Classification

In the generic diagnoses which follow, presumed apomorph (*ie* derived) features or conditions of a character-complex are italicized.

The serial listing of the genera should not be interpreted as having any particular phylogenetic significance. However, the most generalized taxon is taken first, and some of the more specialized lineages are dealt with later in the paper.

ASTATOTILAPIA Pellegrin, 1903

Several endemic species from Lakes Victoria, Kioga, Edward, George, Nabugabo and Kivu must now be added to this genus (see Greenwood, 1979 : 281 *et seq* for redescription and basic diagnosis of the genus). A typical *Astatotilapia* is shown in Fig. 3.

Unfortunately, this additional material in no way clarifies the status of the taxon, nor does it help to establish its monophyly. *Astatotilapia* remains, as before, a genus based on plesiomorph characters widely distributed amongst haplochromine cichlids; the one probable apomorphy (anal ocelli in male fishes) is shared by at least three other lineages (see Greenwood, 1979 : 268 & 284–5).

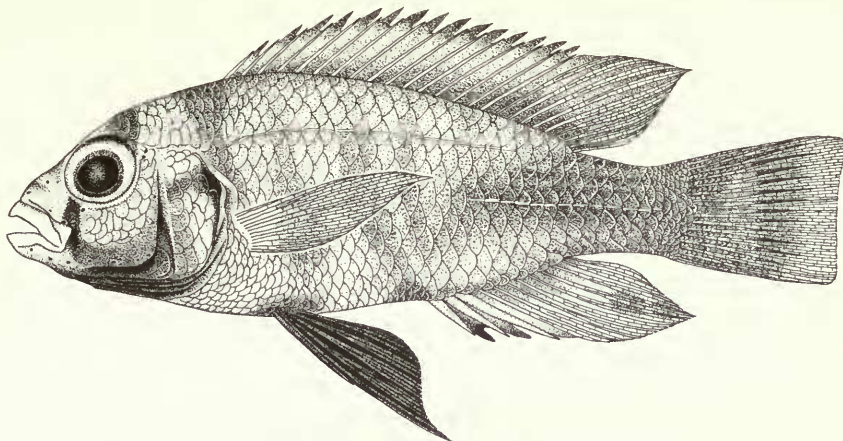


Fig. 3 *Astatotilapia elegans*. Lake George. About natural size.

The endemic *Astatotilapia* species from Victoria–Edward–Kivu differ from their fluviatile congeners in two major features: a higher modal number of lateral line pore scales (32–33 cf. 28–30) and a higher modal number of caudal vertebrae (16 cf. 15). In addition, not all the lacustrine species have several enlarged unicuspid teeth posteriorly in the outer premaxillary row (see Greenwood, 1979 : 282), although one or two such teeth are present in the majority.

There is an overlap in the total range of lateral line scale counts for fluviatile and lacustrine species (28–30, rarely 33, compared with 30–34 in the latter), but no lake species has a scale count in the lower part of the fluviatile range. Likewise, there is an overlap in the ranges for the number of caudal vertebrae, but again higher counts are confined to lake species (14–16 caudal vertebrae in fluviatile species, 15–17 in lake species).

Astatotilapia desfontainesi, from Tunisia and Algeria, is exceptional amongst the fluviatile taxa in having a high lateral line scale count (31–33), but its vertebral counts are typically those of fluviatile *Astatotilapia* species.

In most other respects the redescription of *Astatotilapia*, based on fluviatile taxa, given in Greenwood (1979 : 281–5) covers the species now included in the genus. Note may be made, however, that the range of gill raker numbers is increased to 13 (but the mode remains at 8 or 9), and that one of the newly included species (*A. oregosoma*) has a more slender body form than its congeners (30–34% SL cf. 35–40%).

The maximum adult size range is from 70 to 100 mm standard length.

Certain syncranial characters not discussed in Greenwood (1979) were found to be of value when dealing with the Victoria–Edward–Kivu haplochromines. These may be noted briefly, and are applicable both to the fluviatile and the lacustrine representatives of *Astatotilapia*.

Jaws. Over its posterior half, the lateral wall of each dentary is flared outwards. Consequently the alveolar surface is carried on a narrow, laterally produced shelf projecting slightly beyond the body of the ramus. The length of the entire lower jaw (dentary and anguloarticular) ranges from 31–46% of head length (modal range 40–43%).

The ascending processes of the premaxilla are shorter than the dentigerous arms, usually much shorter (about half the length) but in a few species only fractionally shorter. In all but one species (*A. velifer*, Lake Nabugabo) the dentigerous arms are compressed in cross section; *A. velifer* has the arms very slightly inflated and ovoid in section. No *Astatotilapia* species has

the anterior and anterolateral aspects of the dentigerous arms drawn out into a beak- or shelf-like projection.

The maxilla is relatively short and deep, its articulatory head inclined medially at a distinct angle.

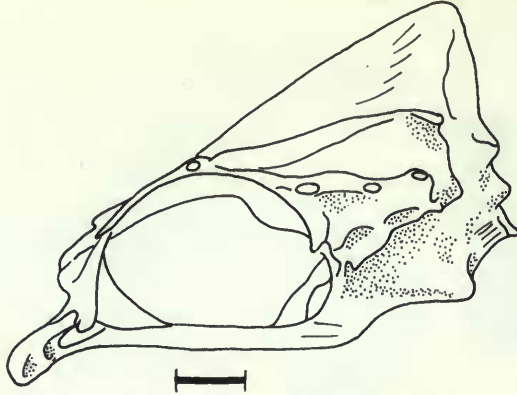


Fig. 4 Neurocranium (left lateral view) of *Astatotilapia macrops*. Scale = 3 mm.

Neurocranium (Fig. 4). Although the overall skull outline, especially the slope of the preorbital face, shows little intralineaage variation, there is some variability in the profile of the supraoccipital crest. Most species have a relatively low crest with a distinctly wedge-shaped outline; in a few species, however, the crest is deeper and consequently its profile approaches the near-pyramidal shape found in members of certain other lineages (*A. bloyeti* typifies this condition in *Astatotilapia*; see Greenwood, 1979: fig. 6).

Preorbital skull depth in *Astatotilapia* ranges from 25–30% of neurocranial length, skull width from 50–61% (modal range 56–60%) and depth of the otic region from 43–50% (modal range 47–50%).

Contained species

Lakes Victoria, Kioga, Edward, George, Nabugabo and Kivu endemics only are listed; for the fluvial species and those occurring in other lakes see Greenwood (1979 : 283–4).

Astatotilapia aeneocolor (Greenwood), 1973. Lake George; see Greenwood (1973 : 150–154).

Astatotilapia barbarae (Greenwood), 1967. Lake Victoria; see Greenwood (1967 : 93–97). Because of its partially paedophagous habits this species was previously associated with the major paedophage lineage *Lipochromis* (see p. 32 below and Greenwood, 1974). Anatomically, however, it shows none of the derived features characterizing *Lipochromis* (see Greenwood, 1967 : 96), and thus cannot be included in that lineage. Amongst *Astatotilapia*, *A. barbarae* is outstanding for its low otic skull depth (ca 43% of neurocranial length).

Astatotilapia brownae (Greenwood), 1962. Lake Victoria; see Greenwood (1962 : 142–9).

Astatotilapia cinerea (Blgr.), 1906. Lake Victoria; see Greenwood (1960 : 239–242).

Astatotilapia eduardi (Regan), 1921. Lake Edward; see Trewavas (1933 : 332). Poll (1932 : 42) considers *Haplochromis vicarius* Trewavas (1933) to be a synonym of this species.

Astatotilapia elegans (Trewavas), 1933. Lakes Edward and George; see Greenwood (1973 : 145–9), and Barel *et al.* (1976).

Astatotilapia engyostoma (Trewavas), 1933. Lake Edward; see Trewavas (1933 : 331–2). A poorly known species represented only by the holotype, a specimen now in very poor condition (see Greenwood, 1973 : 162).

Astatotilapia lacrimosa (Blgr.), 1906. Lake Victoria; see Greenwood (1960 : 230–233).

Astatotilapia latifasciata (Regan), 1929. Lake Kioga; see Regan (1929 : 390).

Astatotilapia macrops (Blgr.), 1911. Lake Victoria and possibly the Victoria Nile; see Greenwood (1960 : 236–9).

Astatotilapia macropsoides (Greenwood), 1973. Lakes Edward and George; see Greenwood (1973 : 162–7).

Astatotilapia martini (Blgr.), 1906. Lake Victoria; see Greenwood (1960 : 245–8). The sharply decurved head profile, and the golden-yellow body coloration in both sexes, make this an outstanding species amongst the *Astatotilapia* of Victoria–Edward–Kivu. Skull morphology is also atypical since the preorbital and orbital depths are above modal, and the preorbital skull profile is decurved and slopes steeply. Dentally and in other osteological features, however, it does not depart from the usual *Astatotilapia* condition. The relationship of *A. martini* can be reviewed when more is known about '*H. cronus*' and '*H. apogonoides*' (see pp. 88 & 89 respectively).

Astatotilapia megalops (Greenwood & Gee), 1969. Lake Victoria; see Greenwood & Gee (1969 : 4–7).

Astatotilapia melanopus (Regan), 1922. Lake Victoria; see Regan (1922 : 165–6). A taxon of uncertain status in the Lake Victoria flock.

Astatotilapia oregosoma (Greenwood), 1973. Lake George; see Greenwood (1973 : 159–162). An unusual species amongst the *Astatotilapia* complex because of its shallow body (depth 30–34% SL, mean 32%) and elongate habitus.

Astatotilapia pallida (Blgr.), 1911. Lake Victoria and possibly the Victoria Nile; see Greenwood (1960 : 233–6).

Astatotilapia piceata (Greenwood & Gee), 1969. Lake Victoria; see Greenwood & Gee (1969 : 7–10).

Astatotilapia schubotziella (Greenwood), 1973. Lake George and probably Lake Edward; see Greenwood (1973 : 188–192). The previously suggested close relationship between this species and *Psammochromis schubotzi* (see p. 56 below, and Greenwood, 1973 : 192) was not corroborated by more detailed anatomical knowledge.

Astatotilapia velifer (Trewavas) 1933. Lake Nabugabo; see Greenwood (1965 : 319–324).

DISCUSSION

Nothing much can be added to the comments already made on this supposed lineage (Greenwood, 1979 : 269, remarks on the *A. bloyeti* species complex, and also pp 284–5). Even information derived from the additional taxa now referred to *Astatotilapia* has failed to isolate a single derived feature uniquely common to all, or even the majority, of *Astatotilapia* species.

Species endemic to the lakes do, however, differ from their fluvial congeners in having higher modal numbers of lateral line scales and caudal vertebrae (see p. 7 above). Phylogenetically speaking, the significance of those features is difficult to assess. Members of all other lineages in the lakes have modes and ranges for these two features comparable with those of lake *Astatotilapia* (or, in some genera, even higher). But, there is, currently, no way of telling whether this should be identified as an ecophenotypic response, or the result of a distant shared common ancestry.

Taken in their entirety, the lacustrine *Astatotilapia* show a little more diversity in their syncranial and dental morphology than do the fluvial species.

Amongst the species of Lakes Victoria, Edward and George there are some whose dental and pharyngeal jaw morphology, and, or, their feeding habits, vaguely foreshadow the definitive characteristics of certain other lineages. For example, the slightly enlarged lower pharyngeal bone (with its enlarged median teeth) in *A. pallida* suggests affinity with *Labrochromis* (see p. 37 below, and Greenwood, 1960 : 234); skull morphology, and a partially paedophagous diet in *A. barbara* suggests *Lipochromis* affinities (see Greenwood, 1974); the unicuspid jaw teeth and partially piscivorous habits of large *A. brownae* hint at a relationship with *Harpogochromis* (see p. 10 below, and Greenwood, 1974); the slender body-form of *A. oregosoma* resembles that in *Yssichromis* (see p. 23 below), and

A. schubotziella has certain features that suggest it might be related to *Gaurochromis* (see p. 32 below, and Greenwood, 1973 : 192).

However, in none of these examples is the resemblance either sufficiently clear-cut, or reflected in unequivocally derived morphological features, for it to be used as a reliable indicator of phyletic relationship. Hence, all these taxa are included in *Astatotilapia* and not in the lineage with some or all of whose members they seem to bear some resemblance.

It has not proved possible to demonstrate intralineaage relationships between the numerous *Astatotilapia* species because the synapomorphies that would permit such an analysis were not discovered.

HARPAGOCHROMIS gen. nov.

TYPE SPECIES: *Hemichromis serranus* Pfeffer, 1896 (Type specimens in the Humboldt Museum, Berlin); see Greenwood (1962 : 152–6).

ETYMOLOGY. The name is derived from the Greek *harpagē*, meaning a robber + *chromis*, a word, when used in such a combination, is now associated with many genera of African Cichlidae; it refers to the predatory habits of species in this lineage.

DIAGNOSIS. Robust and deep to relatively deep-bodied haplochromines (body depth 30–42% of standard length, modal range 34–36%), *reaching a large maximum adult size (146–200 mm SL)*. Mouth generally horizontal or slightly oblique, but sometimes distinctly oblique; *lower jaw long (43–61% of head length, modal range 47–54%)* and with a prominent mental protuberance. Anterior and anterolateral regions of the premaxilla not produced to form a distinct beak or peak.

Neurocranium essentially of the generalized type, *but with a shallower otic region (40–44% neurocranial length cf. 47–50% in the generalized type)* and a higher supraoccipital crest which is generally near pyramidal in outline. Preorbital skull depth 23–28% neurocranial length, mean 25%, skull width 54–60% (no distinct mode), greatest orbital depth 25–31% (modal range 25–28%).

Outer jaw teeth strong and recurved, unequally bicuspid and a few unicuspid in fishes < 90 mm SL, the proportion of unicuspid increasing in larger fishes until, in specimens > 120 mm SL, only unicuspid are present; outer row in premaxilla with 48–80 teeth (modal range 60–70). One or 2 (less commonly 3, rarely up to 5) inner rows of teeth in each jaw.

Cheek fully scaled, generally with 4 or 5 rows of scales (less frequently with 2, 3 or 6 rows).

DESCRIPTION

Habitus (Fig. 5). Most members of this lineage have a deep or moderately deep body (30–42% SL) which is never manifestly compressed. Head shape, and particularly the angle of the mouth, show some intraspecific variation, the mouth angle varying from almost horizontal (*Harpagochromis victorianus*, *H. serranus*, *H. michaeli*) to distinctly oblique (*H. cavifrons*, *H. plagiostoma*, see Fig. 5B).

Anatomically, osteologically and in their dentition, *Harpagochromis* species depart but slightly from the generalized condition typified by species of *Astatotilapia*. All, however, reach a much greater maximum adult size (146–200 mm SL cf. 60–100 mm), and most only attain sexual maturity at a length which is never reached by an *Astatotilapia* (*ie* at a standard length of more than 100 mm in *Harpagochromis*, modally between 120 and 140 mm, compared with lengths of 50–80 mm in *Astatotilapia*). The adult size reached by species of *Harpagochromis* is, with few exceptions, also greater than that attained by members of most other lineages (but see p. 14 below).

In some morphometric features, especially in having a relatively longer lower jaw and, less noticeably, a relatively smaller eye and deeper cheek (two characters generally correlated), *Harpagochromis* species differ from *Astatotilapia*, at least in modal values. The lower jaw in *Harpagochromis* is 43–61% of head length (modal mean values 47–54%), eye diameter 17–29% (modal mean values 20–24%) and cheek depth 22–37% (modal mean values 27–32%). There is a slight overlap in the ranges of these ratios when large specimens of

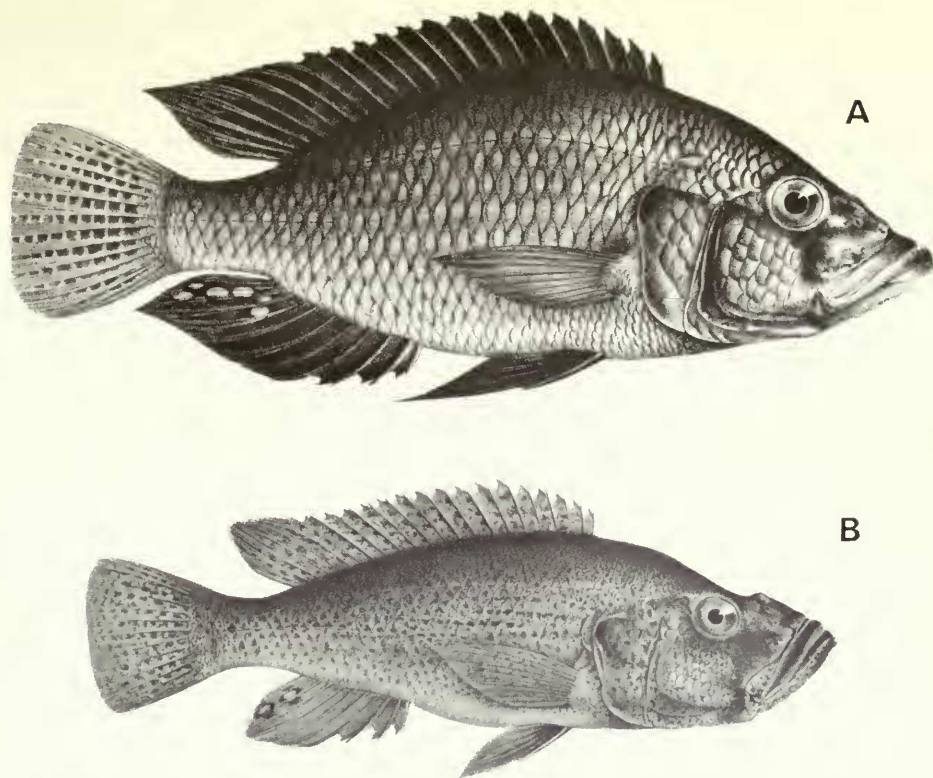


Fig. 5 A. *Harpagochromis spekii*. Lake Victoria. About half natural size. B. *Harpagochromis cavifrons*. Lake Victoria. About three-quarters natural size.

Astatotilapia species are compared with equal-sized *Harpagochromis* individuals. Since the characters in question invariably show either a positive or a negative allometry with body length, this overlap is to be expected. However, the modal value for lower jaw length is always higher for *Harpagochromis*. This might suggest that increased jaw size in *Harpagochromis* is not entirely attributable to allometric relationships with overall body size. In other words, it is in itself a derived feature, which is further emphasised through that allometric relationship.

Squamation. The cheek is fully scaled, usually with 4 or 5 rows of scales (less frequently 2, 3 or 6 rows); there are 30–34 (modal range 32–33) scales in the lateral line series.

Neurocranium (Fig. 6). The neurocranium in *Harpagochromis* is similar to that in *Astatotilapia*, except that the otic region is shallower (40–44% of neurocranial length cf. 47–50%) and the supraoccipital crest is higher and pyramidal in outline. Because the skull is deep preorbitally and orbitally, and since it is wide in the otic region, it is less obviously streamlined than is the skull form characterizing the other major piscivore lineage, *Prognathochromis* (see p. 16). Also, as compared with that lineage, the supraoccipital crest in *Harpagochromis* is taller relative to skull length, and slopes downward and forward more steeply.

Dentition. Fishes over 90 mm SL mostly have strong, somewhat recurved unicuspid teeth in the outer row of both jaws. Smaller specimens have predominantly bicuspid outer teeth, the cusps of unequal size, and the crown and upper neck slightly recurved. There are 48–80 outer teeth in the premaxillary series (modal range 60–70).

Inner row teeth are either tricuspid, unicuspid or a mixture of both types, arranged in 1 or 2 (less frequently 3) rows anteriorly and anterolaterally.

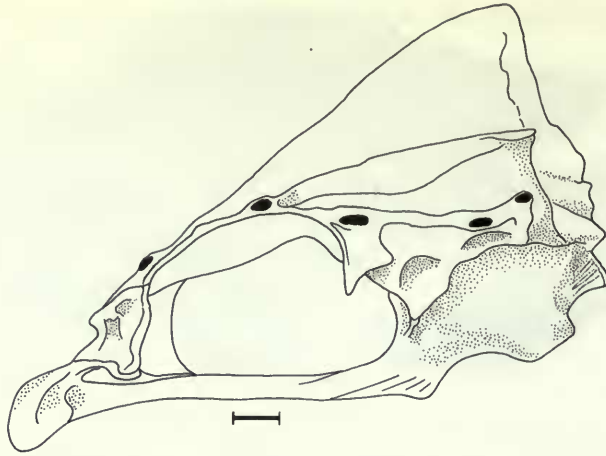


Fig. 6. Neurocranium (left lateral view) of *Harpagochromis maculipinna*; scale = 3 mm.

Jaws. The proportionally long lower jaw has been noted already. In all other respects it barely departs from the *Astatotilapia* type, apart from having a well-developed mental protuberance at the base of the symphysis. In some species the crown of the coronoid process (the ascending dentary limb) has a distinct lateral deflection.

The anterior and immediately lateral regions of the premaxilla are but slightly produced forward (Fig. 7), so that in lateral view it is hardly beaked (cf. *Prognathochromis*, p. 18). The dentigerous arms are very slightly inflated, and have a compressed ovoid cross-section.

Vertebral numbers: 28–31 (mode 30), comprising 12–14 (mode 13) abdominal, and 15–18 (modes 16 or 17) caudal elements (the fused PU_1 and U_1 centra excluded).

Caudal fin. Most species have the posterior margin truncate or weakly subtruncate, but in one species (*H. plagiostoma*) it is obliquely truncate, that is, sloping forward and downward to meet the upwardly curved ventral region.

Contained species

The taxa are arranged in groups approximating to their degree of morphological departure from the generalized '*Astatotilapia*' bauplan.

Harpagochromis serranus (Pfeffer), 1896. Lake Victoria; see Greenwood (1962 : 152–5).

Harpagochromis victorianus (Pellegrin), 1904. Lake Victoria; see Greenwood (1962 : 156–8; plate I).

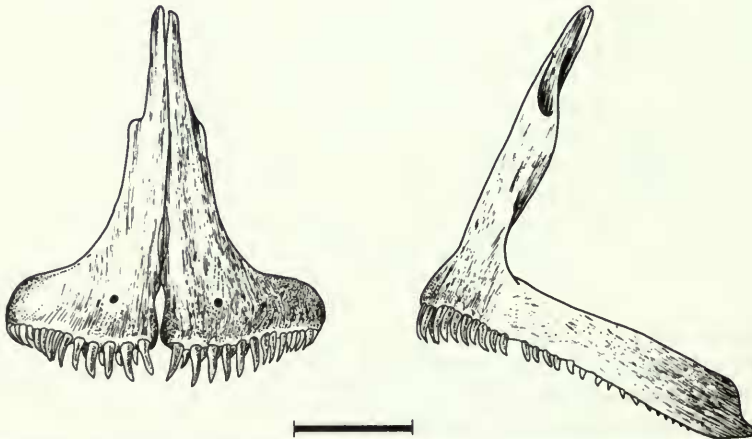


Fig. 7 Premaxilla of *Harpagochromis maculipinna*, seen anteriorly and in left lateral view. Scale = 5 mm.

Harpagochromis nyanzae (Greenwood), 1962. Lake Victoria; see Greenwood (1962 : 159–161).

Harpagochromis spekii (Blgr.), 1906. Lake Victoria and the Victoria Nile; see Greenwood (1967 : 32–38).

Harpagochromis maculipinna (Pellegrin), 1913. Lake Victoria; see Greenwood (1967 : 43–47).

Harpagochromis squamipinnis (Regan), 1921. Lake Edward and George; see Greenwood (1973 : 204–9).

This species differs from all its congeners in Lake Victoria (and all known haplochromine species) in having short rows of small scales extending from the body onto the membrane of the dorsal and anal fins. The scales are closely applied to the fin rays, both spinous and branched (see fig. 31 in Greenwood, 1973 : 206). In its gross morphology *H. squamipinnis* closely resembles *H. serranus* and *H. victorianus* of Lake Victoria. At present no other *Harpagochromis* species are known from Lakes Edward and George.

Harpagochromis boops (Greenwood), 1967. Lake Victoria; see Greenwood (1967 : 47–49).

Harpagochromis pachycephalus (Greenwood), 1967. Lake Victoria; see Greenwood (1967 : 39–42).

Harpagochromis thuragnathus (Greenwood), 1967. Lake Victoria; see Greenwood (1967 : 49–51).

Harpagochromis guiarti (Pellegrin), 1904. Lake Victoria; see Greenwood (1962 : 145–9). The distribution recorded in that paper included Lake Edward; this was based on earlier identifications of material from Lake Edward which most probably does not belong to this species (see Greenwood, 1973 : 232). The identity of the Edward material, and the true distribution of *H. guiarti*, must await the outcome of further research on the haplochromines of Lakes Edward and George.

Harpagochromis artaxerxes (Greenwood), 1962. Lake Victoria; see Greenwood (1962 : 170).

Harpagochromis altigenis (Regan), 1922. Lake Victoria, see Greenwood (1967 : 60–65).

Harpagochromis pectoralis (Blgr.), 1911. Lake Victoria. This species was given the replacement name '*squamulatus*' by Regan (1922), since at that time '*pectoralis*' would have been a junior homonym of *Haplochromis pectoralis* (Pfeffer), 1893. Because Pfeffer's species is now placed in the genus *Ctenochromis*, for which it is indeed the type species (Greenwood, 1979 : 287), the original trivial name for Boulenger's 1911 species can be resurrected.

Harpagochromis pectoralis differs from other members of the lineage in a number of features, but especially in having a more strongly decurved preorbital skull profile. Its relationships with (or within) the *Harpagochromis* lineage may have to be reconsidered when several undescribed and '*pectoralis*'-like species from Lake Victoria have been studied.

The species is redescribed in Greenwood (1967 : 60–65).

Harpagochromis plagiostoma (Regan), 1922. Lake Victoria; see Greenwood (1962 : 199–202).

Harpagochromis cavifrons (Hilgendorf), 1888. Lake Victoria and possibly the Victoria Nile; see Greenwood (1962 : 196–9).

Harpagochromis michaeli (Trewavas), 1928. Lake Victoria; see Greenwood (1962 : 203–6).

Incertae sedis

'*Haplochromis*' *diplotaenia* Regan & Trewavas, 1928, Lake Victoria. This species is known from very few specimens, and no skeletal material is available. Judging from radiographs its

neurocranial architecture is of the *Harpagochromis* type, but the difficulties associated with obtaining accurate measurements from radiographs preclude definite conclusions on that point.

'*Haplochromis*' *paraplagiostoma* Greenwood & Gee, 1969. Lake Victoria. Again, a shortage of osteological material has made it impossible to check several critical features. Although superficially this species does resemble other members of the *Harpagochromis* lineage, it seems advisable to keep the generic placement of '*H.*' *paraplagiostoma* as *incertae sedis* until more specimens are available for study.

'*Haplochromis*' *worthingtoni* Regan, 1929. Lake Kioga. Known only from the holotype (141.0 mm SL), this species closely resembles species of the *Harpagochromis serranus*—*maculipinna* group in all visible anatomical features. From a radiograph its neurocranium also seems to be of a *Harpagochromis* type.

DISCUSSION

The phyletic integrity of this presumed lineage depends on a single synapomorphy, the attainment of a large adult size (with which is, of course, associated a number of other characters, see p. 11 above).

There are indications that members of this lineage, as compared with species of the genus *Astatotilapia*, do have a basically longer lower jaw over and above the relative increase in jaw length effected through its positively allometric growth pattern.

Anatomically, most *Harpagochromis* species retain a generalized level of organization like that in *Astatotilapia*. Only two species, *H. plagiostoma* and *H. cavifrons*, with their very oblique mouths, show some departure from that condition, while a third (*H. pectoralis*) has a slightly derived type of skull architecture.

The possible relationship between *Harpagochromis* and *Prognathochromis* (as suggested in Greenwood, 1974) is discussed on p. 22.

Although the list of *Harpagochromis* species (p. 12) is arranged so that morphologically similar species are grouped together (in order of increasing departure from the *Astatotilapia* level of organization), this should not be taken to imply true phyletic relationships. Such intralinear relationships cannot be determined on the basis of data currently available.

PROGNATHOCHROMIS gen. nov.

TYPE SPECIES: *Paratilapia prognatha* Pellegrin, 1904; see Greenwood (1967 : 78).

ETYMOLOGY. The name is derived from that of the type species.

DIAGNOSIS. Body form variable, from shallow to deep (24–45% standard length) but most species relatively slender (body depth 30–34% SL) and none is markedly compressed. *Lower jaw long* (41–62% head length, modal range 45–53%) and with a prominent mental protuberance; premaxilla distinctly beaked or peaked.

Overall habitus one of a slender, streamlined fish with a large, often oblique mouth, and the head with a relatively acute entry angle. Maximum adult size extending over a wide range of lengths (70–230 mm SL), but most specimens reaching 140–200 mm SL.

Neurocranium (the principal diagnostic feature, particularly for differentiating *Prognathochromis* from *Harpagochromis*), *elongate, slender and shallow, with a low, supra-occipital crest, wedge-shaped in lateral outline. Preorbital skull depth 18.6–23% of neurocranial length (mode 21%), greatest orbital depth 22–28% (modal range 22–23%), depth of otic region 31–42% (no distinct mode), skull width 42–55% (modal range 47–50%), all expressed as ratios of neurocranial length.*

Teeth in outer row of both jaws strong and recurved, mostly unicuspid in fishes > 90 mm SL, unequally bicuspid with some unicuspid in smaller fishes. Thirty-four to 94 outer teeth in the premaxilla, modal range in the nominate subgenus 50–60, but 66–74 in the other subgenus. In that subgenus, whose members have a small adult size (95–120 mm SL), *tricuspid teeth occur laterally and anterolaterally, interspersed amongst the predominantly*

unicuspid outer teeth. The inner teeth in both subgenera are uni- or tricuspid, and are arranged in 2 or 3 (rarely 1, 5 or 6) rows anteriorly and anterolaterally.

Cheek fully scaled, usually with 3 or 4 rows but sometimes 5 or 6, rarely with only 2.

DESCRIPTION

Habitus (Fig. 8). Body form is variable, the depth varying from shallow to relatively deep (24–45% SL) but moderately shallow in the majority of species (modal range 30–34% SL). Except in a few species, the body is not noticeably compressed.

With few exceptions, members of this genus have a 'typical' predator facies (see Fig. 8; and figs 13–15 in Greenwood, 1974), *ie* a slender streamlined body, large mouth and a predominantly unicuspid dentition. In all these features, *Prognathochromis* represents a marked development of the habitus-type beginning to appear in the *Harpagochromis* lineage. No

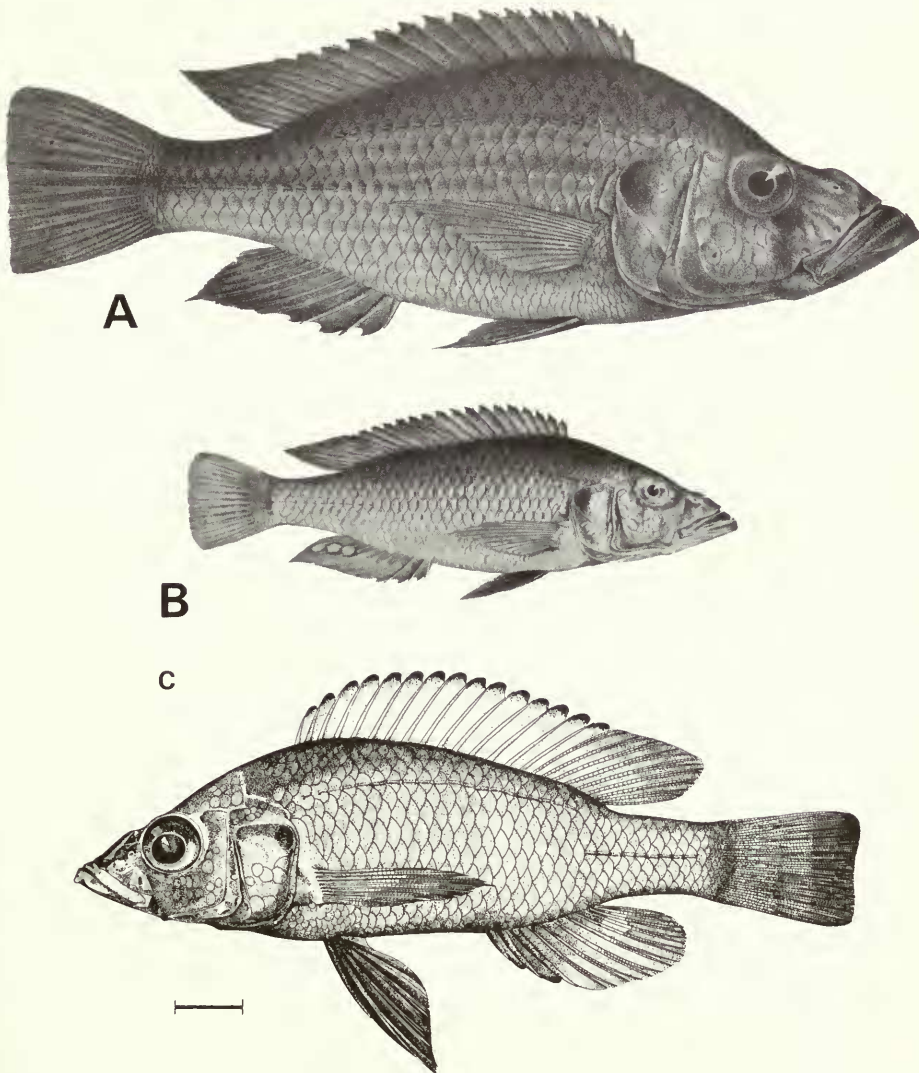


Fig. 8 A. *Prognathochromis* (*P.*) *prognathus*. Lake Victoria. About four-fifths natural size. B. *Prognathochromis* (*P.*) *mento*. Lake Victoria. About half natural size. C. *Prognathochromis* (*Tridontochromis*) *sulphureus*. Lake Victoria. Scale = 1 cm.

member of the *Prognathochromis* line retains the near-*Astatotilapia* habitus which characterizes so many species of *Harpagochromis*.

Nine species attain only a small adult size (70–120 mm SL), but for the others the maximum size lies in the range 140–230 mm SL.

As would be expected, those species reaching a small maximum size have, as compared with their larger congeners, relatively larger eyes and shallower cheeks (24–34% head length, modal range 27–30%, and 16–29%, modal range 19–22% head length, for the characters respectively). In these features they depart but slightly from the generalized condition. Species reaching greater maximum sizes (modally 150–200 mm SL) have relatively smaller eyes (17–26% head, modal range 19–22%) and somewhat deeper cheeks (18–33% head, modal range 24–26%).

The angle of the mouth varies from near horizontal to markedly oblique, and the lower jaw is long (41–62% head, modal range 45–53%). As in *Harpagochromis*, the relative lower jaw length is greatest in larger individuals, but even in those species with a small adult size (*ie* < 110 mm SL), the mean lower jaw length is distinctly greater than that in comparable sized *Astatotilapia* species. It is also greater than in most species of other, but non-piscivorous, groups.

Squamation. The cheek is fully covered by 3 or 4 (less commonly 2, 5 or 6) rows of scales, the lateral line has 30–34 scales (modes 32 or 33), rarely 35.

Neurocranium (Fig. 9). A slender, shallow and generally streamlined neurocranium is found in all species of *Prognathochromis* (see Fig. 9; and fig. 69 in Greenwood, 1974).

Preorbital skull depth is from 18.6–23.1% of neurocranial length (mode 21%), greatest orbital depth 21.7–28.0% (modal range 22–23%), and the greatest width across the otic region 42–55% (modal range 47–50%). Preotic skull length varies from 63–70% (mode 66%) of neurocranial length, and is thus virtually identical with that in *Harpagochromis*.

In most species the supraoccipital crest is low (particularly in relation to that in *Harpagochromis*), and it slopes gently downwards and forwards. The outline of the crest is thus more nearly wedge-shaped than is the pyramidal crest in *Harpagochromis* (and in a few *Prognathochromis* species, eg *P. xenostoma* and *P. flavipinnis*; however, even in these taxa the crest is relatively low and the rest of the skull has proportions typical for the lineage). A wedge-shaped crest characterizes the presumed generalized haplochromine skull (eg *Astatotilapia bloyeti*, see fig. 6 in Greenwood, 1979), but it is relatively lower in *Prognathochromis*.

Within *Prognathochromis* there is a graded range of skull forms (see Greenwood, 1962 : 208, fig. 25; 1967 : 108–115; and 1974 : 98, fig. 69) but even in those species with the least derived skull form (eg *P. melichrous*, *P. dichrourus*, *P. arcanus*), gross neurocranial morphology is quite distinct from that in other lineages.

There is also some variation in the form of the ethmovomerine region. Modally, this part of the skull appears as an almost uninterrupted anterior prolongation of the dorsal skull outline, and the vomer tip lies slightly below the level of the parasphenoid. Exceptionally, the ethmovomerine region is decurved, projecting well below the level of the parasphenoid, and the skull has a more convex dorsal profile than that of the modal type. Examples (Fig. 9B) are seen in *P. dentex*, *P. bayoni* and *P. vittatus*. Intermediate types, however, link the extreme with the modal form.

In the nominate subgenus of *Prognathochromis* (see p. 19), the posterior (*ie* orbital) face of the lateral ethmoid slopes backwards at an angle of 45°–60° with the horizontal; in the other subgenus it is more nearly vertical (75°–80°), the common condition amongst haplochromine lineages. In that subgenus too, the lateral aspects of the bone are more expansive and anteriorly protracted than in the nominate subgenus; again, this is the more usual haplochromine condition.

Characters contributing to the low, slender and streamlined appearance of the skull in *Prognathochromis* (*ie* the shallow preorbital depth, low orbital and otic regions, the low, gently sloping supraoccipital crest, and the narrow otic region) are all derived features, and constitute the principal synapomorphies defining the lineage.

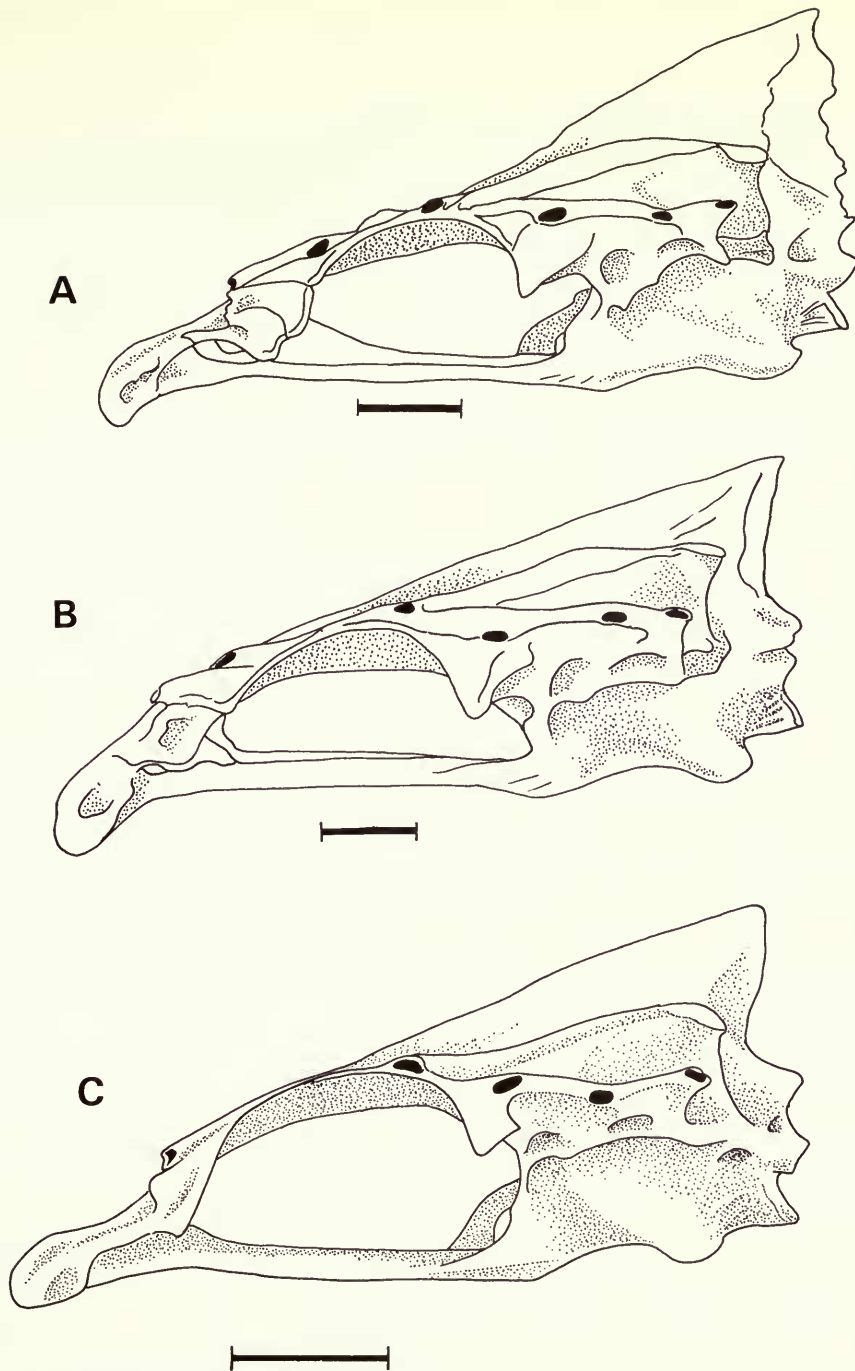


Fig. 9 Neurocranium (in left lateral view) of: A. *Prognathochromis* (*P.*) *mento*. B. *Prognathochromis* (*P.*) *dentex*. C. *Prognathochromis* (*T.*) *sulphureus*. Scale = 5 mm.

Dentition. Specimens over 90 mm SL in most *Prognathochromis* species have a preponderance of strong, recurved, unicuspid teeth in the outer row of both jaws. Some unequally bicuspid teeth may also be present in specimens between 90 and 110 mm SL, but are in a minority, only predominating in fishes less than 80 mm long.

A predominantly unicuspid outer dentition (at least anteriorly in the jaws) also occurs, in some species only, at a length of less than 90 mm. The majority of these species (8 out of 11) belong to a distinct subdivision of the genus (see p. 20) whose members are further distinguished by the occurrence of tricuspid teeth anteriorly and anterolaterally in the outer tooth row, and by their small adult size (96–120 mm SL). These tricuspid teeth are not simply displaced elements from the inner tooth rows, and their presence is considered a derived feature.

Both subdivisions of *Prognathochromis* have the inner teeth arranged in 2 or 3 rows, exceptionally in a single row or as many as 5 or 6 rows. The teeth are generally tricuspid in fishes < 100 mm SL and unicuspid (or mixed uni- and tricuspid) in larger individuals.

Upper jaw. The premaxilla is always beaked. The degree of this anterior and anterolateral extension of the dentigerous arms shows continuous interspecific variation, but is always noticeable (Fig. 10).

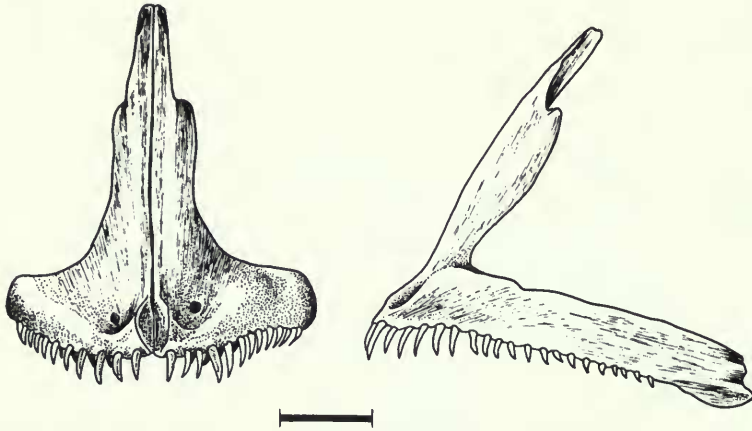


Fig. 10 Premaxilla of *Prognathochromis* (*P.*) *argenteus*, seen anteriorly and in left lateral view. Scale = 5 mm.

Lower jaw. In no species is the dentary foreshortened, but there is considerable interspecific variation in the depth of this bone. Most members of the nominate subgenus have a relatively stout (*ie* deep) dentary, but in all species of the other subgenus the bone is noticeably shallower and more slender. In this group too, the lateral aspect of the dentary is deeply concave; when viewed anteriorly, it has a pronounced upward and outward flare and the alveolar surface projects laterally as a distinct shelf (see Greenwood & Barel, 1978 : 155; and Fig. 11).

A prominent mental protuberance at the ventral end of the symphysis is present in both subgenera.

The crown of the ascending (coronoid) dentary arm is always deflected laterally, most obviously so in species of the nominate subgenus, less markedly in the others. The deflection in both subgenera is stronger than in any *Harpagochromis* species.

The insertion point for the mandibulo-interopercular ligament is prominent and well-developed in the nominate subgenus but poorly developed in the other subgenus.

Lower pharyngeal bone and teeth. The dentigerous surface of this bone is triangular, usually as broad as it is long, but sometimes slightly broader than long.

In one subgenus (see p. 20) the lower pharyngeal bone is relatively narrow and its dentigerous surface has an anteroposteriorly attenuate appearance (Fig. 12; and figs 5, 10 and 12 in Greenwood & Barel, 1978). The pharyngeal teeth in this subgenus are finer and more compressed than those of the nominate subgenus, and the teeth in the two median and the posterior transverse row are, relatively speaking, less enlarged.

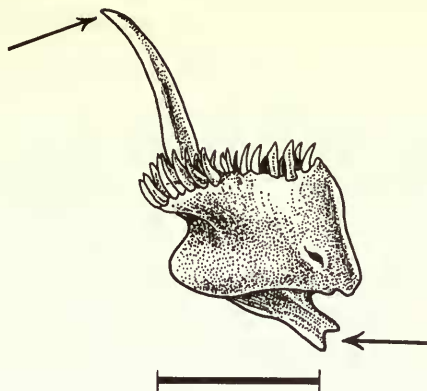


Fig. 11 Anterior view of right dentary in *Prognathochromis* (*T. dolichorynchus*) to show overhang of alveolar shelf, and 'flare' of the dentary's outer wall. Arrows point to: ascending (coronoid) arm of the ramus (upper arrow), and the anterior part of the anguloarticular (lower arrow). Scale = 3 mm.

Vertebral numbers: 28–32 (mode 30), comprising 12–14 (mode 13) abdominal and 15–18 (modes 17 and 18) caudal elements excluding the fused PU_1 and U_1 centra.

Caudal fin. An obliquely truncate fin (see p. 12 above) occurs in some specimens of one species (*P. pseudopellegrini*), but otherwise the fin is truncate or weakly subtruncate.

The two subgenera recognized are:

Subgenus *PROGNATHOCHROMIS* nov.

TYPE SPECIES: *Paratilapia prognatha* Pellegrin, 1904; see Greenwood (1967 : 78).

DIAGNOSIS. *Prognathochromis* without tricuspid teeth in the outer tooth row of either jaw (except, very rarely, as obviously displaced elements from the inner series), usually reaching a large maximum adult size (140–230 mm SL) but only to a length of 93–105 mm in 3 species. First infraorbital (lachrymal) bone with a very slight anterior bullation preceding the anterior infraorbital lateral line tubule, the bullation barely visible without dissection. *Maximum orbital depth of the skull* 22–25% *neurocranial length* (modal range 22–23%). *Lateral ethmoid* relatively narrow, its *posterior face* sloping backwards at an angle of 45°–60° to the horizontal. Lower jaw (especially the dentary) not noticeably shallow, and with a moderately pronounced alveolar shelf visible when the bone is viewed frontally. Lower pharyngeal teeth coarser than those in the other subgenus, the bone itself not distinctly attenuated.

Contained species

Since no intragroup relationships can be determined, the species are listed alphabetically.

Prognathochromis (*Prognathochromis*) *arcanus* (Greenwood & Gee), 1969. Lake Victoria; see Greenwood & Gee (1969 : 52–4).

Prognathochromis (*P.*) *argenteus* (Regan), 1922. Lake Victoria; see Greenwood (1967 : 84–7).

Prognathochromis (*P.*) *bartoni* (Greenwood), 1962. Lake Victoria; see Greenwood (1962 : 161–4).

Prognathochromis (*P.*) *bayoni* (Blgr.), 1909. Lake Victoria; see Greenwood (1962 : 149–52).

Prognathochromis (*P.*) *decticostoma* (Greenwood & Gee), 1969. Lake Victoria; see Greenwood & Gee (1969 : 55–7).

Prognathochromis (*P.*) *dentex* (Regan), 1922. Lake Victoria; see Greenwood (1962 : 167–9)

Prognathochromis (*P.*) *dichrourus* (Regan), 1922. Lake Victoria; see Greenwood (1967 : 65–9).

Prognathochromis (*P.*) *estor* (Regan), 1929. Lake Victoria; see Greenwood (1962 : 164–7).

- Prognathochromis* (*P.*) *flavipinnis* (Blgr.), 1906. Lake Victoria; see Greenwood (1962 : 192–5).
- Prognathochromis* (*P.*) *gilberti* (Greenwood & Gee), 1969. Lake Victoria; see Greenwood & Gee (1969 : 57–60).
- Prognathochromis* (*P.*) *gowersi* (Trewavas), 1928. Lake Victoria; see Greenwood (1962 : 180–3).
- Prognathochromis* (*P.*) *longirostris* (Hilgend.), 1888. Lake Victoria and possibly the Victoria Nile; see Greenwood (1962 : 171–4).
- Prognathochromis* (*P.*) *macrognathus* (Regan), 1922. Lake Victoria; see Greenwood (1962 : 183–6).
- Prognathochromis* (*P.*) *mandibularis* (Greenwood), 1962. Lake Victoria; see Greenwood (1962 : 178–80).
- Prognathochromis* (*P.*) *mento* (Regan), 1922. Lake Victoria; see Greenwood (1962 : 174–8).
- Prognathochromis* (*P.*) *nanoserranus* (Greenwood & Barel), 1978. Lake Victoria; see Greenwood & Barel (1978 : 157–61).
- Prognathochromis* (*P.*) *paraguiarti* (Greenwood), 1967. Lake Victoria; see Greenwood (1967 : 69–72).
- Prognathochromis* (*P.*) *pellegrini* (Regan), 1922. Lake Victoria; see Greenwood (1962 : 186–9).
- Prognathochromis* (*P.*) *percoides* (Blgr.), 1915. Lake Victoria; see Greenwood (1962 : 189–91).
- Prognathochromis* (*P.*) *prognathus* (Pellegrin), 1904. Lake Victoria; see Greenwood (1967 : 78–83).
- Prognathochromis* (*P.*) *pseudopellegrini* (Greenwood), 1967. Lake Victoria; see Greenwood (1967 : 56–60).
- Prognathochromis* (*P.*) *venator* (Greenwood), 1965. Lake Nabugabo; see Greenwood (1965 : 342–6).
- Prognathochromis* (*P.*) *vittatus* (Blgr.), 1901. Lake Kivu; see Regan (1921 : 638).
- Prognathochromis* (*P.*) *xenostoma* (Regan), 1922. Lake Victoria; see Greenwood (1967 : 51–6).

Incertae sedis

Astatotilapia nigrescens Pellegrin, 1909 (Lake Victoria). This taxon, known only from the holotype, has a close superficial resemblance to both *P. (P.) flavipinnis* and *P. (P.) percoides* (see Greenwood, 1967 : 118–19). It is for this reason alone that I am including it, tentatively, as a member of this subgenus.

Subgenus **TRIDONTOCHROMIS** nov.

TYPE SPECIES: *Haplochromis tridens* Regan & Trewavas, 1928 (see Greenwood, 1967 : 97). Lake Victoria.

ETYMOLOGY. The name alludes to the tricuspid teeth which are a feature of the outer tooth row in both jaws.

DIAGNOSIS. *Prognathochromis* species in which *tricuspid teeth occur anteriorly and anterolaterally* (as well as posteriorly) *in the outer tooth rows of, generally, both jaws*; the size and number of these teeth, together with their inevitable presence, militate against their merely being displaced elements from the inner tooth series. *The lachrymal bone (1st infra-orbital) has, in 8 of the 9 species known, an enlarged, ovoid to rectangular bullation occupying the greater part of the bone anterior to the first lateral line tubule, the bulla visible without dissection.* Maximum orbital depth is 23–28% of the neurocranial length (modal range 26–27%), the lateral ethmoid is more expansive than in species of the nominate subgenus, and its posterior face is aligned almost vertically or at an angle of 70°–80° with the horizontal. *The lower pharyngeal bone is narrow, its dentigerous surface having an antero-posteriorly attenuate appearance* (see Fig. 12 and figs 5, 10 & 12 in Greenwood & Barel,

1978); teeth on this bone are fine and compressed. *The lower jaw is shallow, its lateral face having a pronounced upward and outward flare so that the alveolar surface is carried as a prominent shelf overhanging the body of the bone* (see fig. 4 in Greenwood & Barel, 1978).

Members of this subgenus reach a small maximum adult size (95–120 mm SL), becoming sexually mature at a standard length of between *ca* 55–85 mm.

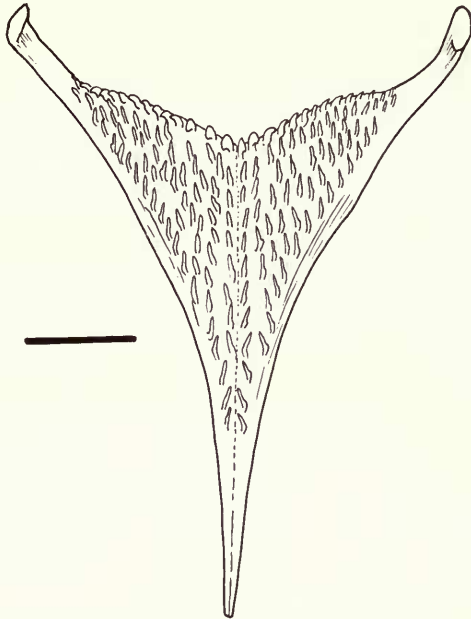


Fig. 12 Lower pharyngeal bone of *Prognathochromis* (*T.*) *crocopeplus* in occlusal view.
Scale = 2 mm.

Contained species

No intragroup relationships can be determined, and the species are therefore listed alphabetically.

Prognathochromis (*Tridontochromis*) *chlorochrous* (Greenwood & Gee), 1969. Lake Victoria; see Greenwood & Gee (1969 : 44–8).

Prognathochromis (*T.*) *crocopeplus* (Greenwood & Barel), 1978. Lake Victoria; see Greenwood & Barel (1978 : 142–8).

Prognathochromis (*T.*) *cryptogramma* (Greenwood & Gee), 1969. Lake Victoria; see Greenwood & Gee (1969 : 48–51).

Prognathochromis (*T.*) *dolichorhynchus* (Greenwood & Gee), 1969. Lake Victoria; see Greenwood & Gee (1969 : 34–40).

Prognathochromis (*T.*) *melichrous* (Greenwood & Gee), 1969. Lake Victoria; see Greenwood & Gee (1969 : 24–8).

Prognathochromis (*T.*) *plutonium* (Greenwood & Barel), 1978. Lake Victoria; see Greenwood & Barel (1978 : 151–5).

Prognathochromis (*T.*) *sulphureus* (Greenwood & Barel), 1978. Lake Victoria; see Greenwood & Barel (1978 : 148–51).

Prognathochromis (*T.*) *tridens* (Regan & Trewavas), 1928. Lake Victoria; see Greenwood (1967 : 97–100).

Prognathochromis (*T.*) *tyrianthinus* (Greenwood & Gee), 1969. Lake Victoria; see Greenwood & Gee (1969 : 40–4).

Incertae sedis

Haplochromis eutaenia Regan & Trewavas, 1928. The type and only specimen of this species is now rather damaged, particularly about the jaws. As a result the dentary is broken and there are almost no outer series teeth in either jaw. The remaining teeth are bicuspid, but the morphology of the dentary, the overall proportions of the specimen, and what little I can learn about its neurocranial architecture, all suggest that the species could be referred to this subgenus of *Prognathochromis*.

Lake Victoria; see Regan & Trewavas (1928 : 225–6).

DISCUSSION

The characteristic and derived skull form in *Prognathochromis* (see above, p. 16) seems to provide a strong argument for the monophyly of the lineage. Certainly it would be more parsimonious to consider this to be so than to argue that such a distinctive skull form had evolved independently and on several occasions. But, as is so often the case with the Victoria–Edward–Kivu haplochromines, there are few other unequivocally synapomorphic features to back-up the single, diagnostic one.

Again, an absence of synapomorphic characters makes it difficult to identify the sister group of *Prognathochromis*. In an earlier attempt (Greenwood, 1974), certain paedophagous species were tentatively identified as the sister taxon of *Prognathochromis* (then represented by what is now the nominate subgenus).

A more critical analysis of the features on which that suggestion was based, shows that it is no longer tenable; some of the characters involved proved to be plesiomorphies, and others to be autapomorphies.

I have also not been able to find new features that would corroborate my suggestion that *Prognathochromis* and *Harpagochromis* are closely related (Greenwood, 1974). *Prognathochromis* could, on available anatomical evidence, be derived from an *Harpagochromis* or an *Astatotilapia*-like ancestor. However, since in certain respects the skull form in *Harpagochromis* does depart from the generalized *Astatotilapia* type towards that of *Prognathochromis*, there may be grounds for suspecting some relationship between the two lineages. Unfortunately, since there are no other features to support (or negate) this idea, it must remain as no more than a suggestion.

In the same tentative phylogeny (Greenwood, 1974 : fig. 70), the *Tridontochromis* division of *Prognathochromis* was thought to have a rather distant relationship with the nominate subgenus. It was, indeed, allied with a taxon now accorded the status of a monotypic genus, namely *Allochromis welcommei* (see p. 57); the two taxa were, at that time, considered to be the sister group of the *Haplochromis riponianus* complex here included in the genus *Psammochromis*, see p. 53.

First doubts about these proposed relationships were expressed by Greenwood & Barel (1978 : 156), and are confirmed by the research embodied in this paper (see below, p. 60).

For the moment, all that can be established on the basis of synapomorphic characters is the sister-group relationship between the two divisions of *Prognathochromis* itself; their affinities with the other haplochromine lineages from Victoria–Edward–Kivu have still to be discovered.

Intralineage relationships remain undetectable at the level of investigation employed so far. Each subgenus has its morphologically outstanding taxa, but the majority differ from one another only in such features as male coloration and certain morphometric characters.

Within the subgenus *Tridontochromis*, however, *Prognathochromis* (*T.*) *melichrous* stands apart because of the greater number of plesiomorph features it displays, and the skull architecture in all species is less derived than in species of the nominate subgenus. The intralineaage dichotomy would seem to have occurred early in the history of the genus.

YSSICHRMIS gen. nov.

TYPE SPECIES: *Haplochromis fusiformis* Greenwood & Gee, 1969. Lake Victoria.

ETYMOLOGY. From the Greek *yssos*, javelin, + *chromis*, alluding to the slender, elongate body form.

DIAGNOSIS. *Shallow bodied, elongate haplochromines (body depth 23–30% SL, modal range 27–29%, caudal peduncle 17–25% of standard length, modal range 19–22%, its depth contained 1.7–2.1 times (modally 1.8–2.0) in its length), reaching a small maximum adult size (85–110 mm SL).*

Neurocranium of the generalized type with a low, wedge-shaped supraoccipital crest. Premaxilla not beaked anteriorly; *edentulous over the posterior* $\frac{1}{4}$ – $\frac{1}{3}$ of its dentigerous arms.

Teeth in the outer premaxillary row compressed and unequally bicuspid, those in the dentary similar but with a few tricuspids posteriorly and laterally; 28–64 teeth (no distinct modal number) in the outer row of the premaxilla.

Lower pharyngeal bone slender and elongate, all its teeth fine and compressed.

Lateral line with 32–37 scales (modal range 33–35); cheek fully scaled, with 3 or 4 (rarely 2) rows.

DESCRIPTION

Habitus (Fig. 13). The body is shallow and elongate, the head profile in lateral view moderately acute. Maximum adult size recorded for each of the three constituent species is 110 mm, 93 mm and 85 mm SL respectively.

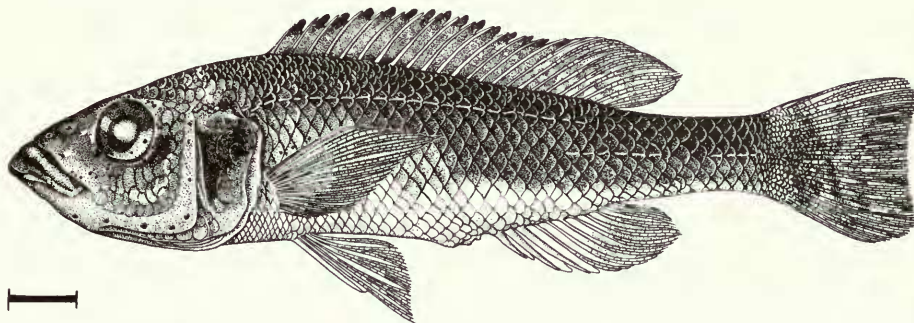


Fig. 13 *Yssichromis fusiformis*. Lake Victoria. Scale = 1 cm.

Superficially, members of this genus resemble those of the *Prognathochromis* lineage, especially members of the subgenus *Tridontochromis*. However, *Yssichromis* species retain several generalized features in the syncranium (see below), and the lower jaw length is shorter, although some overlap does occur (*viz* 35.7–43.8% head length, modal range 40–42% cf. 41–62%, modal range 45–53%).

Neurocranium. Neurocranial architecture in this genus is basically of the generalised type (see fig. 18 in Greenwood & Gee, 1969). In one species (*Y. pappenheimi*), however, the preorbital and orbital depths, and the maximum otic width, are reduced and approach the condition found in *Prognathochromis* (which skull-type that of *Y. pappenheimi* also resembles in having a straight rather than a gently curved preorbital skull profile).

The supraoccipital crest in all species is relatively low and wedge-shaped in profile, but it is not as low as that in *Prognathochromis*.

Upper jaw. The premaxilla is not produced anteriorly into a definite beak. Posteriorly over about its last $\frac{1}{4}$ – $\frac{1}{3}$ each horizontal dentigerous arm is edentulous in all known specimens of *Y. pappenheimi*, and, apart from the rare exception, is edentulous in the other two species as well.

Lower jaw. The mouth is slightly to moderately oblique (20°–35°), with the tip of the lower jaw not, or but marginally projecting beyond the upper jaw.

The dentary departs but little from the generalized type (and is thus relatively deeper than in *Tridontochromis* species). It does, however, have a well-defined upward and outward flare

to the lateral walls when viewed frontally, and in this feature closely approximates to the dentary in *Tridontochromis*. Two of the three species (*Y. pappenheimi* is the exception) have a poorly defined mental protuberance at the symphysis, which is visible in skeletal material but barely detectable in whole fishes.

Dentition. Most outer row teeth in both jaws are compressed and unequally bicuspid; posteriorly in the lower jaw there are often some tricuspid teeth, and tricuspid or unicuspid are sometimes present posteriorly in the upper jaw. Posterior teeth in both jaws are either smaller than those situated anteriorly or may be of approximately the same size, even when unicuspid. (The generalized condition, as seen for example in *Astatotilapia* and some other genera, is for the posterior few teeth to be enlarged.)

Teeth forming the inner row or rows are tricuspid and small.

Lower pharyngeal bone and teeth. The bone is narrow and slender, its dentigerous surface slightly broader than it is long. Two species (*Y. pappenheimi* and *Y. fusiformis*) have the transverse posterior margin of the bone deeply indented so that it is acutely 'V' shaped rather than broadly 'V' shaped (the usual condition in all genera except those with hypertrophied pharyngeal bones, and in the third *Yssichromis* species, *Y. laparogramma*).

All lower pharyngeal teeth are fine, laterally compressed, and weakly cuspidate.

Contained species

Yssichromis fusiformis (Greenwood & Gee), 1969. Lake Victoria; see Greenwood & Gee (1969 : 32–34).

Yssichromis laparogramma (Greenwood & Gee), 1969. Lake Victoria; see Greenwood & Gee (1969 : 28–32).

Yssichromis pappenheimi (Blgr.), 1914. Lakes Edward and George; see Greenwood (1973 : 199–204).

DISCUSSION

Although superficially resembling certain species of *Prognathochromis*, *Yssichromis* cannot be considered a member of that lineage because it does not share with it any derived features in skull architecture or lower jaw proportions.

Yssichromis is an isolated lineage defined by its autapomorphic features (shallow, elongate body, and posteriorly edentulous premaxilla), but otherwise is of a generalized type.

Within the genus, *Y. pappenheimi* from Lakes Edward and George is apparently the most derived species, judging from its skull shape, and *Y. laparogramma* (Lake Victoria) the most plesiomorphic one; *Y. fusiformis*, also from Lake Victoria, occupies an intermediate position in this morphocline.

PYXICHROMIS gen. nov.

TYPE SPECIES: *Haplochromis parorhostoma* Greenwood, 1967. Lake Victoria.

ETYMOLOGY. From the Greek *pyx* (later form of *pyge*), the rump, an allusion to the rump-like protuberance of the nuchal musculature, and, punningly, to the gnome-like physiognomy of the known species.

DIAGNOSIS. Small relatively deep-bodied and compressed haplochromines (body depth 35–42% SL; maximum adult size 117 mm SL), with a very oblique lower jaw (sloping upwards at 50°–70° to the horizontal), a sharply concave dorsal head profile, and the dorsal surface of the snout virtually horizontal. The very characteristic profile of these fishes is contributed to by the bulging anterior portion of the cephalic epaxial musculature (see Fig. 14).

The anatomy of the upper jaw is distinctive (see p. 25).

DESCRIPTION

Habitus (Fig. 14). The external features of *Pyxichromis* are highly characteristic. Considering the small adult size attained, the eye diameter (22–28% head length) is small, especially in comparison with that of certain piscivorous groups (eg *Prognathochromis*

(*Tridontochromis*) species) and in *Astatotilapia* and *Haplochromis*; in contrast, the cheek depth in *Pyxichromis* (24–32% head length) is greater.

Members of the genus are sexually mature at a standard length of *ca* 70 mm, and are not known to exceed a length of 117 mm.

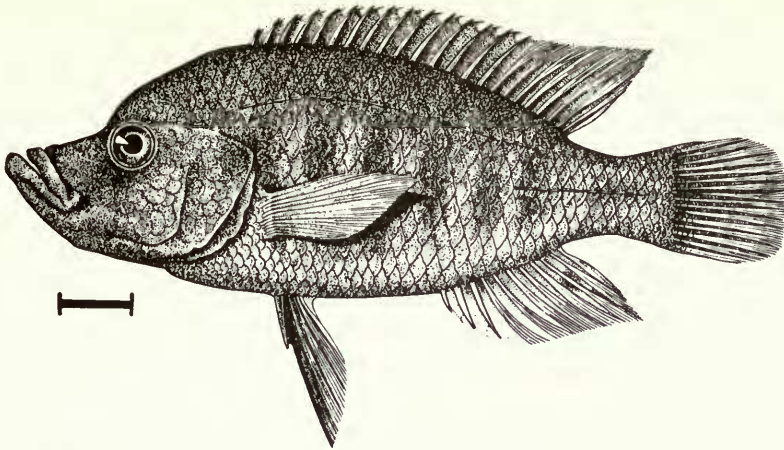


Fig. 14 *Pyxichromis parorthostoma*. Lake Victoria. Scale = 1 cm.

Anatomy. Unfortunately, very few *Pyxichromis* specimens are available and consequently knowledge of its anatomy and osteology is confined to information gleaned from partial dissections and from radiographs.

Neurocranium. Skull form is essentially of the *Astatotilapia* type except that the supra-occipital crest is relatively more expansive, a probable correlate of the somewhat hypertrophied nuchal muscle mass.

Upper jaw. An unusual feature of *Pyxichromis* is the near-horizontal alignment of the dorsal snout surface. Amongst other members of the Victoria–Edward–Kivu haplochromine complex the snout profile slopes downwards and forwards, albeit at various angles, but it is never horizontal. The angle at which the snout descends in these other species virtually parallels the slope of the underlying ethmovomerine region of the skull.

In *Pyxichromis* the ethmovomerine region slopes at almost the same angle as it does in the skulls of *Harpagochromis* and *Prognathochromis* species. That the upper snout profile is, nevertheless, horizontal in *Pyxichromis* can be explained by the hypertrophy of certain articulatory menisci and other surfaces associated with the maxillae and premaxillae.

For example, the median rostral cartilage is much deeper than it is in other taxa, and its ventral face (which is apposed to the sloping ethmovomer) is angled so that its dorsal surface (in contact with the premaxillary process) lies horizontally, not sloping forward and downward as it would otherwise do if the anterior part of the cartilage were not deeper than the posterior part. The premaxillary processes are thus elevated above the ethmovomerine surface and, since the upper surface of the cartilage is almost horizontal, held horizontally as well.

As a result of this arrangement there is a considerable gap anteriorly between the processes and the rostral part of the dorsal ethmoid surface. The premaxillary processes are supported in this region by an hypertrophy of the membrane and cartilage cushion surrounding the condyle of the medially directed posterior process on the maxillary head (the neurocranial process of Barel *et al.*, 1976). More support is derived from the enlarged cushion of tissue capping the anteroventral process of the maxilla (Barel *et al.*'s 'premaxilliad wing').

Thus, when the mouth is closed, the premaxilla is supported, and held away from the ethmovomer, by enlarged articulatory points at three places: posteriorly by the rostral cartilage, near its midpoint by the neurocranial process, and anteriorly (where the ascending

processes join the body of the bone) by a pad of tissue on the premaxilliad wing of the maxilla.

The alignment and relative enlargement of these three surfaces is such that the premaxillary processes lie almost horizontally, despite the forward and downward slope of the ethmoid and vomer against which two of them articulate.

Lower jaw. As far as I can determine from limited dissections and from radiographs, the lower jaw is not unusual (although I suspect that there are some specialized features in the anguloarticular-quadrato joint). When compared with similar-sized specimens of species belonging to the non-piscivorous lineages (especially *Astatotilapia*), the lower jaw in *Pyxichromis* is somewhat longer (48–57% head length). This is a derived feature shared with both *Harpagochromis* and *Prognathochromis* (see pp. 10 & 16). The jaw is narrow (its maximum width contained more than twice in the length), a correlate of the generally compressed body-form.

Dentition. In fishes > 70 mm SL, the outer teeth are mostly slender and unicuspid, but there are interspecific differences in tooth shape and orientation. Only one smaller fish is known (a 67.5 mm SL specimen of *P. orthostoma*); anteriorly and anterolaterally in the upper jaw its outer teeth are bicuspid (as they are throughout the lower jaw) but are short and tricuspid laterally and posterolaterally. With only one small specimen known, the significance of these tricuspid outer teeth cannot be evaluated.

Lower pharyngeal bone and teeth. These are virtually identical with those of *Harpagochromis* and *Prognathochromis* (see p. 18).

Caudal fin. One species (*P. orthostoma*, Lake Kioga system) has a truncate fin, the other species (*P. parorthostoma*; Lake Victoria) has the fin strongly subtruncate, almost rounded.

Contained species

Pyxichromis orthostoma (Regan), 1922. Lake Salisbury, Kioga system; see Greenwood (1967 : 100–2).

Pyxichromis parorthostoma (Greenwood), 1967. Lake Victoria; see Greenwood (1967 : 103–5).

DISCUSSION

Because of its peculiar autapomorphic features, and within the limits imposed by inadequate anatomical and osteological data, it is particularly difficult to assess the affinities of *Pyxichromis*.

Its high relative jaw length, especially in a species with a small maximum adult size, suggests a possible relationship with *Harpagochromis* and *Prognathochromis*. As far as can be told, neurocranial form in *Pyxichromis* is of the near-generalized type and like that found in *Harpagochromis* (see p. 11). Except for the narrow otic region, the neurocranium shows none of the derived features characterizing the skull of *Prognathochromis* (ie low preorbital skull depth, low orbital depth, and a relatively shallow, gently sloping supraoccipital crest).

Pyxichromis does, however, share with *Prognathochromis* the derived features of a unicuspid dentition in small individuals, the presence of some tricuspid outer teeth laterally in the jaw (at least in one specimen, the smallest known) and, of course, a relatively, long lower jaw.

LIPOCHROMIS Regan, 1920

TYPE SPECIES: *Paratilapia obesus* Boulenger, 1906. Lake Victoria; for details of synonymy etc, see Greenwood (1959b : 182–3).

DIAGNOSIS. Haplochromine fishes with an adult size range of 130–170 mm SL, and a varied body form (see Figs 15A & B). All are characterized by having a thick-lipped, *widely distensible and protractile mouth, and small teeth deeply embedded in the oral mucosa (often invisible without dissection)*.

The nominate subgenus is characterized by many of its outer row jaw teeth having the crowns reflected labially (not buccally as is usual), and by its broadly rounded lower jaw. The

other subgenus is recognizable by its peculiarly boat-shaped lower jaw which narrows abruptly over about its anterior third so that this part of the jaw closes within the upper jaw; no outer row jaw teeth have their crowns curved labially, and are either erect or recurved.

The neurocranium is essentially of the generalized type, but does have a relatively tall and expansive supraoccipital crest which is near-pyramidal in lateral outline.

DESCRIPTION

Habitus (Fig. 15). Body form is variable, especially with regard to the head and snout profiles; these range from heavy and blunt ('pug-headed'), to slender and subacute (see Figs 15A & B respectively). Body depth ranges from 27–47% of standard length, with some species (as currently defined) showing considerable intraspecific variation (eg 33–47% in *L. obesus*, and 32–43% in *L. maxillaris*). In general, deep-bodied species are pug-headed, and slender bodied ones have a more refined profile.

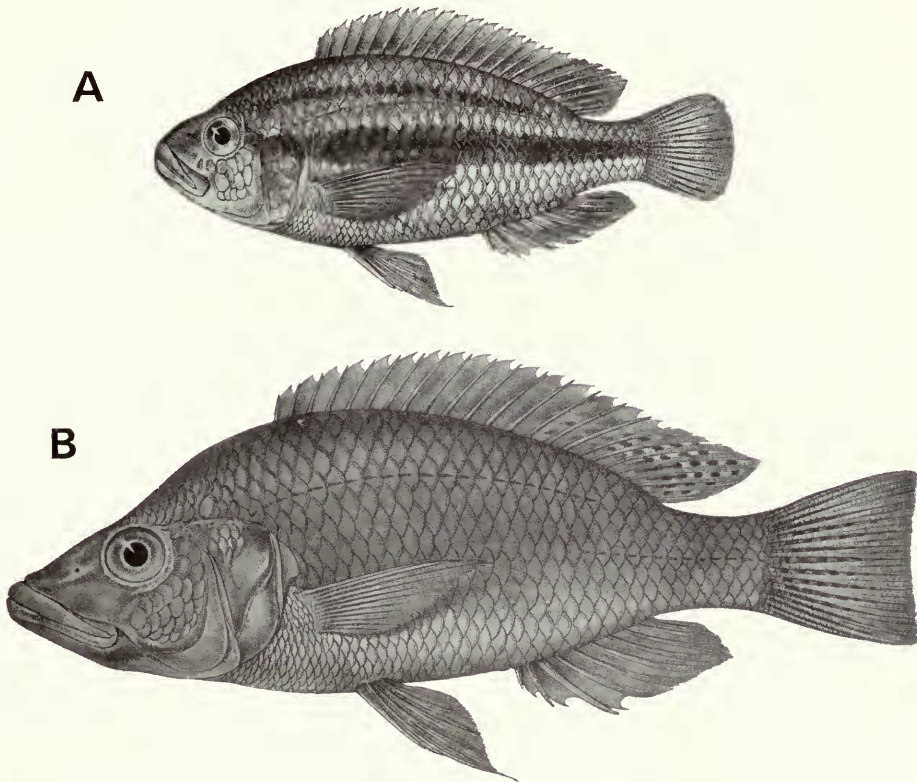


Fig. 15 A. *Lipochromis (Lipochromis) obesus*. Lake Victoria. About two-thirds natural size. B. *Lipochromis (Cleptochromis) parvidens*. Lake Victoria. About two-thirds natural size.

Maximum adult size ranges from 130–170 mm SL, with sexual maturity reached at between 85 and 105 mm SL depending on the maximum adult size for a particular species.

Neurocranium. Basically, the skull is of the near-generalized type found in species of the *Harpagochromis* group (see p. 11) but it retains the deeper otic region of the more generalized skull (see Greenwood, 1974 : fig. 45, excluding skull of *H. barbarae*).

As in *Harpagochromis*, the supraoccipital crest in *Lipochromis* species is high, with a near-pyramidal profile, but it is more expansive than in the majority of *Harpagochromis* species.

Greatest departure from the modal *Lipochromis* skull type is seen in *L. obesus*, where the orbital depth is greater and consequently the preorbital skull profile slopes at a greater angle.

Dentition. All jaw teeth are deeply embedded in the thickened oral mucosa so that, at most, only the crowns of the teeth are visible; often the inner rows are completely buried.

Two distinct forms of outer teeth are present. In one, the tip of the crown is inclined anteriorly or laterally (see below) whilst in the other it is either vertical or fairly strongly recurved (*ie* directed buccally; see below p. 31).

Most outer row teeth in fishes between 70 and 100 mm SL are weakly bicuspid (with, in certain species, some unicuspid and weakly bicuspid also present); above that size the majority of teeth are unicuspid, although in one species (*L. taurinus*) bicuspid predominate even in the largest individuals (see Greenwood, 1973 : 194).

The inner rows, usually 1 or 2, are composed of tricuspid teeth (with a few unicuspid) in fishes <80–100 mm SL, and predominantly of unicuspid in larger individuals.

Compared with the teeth in equal-sized specimens from other lineages, those of *Lipochromis* are shorter (as little as half the height of teeth in members of the piscivorous lineages *Harpagochromis* and *Prognathochromis*); teeth in *Lipochromis* are also often finer (although in some species they are stouter) than in species of the latter genera.

Modally, the total number of teeth in the outer row of the premaxilla is less than in comparable-sized specimens of *Harpagochromis* and *Prognathochromis*, the number ranging from 30–62, but generally about 40. A comparable reduction in the number of outer teeth in the dentary is also noted in *Lipochromis*.

Most individuals in certain species have almost the posterior third of the premaxilla devoid of teeth; when premaxillary teeth are present posteriorly in these taxa, they are widely spaced, as they are in those species with a completely toothed premaxilla.

Lip tissue is well-developed in all species, and the inner aspect of the upper lip is so arranged that it generally covers, or partly covers, the tips of the outer teeth in the upper jaw.

Mouth. The mouth is a very distinctive feature in all *Lipochromis* species, in particular the wide lateral gape of the upper jaw in a fully-opened mouth; in one subgenus this distensibility of the upper jaw is combined with a marked protrusibility.

In all species the lips are thickened, but the bullate posterior end of the maxilla is obvious, even when the mouth is closed.

The orientation of the mouth is slightly oblique in most species, more obviously so in one (*L. microdon*). The lower jaw may project a little way beyond the upper jaw, particularly in those species with an acute head profile.

Relative lower jaw length in *Lipochromis* (38–56% of head length, modal range 42–48%) overlaps that in *Harpagochromis* and *Prognathochromis*, but modally it is shorter. Similarly, its length range overlaps that of most other lineages but in these instances the mode for *Lipochromis* is somewhat higher.

Upper jaw. Posteriorly the maxilla is markedly bullate, its lateral face convex and the inner face concave. The ventral margin over the entire bone, except in the bullate region, is distinctly thickened. Some variation exists in the degree to which the anterior half of the bone is incurved relative to the posterior portion; in most species the curvature is very noticeable, especially so in members of the nominate subgenus (see below, p. 30).

A prominent feature of the premaxilla is the stoutness of its dentigerous arms, which are almost cylindrical in cross-section over the greater part of their lengths. The ascending processes are either as long as the dentigerous arms or are distinctly shorter, a feature positively correlated with the degree of mouth protrusibility.

Lower jaw. The dentary is bullate in the region surrounding its bifurcation into ascending (coronoid) and horizontal arms. This horizontally directed, dorsoventrally compressed swelling is produced forward for almost half the anterior length of each ramus as a thick, shelf-like lateral projection.

The tip of the ascending process has a definite, but interspecifically variable, deflection laterally. A similar deflection occurs in *Prognathochromis*, particularly in members of its nominate subgenus, but in no species is it so noticeable as it is in most *Lipochromis* species. The insertion for the mandibulo-interopercular ligament is prominent and well-developed (to a level comparable with that in *Prognathochromis* (*Prognathochromis*) species).

Two extreme forms of lower jaw morphology are found amongst *Lipochromis* species (see Fig. 16). In one (the *obesus* type) the anterior margin of the jaw is broadly rounded (most clearly so in *L. obesus*); when viewed from below, the alveolar surface appears as a broad shelf projecting above and beyond the ventral half of each ramus, the lateral wall of which is sharply angled towards the midline.

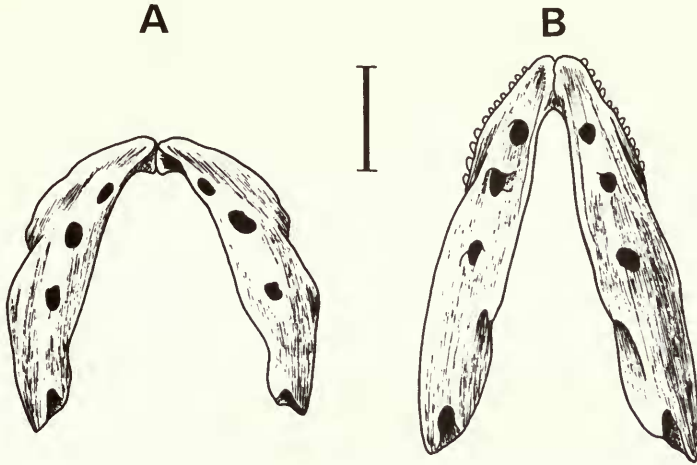


Fig. 16 Dentary in ventral view, of: A. *Lipochromis* (*L.*) *obesus*, and B. *Lipochromis* (*C.*) *parvidens*. Scale = 5 mm.

In the second, or *parvidens* type, the entire forward portion of the lower jaw anterior to the dentary bifurcation narrows rapidly; the alveolar 'shelf' is thus much less obvious and the anterior jaw outline is more acute (Fig. 16B). Also, since the ventral half of each ramus is, as it were, pinched medially, this anterior narrowing is emphasized and the ventral contours of the rami are rounded. In section, the jaw is rather boat-shaped, especially when viewed from in front. (In nautical terms, the shape is like that of a pram seen bow-on.)

Although the extreme conditions, as represented by *L. obesus* and *L. parvidens*, are very distinctive, some species have a jaw shape that almost bridges this morphological gap (see, for example, the lower jaws in *L. maxillaris* and *L. cryptodon*; Greenwood, 1959 : 189, 192 & 198–200).

Lower pharyngeal bone and dentition. The bone is broad and short, its dentigerous surface triangular and as broad as, or more often, broader than it is long. The teeth are fine and weakly bicuspid, with only those of the posterior transverse row, and some posteriorly in the two median rows, coarser than the others.

Taking into account the differences in dentition and in jaw morphology, it would seem that intragroup relationships of *Lipochromis* are best expressed by recognizing two subgenera. This action reflects and corrects an earlier view (Greenwood, 1974) that the paedophage trophic radiation (here represented by the genus *Lipochromis*) was of diphyletic origin. Further consideration of that idea has led me to give greater phylogenetic emphasis than before to the derived features shared by all *Lipochromis* species (*viz* buried teeth reduced in size and number, coupled with great distensibility and protrusibility of the upper jaw), and to the lack of characters suggesting an alternate relationship for any or all of the species involved. Hence, the recognition of one lineage comprising two subdivisions.

Subgenus *LIPOCHROMIS* Regan, 1920

TYPE SPECIES: *Pelmatochromis obesus* Blgr., 1906 (see Greenwood, 1959b : 182–8).

Members of this subgenus are characterized by the presence, in the outer tooth row, of stout uni- or bicuspid teeth whose crowns are inclined labially (*ie* anteriorly or laterally depending

on their position in the jaw). Such teeth (Fig. 17) usually are the predominant type in the lower jaw; if present in the upper jaw they are intercalated amongst the more numerous recurved (*ie* buccally directed) or erect and conical teeth. Bicuspid teeth are the commonest type in fishes < 100 mm SL, but in one species (*L. taurinus* from Lakes Edward and George) most teeth are bicuspid even in specimens 140 mm long. Compared with the teeth in members of the other subgenus, those in *Lipochromis* are stouter and shorter.

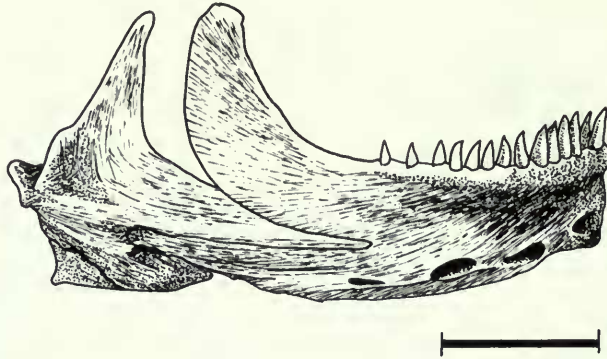


Fig. 17 Dentary (right) of *Lipochromis (L.) obesus* to show labial curvature of certain outer row teeth. Scale = 5 mm.

The lower jaw, save in one species, is of the *obesus* type (see above, and Fig. 16A), although in the majority of species it is not as broad anteriorly as it is in *L. (L.) obesus* itself. With the same exceptional species, the lower jaw does not close within the upper. The exception, *L. (L.) melanopterus*, was known only from the holotype; however, material collected recently in Lake Victoria indicates that it is not, as once was thought, an aberrant specimen (see Greenwood, 1959*b* : 192–4). As far as could be determined from superficial examination, radiographs and limited dissection on the holotype, the dentary in *L. (L.) melanopterus* is essentially of the *parvidens* type (see above p. 29) a conclusion confirmed from the examination of new material. In its dentition, head shape and oral features, however, *L. (L.) melanopterus* is typically a member of the nominate subgenus.

Regan's (1920) original description of *Lipochromis* (based solely on the species *obesus*) gave as the only diagnostic feature '... Lower jaw shutting within the upper'. The type specimen of *Pelmatochromis obesus*, the only specimen available at that time, is very atypical and also rather poorly preserved. Certainly the lower jaw does seem to shut within the upper, but in my view this is more likely to be a preservation artefact than the natural condition (see also Greenwood, 1959*b* : 183). In none of the 47 other specimens on which my redescription of the species was based does the lower jaw fail to occlude with the upper.

Species of *Lipochromis (Lipochromis)* have a 'pug-headed' morphotype unlike the more elegant head form in all known species of the second subgenus.

The mouth is moderately protractile but is markedly distensible laterally. The pre-maxillary ascending processes are much shorter than the dentigerous arms of the bone (even in *L. (L.) melanopterus*), hence, presumably, the comparatively restricted protusibility of the upper jaw.

Contained species

The taxa are listed in order of their apparently increasing level of derivation.

Lipochromis (Lipochromis) taurinus (Trewavas), 1933. Lakes Edward and George; see Greenwood (1973 : 192–6).

Lipochromis (L.) maxillaris (Trewavas), 1928. Lake Victoria; see Greenwood (1959*b* : 189–192).

Lipochromis (*L.*) *obesus* (Blgr.), 1906. Lakes Victoria and Kwania (Uganda); see Greenwood (1959b : 182–8).

Lipochromis (*L.*) *melanopterus* (Trewavas), 1928. Lake Victoria; see Greenwood (1959b : 192–4).

Subgenus *CLEPTOCHROMIS* nov.

TYPE SPECIES: *Paratilapia parvidens* Blgr., 1911. Lake Victoria (see Greenwood, 1959b : 194–8).

ETYMOLOGY. From the Greek *kleptes*, a thief, + *chromis*, with reference to the paedophagous habits of its member species.

Species of this subgenus are characterized by the unusual form of the dentary, and by the outer row of jaw teeth being mainly slender, recurved, often strongly recurved unicuspid in specimens over *ca* 100 mm SL, and weakly recurved bicuspid in smaller fishes; in no species are there any teeth with anteriorly or laterally directed crowns (cf. subgenus *Lipochromis*).

The lower jaw, at least anteriorly, closes within the upper, and has a boat-shaped dentary of the 'parvidens' type (see above p. 29 and Fig. 16B). The mouth is both markedly distensible and protractile.

In all known species the ascending premaxillary processes are as long as, or longer than the dentigerous arms of that bone.

Contained species

The taxa are arranged in their apparently increasing order of derivation.

Lipochromis (*Cleptochromis*) *cryptodon* (Greenwood), 1959. Lake Victoria; see Greenwood (1959b : 198–200).

Lipochromis (*C.*) *microdon* (Blgr.), 1906. Lake Victoria; see Greenwood (1959b : 200–3).

Lipochromis (*C.*) *parvidens* (Blgr.), 1911. Lake Victoria; see Greenwood (1959b : 194–8).

DISCUSSION

The genus *Lipochromis* comprises two groups of embryonic and larval cichlid-eating haplochromines (the paedophages) discussed in Greenwood (1959b & 1974 for the species of Lake Victoria) and 1973 for the Edward–George species. They are now united in a single lineage because of their presumed synapomorphies, namely: jaw teeth deeply embedded in the thickened oral mucosa, the teeth reduced in size (relative to those in comparable sized specimens from other lineages) and often absent from the posterior part of the premaxilla, the mouth widely distensible (through a mechanism effecting a marked lateral displacement of the upper jaw moieties when the mouth is opened), a highly protrusible premaxilla, the pronounced bullation of the posterior maxillary arm, and the thickened ventral margin of the maxilla.

There are two other derived characters shared by all members of this lineage: the premaxillary dentigerous arms are inflated, and the dentary is greatly swollen posteriorly in the region of its bifurcation into ascending and horizontal arms. However, there is evidence indicating that these features could be the result of convergent trends associated with the evolution of a jaw that is much involved in the handling of prey objects. Probably in the case of *Lipochromis* those jaw features are truly synapomorphic, but since the possibility of their convergent evolution in other genera exists, they are unreliable indicators of any relationship between *Lipochromis* and lineages showing the same features (see discussions on pp. 52, 71 & 75).

Previously (Greenwood, 1974) I postulated a diphyletic origin for the paedophage trophic radiation. Some of the cranial characters on which that argument was based are now seen to be plesiomorphous, and the dental features used are probably associated with the large adult size attained by the paedophage species. Thus, there seem to be no adequate grounds for suggesting that *Lipochromis* might share a recent common ancestry with *Harpagochromis* and *Prognathochromis* (the lineages in which most of the species linked with the paedophages in my earlier analysis are now placed; see Greenwood, 1974, fig. 70 and discussions in

the text). Indeed, I can find no unequivocally apomorph features that would allow one reasonably to identify the sister group of *Lipochromis*.

Two paedophage (or partly paedophagous) species, '*H*' *cronus* and '*H*' *barbarae* were formerly associated with, respectively, the '*obesus*' and '*parvidens*' lineages recognized by Greenwood (1974). Since neither of these species has any of the synapomorphic features characterizing *Lipochromis*, neither is currently included in *Lipochromis* (see p. 8 and p. 88 for '*barbarae*' and '*cronus*' respectively; also Barel, Witte & van Oijen (1976) for a comparative anatomical study of the palate in '*H*' *barbarae* and various *Lipochromis* species).

Within the *Lipochromis* lineage it is only possible to note that, for the species so far described, *L. (L.) taurinus* from Lake Edward and George has the least derived dental morphology for taxa in its subgenus, and that *L. (C.) parvidens* shows the greatest jaw distensibility and tooth reduction amongst members of its subgenus.

When the several species recently collected in Lake Victoria are studied further it may be possible to produce a more satisfactory indication of intral lineage relationships (personal observations based on material collected by the Leiden University research team).

GAUROCHROMIS gen. nov.

TYPE SPECIES: *Haplochromis empodisma* Greenwood, 1960. Lake Victoria.

ETYMOLOGY. From the Greek '*gauros*', haughty + *chromis*, alluding to the physiognomy in at least four of the member species.

DIAGNOSIS. Deep to relatively deep-bodied haplochromines (body depth 30–44% SL, modal range 38–39%), with a straight or slightly concave but steeply sloping dorsal head profile interrupted by the prominent ascending process of the premaxilla. Mouth horizontal or slightly oblique, lips not thickened, and the teeth small, fine and numerous but rarely contiguous.

Premaxilla with compressed (*ie* not inflated) dentigerous arms that are longer than the ascending processes, and which are not produced anteriorly into a beak or shelf.

Outer teeth in both jaws (particularly when compared with those in Labrochromis and Astatotilapia) finer, more compressed, shorter and closer set, with 44–82 (modal range 60–70) in the premaxillary outer row. Fishes <90 mm SL have unequally bicuspid teeth (the major cusp acutely pointed but sometimes obscured by a dark brown accretion), *the crown barely broader than the neck.* Larger fishes have a mixed dentition of weakly bicuspid and unicuspid teeth, the latter predominating in the largest specimens. An exclusively unicuspid outer dentition has never been recorded.

Inner row teeth small, generally tricuspid, and arranged in 1 or 2 (less frequently 3) rows anteriorly and laterally in both jaws; separated from the outer row by a distinct space.

Two kinds of lower pharyngeal bone occur. One is slender, narrow and relatively elongate, with all or the majority of its teeth fine and compressed. A few teeth in the two median rows may be coarser than the others, but none is molariform or submolariform.

The second type of lower pharyngeal bone is distinctly hypertrophied and stout, and has thick, short, articular horns. The two median tooth rows are composed of enlarged and molariform teeth, and usually there are several other rows containing enlarged and submolariform (or even molariform) teeth. Fine, compressed and distinctly unicuspid teeth are virtually confined to the posterolateral angles of the dentigerous surface.

DESCRIPTION

Habitus (Fig. 18). Although not particularly deep-bodied (depth 30–44% SL, modal range 38–39%) the total impression gained from a specimen of *Gaurochromis* is one of a deep-bodied fish. The premaxillary ascending processes are prominent and break the outline of steeply sloping dorsal head profile, giving the fish a distinctive 'Roman nose'. The lips are not thickened, and the mouth is horizontal or slightly oblique.

The maximum adult size range is 90–117 mm SL.

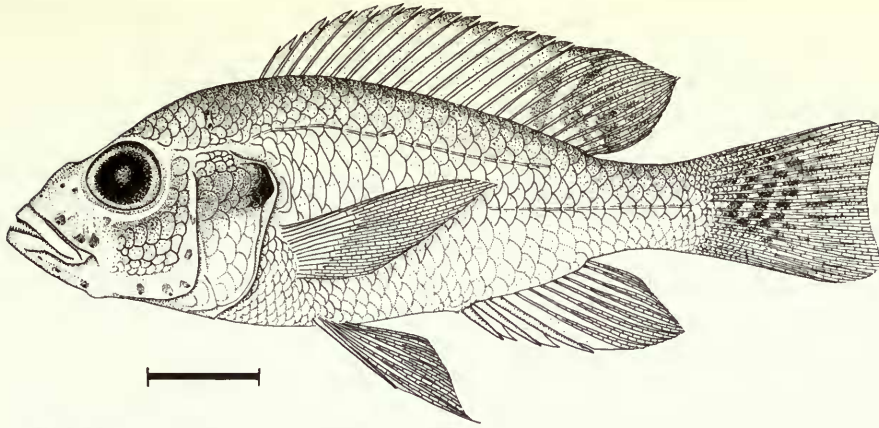


Fig. 18 *Gaurochromis (Gaurochromis) angustifrons*. Lake George. Scale = 1 cm.

Neurocranium Skull architecture is of the generalized type, with a straight and moderately sloping dorsal profile; preorbital depth ranges from 19–27% neurocranial length (being lowest in *G. angustifrons* from Lakes Edward and George), the mode lying in the lower part of the range for taxa with a generalized skull type. The height of the supraoccipital crest varies from low to relatively low, the bone being wedge-shaped in lateral profile.

In some species the neurocranial apophysis for the upper pharyngeal bones is hypertrophied (see p. 36).

Dentition. Teeth in both jaws are fine, slender and compressed. Those in the outer row are slightly recurved and, especially in the anteroposterior dimensions of the crown, noticeably finer than the teeth in similar-sized specimens from other taxa; in general these teeth are also shorter.

Most outer teeth in fishes <90 mm SL have the generalized type of unequally bicuspid crown which is marginally broader than its subcylindrical neck; the major cusp is acutely pointed. Some slender, compressed unicuspid teeth may be present in fishes less than 90 mm long, and weakly bicuspid teeth may also occur. The latter are the predominant teeth in larger fishes. An entirely or even a mainly unicuspid outer dentition has not been recorded in large individuals (*ie* >100 mm SL) of any *Gaurochromis* species (see Greenwood, 1960 : 264; 1965 : 326; 1973 : 180).

The outer teeth are close-set but rarely contiguous, with 44–82 (modal range 60–70) in the premaxilla. Although the range overlaps that of *Astatotilapia*, *viz* 34–74 (and thus the presumed primitive numbers), the modal range is higher in *Gaurochromis* (60–70 *cf.* 48–54).

Inner row teeth are small and usually tricuspid, but some weakly tricuspid and even unicuspid teeth may be present in fishes > 100 mm SL. The teeth in both jaws are arranged in 1 or 2 (less commonly 3) rows anteriorly and anterolaterally, and a single row posteriorly.

Upper jaw. The maxilla is slender and elongate, its articular head with a fairly marked medial curvature relative to the shaft of the bone.

The dentigerous arms of the premaxilla are compressed, and are longer than the ascending processes. Anteriorly, the bone is not produced into a shelf or beak.

Lower jaw. In two species (*G. empodisma* and *G. simpsoni*) the dentary is slender and relatively shallow, its alveolar surface produced laterally into a narrow but distinct shelf; in the third species (*G. angustifrons*), the shelf is less obvious but is nevertheless clearly defined, more so than in the generalized condition.

The lower jaw length is 38–49% head (modal range 41–44%) thus overlapping the range in the generalized taxon *Astatotilapia* and in other but trophically specialized non-piscivorous lineages; however, the upper part of its range exceeds that in those taxa, and the modal range is also higher.

Lower pharyngeal bone. Two distinct types of lower pharyngeal bone (with correlated differences in the upper bones) occur in *Gaurochromis*.

In one type (Fig. 19) the bone is slender and narrow, with a long anterior shaft and fine, elongate articular horns. Its dentigerous area is attenuated, the lateral margins narrowing rapidly to produce an outline which is nearer that of an isosceles than an equilateral triangle. This overall attenuation is seen most clearly when the bone is superimposed onto one from a similar-sized specimen of some other lineage, for example, any species of *Astatotilapia*.

There is some intrageneric variation in the degree of attenuation, with the bone in *G. angustifrons* being the narrowest and most attenuated (see Greenwood, 1973 : fig. 19).

The lower pharyngeal teeth are fine, slender, and compressed, with weakly cuspidate and not greatly protracted crowns; even those teeth forming the posterior transverse row are strongly compressed so that they do not appear to be relatively enlarged (as is the case in most other lineages). Teeth forming the median rows are sometimes slightly coarser than their lateral counterparts, but none can be described as enlarged.

Except in the posterolateral angles of the bone, the teeth are not densely arranged; consequently the occlusal surface does not have the appearance of a fine dental felt.

The other type of lower pharyngeal bone (and dentition) differs markedly from the slender, attenuate bone described above (Fig. 20). It is moderately hypertrophied and stout (almost massive in some specimens), thus in many respects resembling the type of bone found in the genus *Labrochromis* (see p. 40).

At least the two median rows (and often the two rows lateral to them as well) are composed of enlarged and molariform teeth. In *Gaurochromis obtusidens* nearly all the other teeth are somewhat enlarged, with molariform or submolariform crowns, only those in the posterolateral angles of the bone being distinctly finer and cuspidate.

There appears to be a related species (currently undescribed) in which the bone is less massive and has fewer enlarged and molariform teeth outside the median series.

Neither *Gaurochromis obtusidens*, nor the undescribed species have the entire bone or its dentigerous surface so characteristically attenuated as it is in the other species. Yet, when compared with *Labrochromis*, the bone is narrower relative to its length (Fig. 21) and the dentigerous area is more nearly isoscelene than equilateral. Also, the articular horns, though stouter than in the other *Gaurochromis*, are neither as short nor as massive as those in *Labrochromis*.

Based on these intralineage differences in pharyngeal bone morphology and dentition, two divisions of *Gaurochromis* are recognised, each characterized by its autapomorphic features.

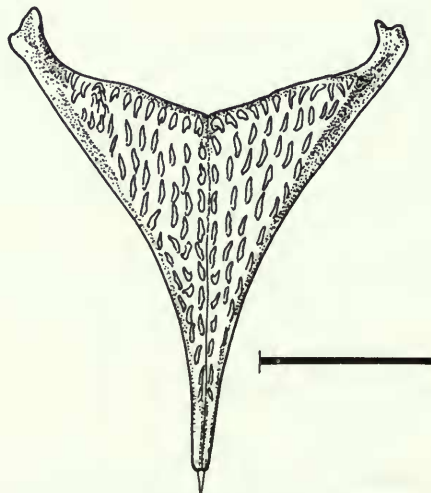


Fig. 19 Lower pharyngeal bone of *Gaurochromis (Gaurochromis) simpsoni*, in occlusal view. Scale = 3 mm.

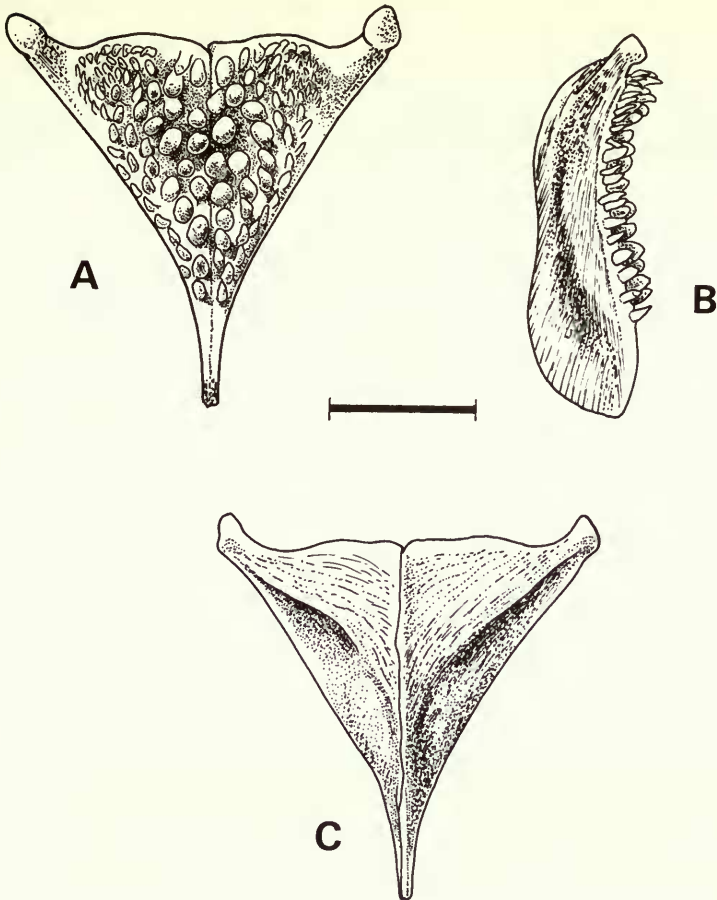


Fig. 20 Lower pharyngeal bone of *Gaurochromis* (*Mylacochromis*) *obtusidens* in: A. Occlusal. B. Right lateral. C. Ventral view. Scale = 5 mm.

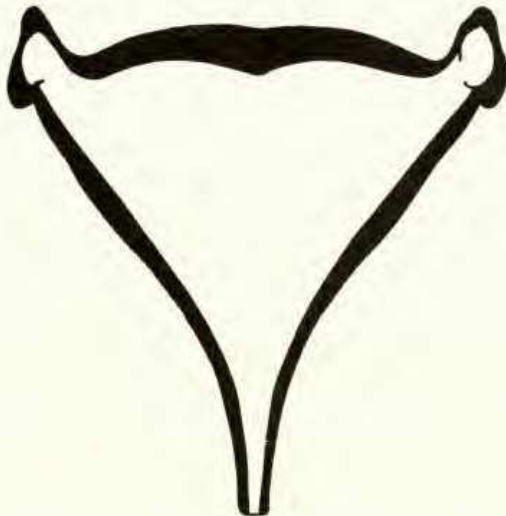


Fig. 21 Outline of lower pharyngeal bone, in occlusal view, of *Gaurochromis* (*Mylacochromis*) *obtusidens* (white) superimposed on that of *Labrochromis ishmaeli* (in black). Both bones are from adult specimens of the same standard length.

Subgenus **GAUROCHROMIS** nov.

TYPE SPECIES: *Haplochromis empodisma* Greenwood, 1960. Lake Victoria.

DIAGNOSIS. *Gaurochromis* species with a slender, attenuated and fine lower pharyngeal bone without molariform lower pharyngeal teeth. The dentigerous area of the bone is narrower than it is long.

Contained species

Gaurochromis (Gaurochromis) empodisma (Greenwood), 1960. Lake Victoria; see Greenwood (1960 : 262–6).

Gaurochromis (G.) simpsoni (Greenwood), 1965. Lake Nabugabo; see Greenwood (1965 : 325–9).

Gaurochromis (G.) angustifrons (Blgr.), 1914. Lakes Edward and George; see Greenwood (1973 : 177–83).

Subgenus **MYLACOCCHROMIS** nov.

TYPE SPECIES: *Haplochromis obtusidens* Trewavas, 1928. Lake Victoria.

ETYMOLOGY. From the Greek *mylakris*, a millstone, + *chromis*, referring to the enlarged pharyngeal jaws and dentition.

DIAGNOSIS. *Gaurochromis* in which the lower pharyngeal bone is enlarged and stout, with at least the two median tooth rows composed of enlarged and molariform teeth; often with many additional teeth enlarged and molariform or submolariform, and others coarse and somewhat enlarged but still cuspidate.

The neurocranial apophysis for the upper pharyngeal bones has an expanded articular surface (both the parasphenoid and the basioccipital facets contributing to this enlargement), and strengthened, bullate lateral walls (especially the prootic component).

Contained species

Gaurochromis (Mylacochromis) obtusidens (Trewavas), 1928. Lake Victoria; see Greenwood (1960 : 266–9).

Research in progress at the University of Leiden, Netherlands, indicates that there is probably a second species of *Mylacochromis* in Lake Victoria (Dr C. D. N. Barel, *pers. comm.* and personal observations).

DISCUSSION

In its overall level of anatomical differentiation (except for its larger adult size), *Gaurochromis* departs but slightly from the generalized condition seen in *Astatotilapia* species. Even in its oral dentition (p. 33) *Gaurochromis* has retained the basic bicuspid tooth form and the basic dental pattern. Its derived dental features involve a reduction in tooth size (the teeth becoming finer, shorter and more slender) combined with an increase in the number of outer row teeth in both jaws.

Departure from the generalized haplochromine condition is also seen in the attenuated and fine lower pharyngeal bone in members of the nominate subgenus (p. 34) and, in the opposite direction, by the still relatively attenuate but greatly enlarged pharyngeal bone and molariform teeth in the subgenus *Mylacochromis* (see above).

For these various reasons I conclude that the species here grouped under the name *Gaurochromis* represent a monophyletic lineage distinct from *Astatotilapia*, with which genus it shares only features plesiomorphic for the Victoria–Edward–Kivu haplochromines in general.

When compared with the pharyngeal mill in *Labrochromis* (p. 40 and Fig. 21), that of *Gaurochromis (Mylacochromis)* species is less robust (particularly so in the undescribed taxon). This difference is apparent in specimens of all sizes, but it is more especially obvious in larger individuals.

Enlargement of the pharyngeal bones and dentition in *Gaurochromis (M.) obtusidens*

prompted an earlier suggestion (Greenwood, 1960 : 265 & 268) of a possible relationship between this species and the genus *Labrochromis* (then known only from two species, *Haplochromis ishmaeli* and *H. pharyngomylus*). In turn, the resemblance between *Gaurochromis* (*M.*) *obtusidens* and *Gaurochromis* (*G.*) *empodisma* was thought to indicate a direct phyletic linkage between *Labrochromis* and the generalized *Astatotilapia* species of the Lake Victoria flock (Greenwood, 1960 : 265 & 268).

Later studies (Greenwood, 1974; and p. 42 below), indicated, however, that *Gaurochromis* (*G.*) *empodisma* and *G. (M.) obtusidens* belong to a distinct lineage and were unlikely to be linked with '*Haplochromis*' *ishmaeli* and '*H.*' *pharyngomylus* through recent common ancestry. This conclusion is apparently corroborated by the peculiar dental features of *Gaurochromis* species belonging to both subdivisions of the genus (see p. 33 above).

These features (and the form of the lower pharyngeal bone in *Gaurochromis* (*Gaurochromis*) species) also negate the idea that '*Haplochromis*' *erythrocephalus* (see p. 46) has a recent shared common ancestry with *Gaurochromis* (*G.*) *empodisma*, and also that '*Haplochromis*' *acidens* could be included, as a sister group, in the same major lineage (see Greenwood, 1974 : fig. 70). Incidentally, '*Haplochromis*' *erythrocephalus* is the '... small undescribed species' that was considered to be the nearest living relative of *G. (G.) empodisma* when that taxon was first described (Greenwood, 1960 : 265).

To summarize, *Gaurochromis* appears to be an independent lineage whose sister-group relationships cannot yet be determined. Its once supposed relationships with *Labrochromis* are no longer supported because the shared specialization, an enlarged pharyngeal mill, is more parsimoniously explained as the result of convergent evolution.

Within the nominate subgenus *Gaurochromis*, *G. (G.) angustifrons*, from Lakes Edward and George, has the most derived pharyngeal bone morphology (see Greenwood, 1973 : fig. 19) and also differs from its congeners, probably in an apomorphic way, in having a marked sexual dimorphism in adult size range, males being much smaller than females (Greenwood, 1973 : 182).

***LABROCHROMIS* Regan, 1920**

TYPE SPECIES: *Haplochromis ishmaeli* Blgr., 1906 (not *Tilapia pallida* Blgr., 1911, as cited by Regan 1920, p. 45, footnote). Lake Victoria.

Regan (1920) apparently defined *Labrochromis* on the basis of a single specimen (BMNH 1911.3.3 : 132), a skeleton prepared from one of the paratypical series of *Tilapia pallida* Blgr., 1911. This specimen and one other paratype were misidentified by Boulenger (see Greenwood, 1960 : 275); both are clearly referable to *Haplochromis ishmaeli* Blgr., 1906, a fact implicitly recognized by Regan in 1922. In that paper Regan remarks apropos of *H. ishmaeli*, '... The remarkable pharyngeal dentition might well be held to justify the genus *Labrochromis* (Regan, 1920) were it not that in all other characters the species is nearly identical with *H. cinereus*' (Regan, 1922 : 170).

Amongst the species synonymized with *H. ishmaeli*, Regan (1922 : 169) includes '... *Tilapia pallida* (part) Blgr., Cat. Afr. Fish. 3 : 231', but does not state specifically whether the skeletal preparation in question was included in that 'part'. However, judging from Regan's (1922) comments on *Labrochromis* quoted above, it seems reasonable to conclude that the skeleton was indeed included in the '*pallida*' material reidentified as '*ishmaeli*'.

The holotype of Boulenger's *Tilapia pallida* represents a quite distinct taxon (see Greenwood, 1960 : 233-6; and p. 43 below), one showing none of the diagnostic features for *Labrochromis* mentioned by Regan, nor any of those to be considered below.

DIAGNOSIS. Haplochromines characterized by a massive hypertrophy of the pharyngeal mill (especially the lower pharyngeal bone and its dentition), and having stout but generalized jaw teeth.

The lower pharyngeal bone is massive, relatively short and broad, the dentigerous surface

concave, and the articular horns short and stout. Its dentition is composed almost entirely of stout molariform teeth; a few smaller submolariform or cuspidate teeth sometimes occur in the posterolateral angles of the dentigerous field, or as the teeth forming the perimeter of that field.

The neurocranium is of the generalized type but has a somewhat more decurved preorbital profile and a relatively higher supraoccipital crest whose outline is nearer pyramidal than wedge-shaped. The apophysis for the upper pharyngeal bones is enlarged and stout, its expansive articular surface almost square in outline. As compared with the generalized type of apophysis, the basioccipital facets make a much larger contribution to the articular area, and the walls of the apophysis (particularly the prootic part) are manifestly strengthened.

Outer jaw teeth, as compared with those in *Gaurochromis*, are coarser and less numerous (30–70, modal range 36–50, in the premaxilla).

Differences in the morphology and number of the jaw teeth, and the presence of a broader, more massive and more extensively molarized pharyngeal mill, are the features most readily distinguishing *Labrochromis* from *Gaurochromis*.

DESCRIPTION

Habitus (Fig. 22). In their overall appearance, members of the genus *Labrochromis* have a typically generalized facies, but most species do have a rather 'heavy headed' appearance.

Maximum adult size ranges from 90–140 mm SL.

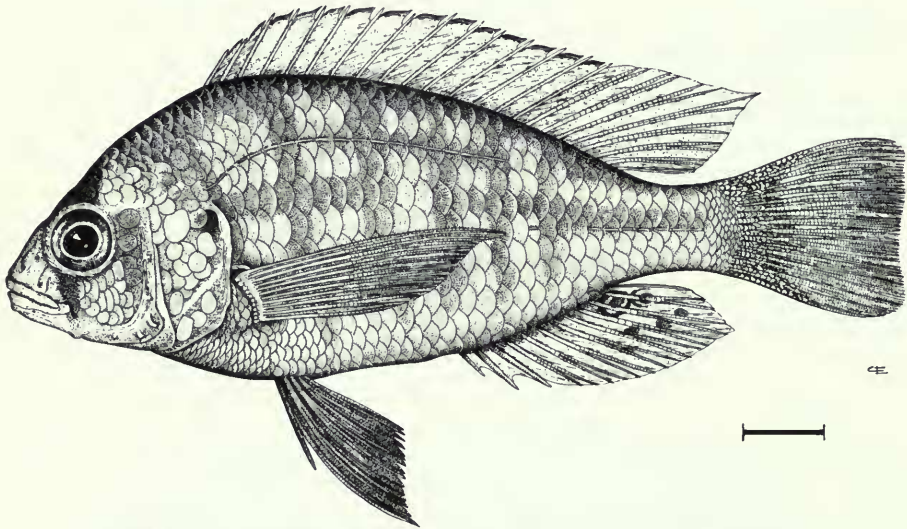


Fig. 22 *Labrochromis teegelaari*. Lake Victoria. Scale = 1 cm.

Neurocranium. The skull departs slightly from the generalized *Astatotilapia* type in having the preorbital profile gently curved (rather than straight), and the supraoccipital crest relatively high and near-pyramidal rather than wedge-shaped in profile. However, in one species (*L. ptistes*), the skull is more like the generalized kind in these features (see Greenwood & Barel, 1978 : fig. 20).

All *Labrochromis* have a stout and well-developed ventral articular apophysis for the upper pharyngeal bones, which exhibits relatively little interspecific variation in its form. Particularly noticeable are the expanded articular surface (almost square in outline), the enlarged parasphenoidal and basioccipital facets (Fig. 23), and the strengthened, somewhat bullate lateral walls (especially that part contributed by the prootics).

As the individual grows so the apophysis becomes relatively more massive. However, even in the smallest specimens examined, the basioccipital facets are larger, and the total area of the apophysis greater than in a similar-sized specimen from any other lineage (including

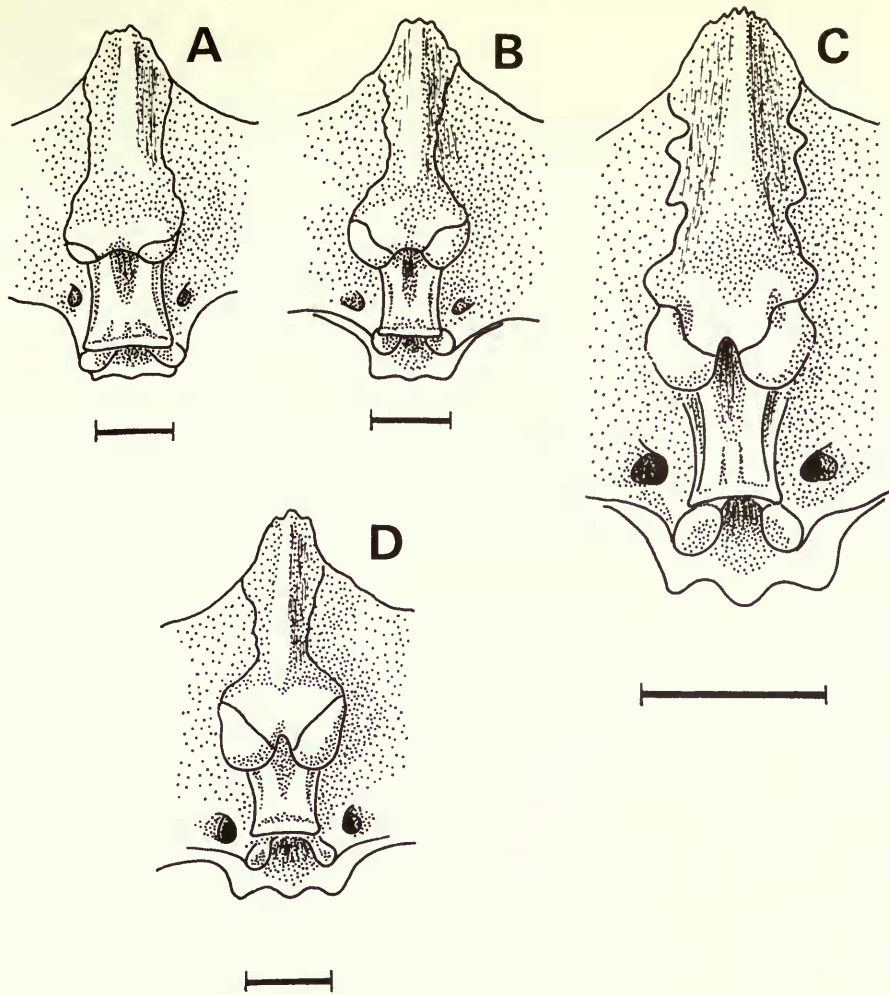


Fig. 23 Structure of the neurocranial apophysis for the upper pharyngeal bones (the pharyngeal apophysis) in various genera. A. *Gaurochromis* (*G.*) *empodisma* (typical of condition found in most haplochromine species). B. *Gaurochromis* (*M.*) *obtusidens* (see p. 36). C. *Labrochromis humilior* (the *Labrochromis* species with the least hypertrophied pharyngeal jaws in that lineage). D. *Labrochromis ishmaeli* (massive pharyngeal jaws and dentition). Scale = 3 mm.

Gaurochromis [p. 36 above], but excluding *Astatoreochromis*, see Greenwood, 1979b : 285–6 and also 1959a : 165–176; 1974 : fig. 44). This ontogenetic change in the apophysis is correlated with the size-related hypertrophy of the upper and lower pharyngeal bones and dentition.

Closest approximation to the *Labrochromis* apophyseal type is found in one species of the subgenus *Gaurochromis* (*Mylacochromis*), see above, p. 36, but the differences, even if less well-marked, are nevertheless apparent.

Dentition. Teeth in the outer row of both jaws are mostly of the basic bicuspid type, moderately stout to stout, slightly recurved, the neck subcylindrical, and the crown not markedly compressed. The minor cusp is small and the major one equilateral in outline. Some unicuspid teeth (otherwise similar in their morphology to the bicuspid) occur in specimens of all species at a length of ca 70–80 mm, the proportion increasing with the fish's length. However, even in fishes > 100 mm SL, an exclusively unicuspid jaw dentition is uncommon.

There are 30–70 teeth in the outer premaxillary row, but the modal range is *ca* 36–50. Although the range overlaps that for *Gaurochromis* (44–82, see p. 33), the modal numbers in *Labrochromis* are lower (36–50 cf. 60–70). Outer jaw teeth in the latter genus are also stouter, stockier and less compressed than in *Gaurochromis*, and thus are more akin to the generalized tooth form.

Teeth forming the inner rows are small, tricuspid, and are arranged in from 1–3 (rarely 4) rows anteriorly and anterolaterally in both jaws.

Mouth. The mouth is horizontal or very slightly oblique, the lips not thickened, and the jaws equal anteriorly except in *L. humilior* where the lower jaw is usually a little shorter than the upper.

Upper jaw. As compared with the maxilla in *Gaurochromis*, that in *Labrochromis* is shorter and deeper, but its articular head has about the same degree of medial curvature (see p. 33).

The relative height of the ascending premaxillary processes ranges from shorter than the dentigerous arms of the premaxilla to as long as or slightly larger than those arms. The dentigerous arms are compressed, and anteriorly the bone is not produced into a beak or shelf.

Lower jaw. The dentary is slender and shallow, with almost the posterior half (sometimes a little less) of its alveolar surface produced into a slight lateral shelf; anteriorly there is no shelf-like projection because the body of the ramus merges gradually with the alveolar surface.

The anguloarticular complex is of the generalized type (see p. 6).

The length of the lower jaw is from 34–44% head length (modal range 37–40%), that is, within the generalized range and, at least modally, shorter than in *Gaurochromis*.

Lower pharyngeal bone and teeth (Fig. 24). In all *Labrochromis* species the lower pharyngeal bone is massive and strong, the extensive hyperossification imparting to the ventral surface a characteristic bulbous appearance (see Fig. 24C). Its articular horns are short and stout, and the posterior margin of the bone lying between them is always strongly convex, save for a slight median depression (Fig. 24C).

Because the degree of lower pharyngeal hypertrophy is positively correlated with the fish's size, 'typical' *Labrochromis* bone-form is best seen in specimens over 80 mm SL. But, even in the one species reaching only a small maximum adult size (*L. humilior*, *ca* 90 mm SL), the lower pharyngeal is seen to be much hypertrophied when compared with the bone from similar-sized specimens in other lineages (including *Gaurochromis* (*M. obtusidens*; see p. 34). It also shows the characteristic bulbous ventral profile, and the short, stout articular horns characteristic of larger specimens (see Greenwood, 1960 : fig. 11; and 1974 : fig. 5C).

In some *Labrochromis* species the broadly triangular dentigerous surface is barely concave but in others it is markedly so, with a deep and extensive central pit (see Greenwood & Barel, 1978 : figs 26 & 30). The outline of the toothed surface is, relatively speaking, wider overall than in *Gaurochromis* (*Mylacochromis*) and, when viewed occlusally, it narrows gradually rather than rapidly from its maximum posterior width to the narrow anterior angle (Fig. 21). Generally the toothed area is as long as it is broad, but sometimes it is broader than long. In a few species, the surface, after beginning to narrow, actually broadens slightly at a point about two-thirds of the way along its antero-posterior length before it narrows again near the base of the short and deep anterior keel (see Greenwood & Barel, 1978 : figs 21 & 30).

Two outstanding features of the lower pharyngeal dentition in all *Labrochromis* species are the large size of the molariform teeth and, except in *L. humilior*, the extent to which pharyngeal molarization has proceeded. (These latter remarks, of course, are based on larger individuals; molarization is less pronounced in fishes < 60 mm SL).

Apart from a few compressed and bi- or unicuspid teeth situated in the posterolateral angles of the dental field, and the teeth comprising the perimeter series (*ie* the outermost one or two teeth in each transverse row), all the remaining teeth are molariform. Teeth within the central area are the most enlarged, and rarely show any trace of the low cusp that usually is

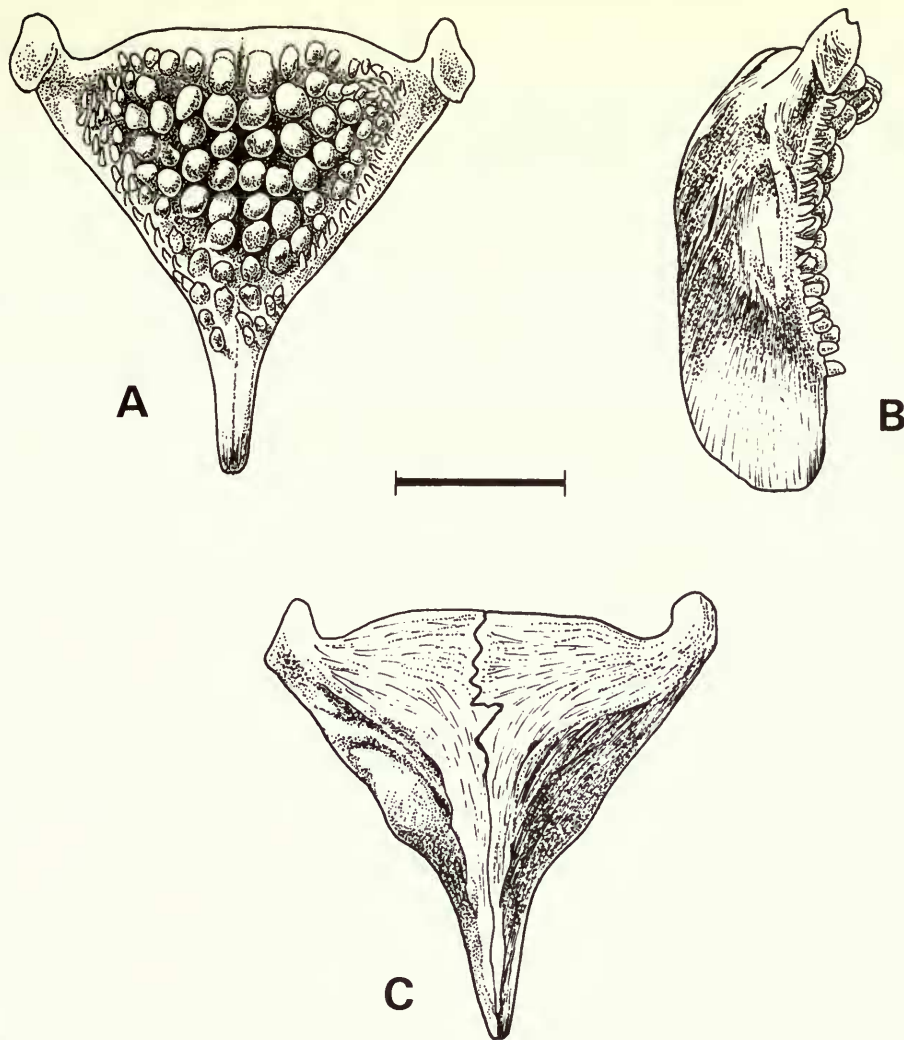


Fig. 24 Lower pharyngeal bone of *Labrochromis ishmaeli* in: A. Occlusal, B. Right lateral, C. Ventral view. Scale = 3 mm.

present on smaller molariform teeth. Loss of this cusp is at least partly attributable to wear, but even in newly erupted teeth it is insignificant.

Labrochromis humilior has proportionately fewer enlarged and molariform teeth, and these are restricted to the median rows. But, it must be stressed, these teeth are greatly enlarged, particularly when compared with the coarser teeth occurring in the median rows of the bone in other lineages (including comparable-sized specimens of *Gaurochromis (Mylacochromis) obtusidens*).

Specimens of *Labrochromis humilior* reach a maximum adult size of only *ca* 90 mm SL. When compared with like-sized individuals from other *Labrochromis* species the pharyngeal dentition is virtually identical (as is the degree to which the lower pharyngeal bone is hypertrophied). It is for these reasons (and because of its oral dentition) that I have included 'humilior' in *Labrochromis* and not *Gaurochromis*.

All *Labrochromis* species have a correlated hypertrophy and molarization of the upper and lower pharyngeal elements.

Contained species

The taxa are grouped approximately in the order of their increasing pharyngeal mill hypertrophy and molarization.

Labrochromis humilior (Blgr.), 1911. Lake Victoria and the Victoria Nile; see Greenwood (1960 : 248–52).

Labrochromis ptistes (Greenwood & Barel), 1978. Lake Victoria; see Greenwood & Barel (1978 : 164–9).

Labrochromis mylodon (Greenwood), 1973. Lakes Edward and George; see Greenwood (1973 : 172–7).

Labrochromis ishmaeli (Blgr.), 1906. Lake Victoria; see Greenwood (1960 : 275–9).

Labrochromis pharyngomylyus (Regan), 1929. Lake Victoria; see Greenwood (1960 : 270–5).

Labrochromis teegelaari (Greenwood & Barel), 1978. Lake Victoria; see Greenwood & Barel (1978 : 169–74).

Labrochromis mylergates (Greenwood & Barel), 1978. Lake Victoria; see Greenwood & Barel (1978 : 174–9).

Incertae sedis

Tilapia adolphifrederici Blgr., 1914. Lake Kivu.

I have been unable to examine the holotype of this species, a specimen once housed in the Berlin Museum but which may have been lost during the 1939–45 war. In his original description, Boulenger (1914) makes no reference to the lower pharyngeal bone of this fish, and it has not been mentioned in any subsequent redescription of the taxon (see Regan, 1921 : 637; Poll & David, 1937 : 259; Poll, 1939 : 9).

In the three BM(NH) specimens (one a skeleton), reg. nos: 1935.8.26 : 18–20, the pharyngeal mill is hypertrophied and the lower pharyngeal dentition is molarized (to an extent equaling that in *Gaurochromis* (*Mylacochromis*) *obtusidens* specimens of a comparable size). The morphology of the oral teeth, the number of outer teeth in both jaws, the shape of the dentary, and the proportions of the toothed surface on the lower pharyngeal bone are, however, of the *Labrochromis* and not the *Gaurochromis* types.

Judging from various published comments on this taxon (especially those of Regan, 1921; and Poll & David, 1937), it seems likely that at least two taxa have been confused under one name. Until more material, and the holotype, have been examined in detail, it seems inadvisable to place *Tilapia adolphifrederici* formally in *Labrochromis*. Nevertheless, the three BM(NH) specimens noted here can be referred to that genus.

Haplochromis placodus Poll, 1939, from the river Molindi, near Lake Kibuga, Zaire (Lake Edward drainage basin).

This species is known only from the holotype, and thus little detailed information is available on its anatomy. Considering the greatly enlarged and extensively molarized lower pharyngeal bone, and the nature of the oral dentition, the species probably should be included in *Labrochromis* (see also Greenwood, 1973 : 176).

DISCUSSION

Apart from the hypertrophied pharyngeal mill (and correlated modifications to the pharyngeal apophysis on the skull base) members of this lineage share no other derived features indicative of their monophyletic origin. Some doubt can even be cast in this instance on the hypertrophied pharyngeal mill being a true synapomorphy.

An enlarged lower pharyngeal bone, coupled with some degree of dental molarization, occurs in other lineages amongst the Victoria–Edward–Kivu haplochromines, and amongst haplochromine lineages from other areas as well. *Gaurochromis* (*Mylacochromis*) *obtusidens* is an example from the Victoria area, whilst *Astatoreochromis* species furnish examples from that region and beyond. Within the polyspecific lineage *Thoracochromis*, *Th. pharyngalis*

and *Th. mahagiensis* are examples from Lakes Edward and Albert, whilst species of the *Serranochromis* subgenus *Sargochromis*, together with the monotypic *Pharyngochromis darlingi*, are examples from the more southerly parts of Africa (see Greenwood, 1979).

Because these lineages do not appear to be more closely related to one another (or to *Labrochromis*) than they are to any other lineage, and since in some cases (eg in *Thoracochromis*) the species with hypertrophied mills are related to others without that specialization, the evolution of this character must have occurred independently on a number of occasions.

Thus, in the absence of unifying synapomorphies uniquely shared by all *Labrochromis* species, one cannot consider the presence of an hypertrophied pharyngeal mill (and various correlated characters) as unequivocal indicators of monophyly for the genus.

Labrochromis (in particular the species *ishmaeli* and *pharyngomylus*), has, in the past, been considered a derived relative of *Gaurochromis* (*M.*) *obtusidens* (see Greenwood, 1954 : 412-13; in that discussion, for *H. michaeli* read *H. empodisma*, see Greenwood, 1960 : 262, 266 & 269).

Later (Greenwood, 1974 : 72-4), it was suggested that *Labrochromis* (as represented by *ishmaeli* and *pharyngomylus*) and *Gaurochromis* (represented by *empodisma* and *obtusidens*) probably belonged to separate lineages. This suggestion is apparently borne out by the dental and pharyngeal differences discussed above (p. 40), differences which are apomorphic features serving to distinguish all *Gaurochromis* from every *Labrochromis* species. This general situation would still hold even if *Labrochromis* proves to be a non-monophyletic assemblage (see above).

Amongst *Labrochromis* species, *L. humilior* (Lake Victoria), with its small adult size and moderate degree of pharyngeal development, seems to be the least derived taxon. *Labrochromis ptistes*, *L. ishmaeli*, *L. pharyngomylus*, *L. teegelaari* (all from Lake Victoria) and *L. mylodon* (Lakes Edward and George) are at approximately the same level of anatomical derivation, whilst *L. mylergates* (Lake Victoria) appears to be the most derived species in the genus (see Greenwood & Barel, 1978 : 176-7).

In a previous analysis of the Lake Victoria flock (Greenwood, 1974 : fig. 70), *Haplochromis pallidus* (now *Astatotilapia pallida*, p. 9) was considered to be the plesiomorph sister taxon of three species now included in *Labrochromis*. This supposed relationship was based on *pallida* having somewhat enlarged median teeth on its slightly enlarged lower pharyngeal bone, and on the overall dental and syncranial similarities shared with the other species. It is apparent that the latter features are symplesiomorphies (and thus of no value as phyletic indicators), and that the pharyngeal characters are of equivocal significance. Several species have pharyngeal features like those of *A. pallida*, but in none (including *A. pallida*) is the bone so hypertrophied, nor its teeth so extensively molarized as in *Labrochromis humilior*, the least derived member of that genus. In other words, there are no clear-cut synapomorphies allowing one to postulate a recently shared common ancestry between *Astatotilapia pallida* and *Labrochromis*; at best the available evidence is but faintly suggestive of such a relationship.

***ENTEROCHROMIS* gen. nov.**

TYPE SPECIES: *Haplochromis erythrocephalus* Greenwood & Gee, 1969. Lake Victoria.

ETYMOLOGY. From the Greek *enteron*, the bowel, + *chromis*, referring to the long intestine in members of this lineage.

DIAGNOSIS. Small haplochromines (maximum adult size range 68-88 mm SL), with a generalized body form, head shape and syncranial skeleton, but *with a long, much coiled intestine that is at least 3 or 4 times longer than the standard length.*

From other haplochromines with a long intestine, *Enterochromis* is distinguished as follows:

From *Xystichromis* (p. 46), by its narrow bands of inner jaw teeth (1-3 rows) separated

from the outer row by a distinct interspace, the crowns of the outer teeth distinctly broader than the neck of the tooth, and by having *the anterior opening to the nasal lateral line canal as large as the nostril*.

From *Neochromis* (p. 49) by its straight and sloping dorsal head profile (compared with a strongly decurved one), its narrow bands of inner teeth separated from the outer series by a distinct interspace, by its unequally bicuspid, and not equally or subequally bicuspid teeth, by its elongate and not foreshortened and laterally bullate dentary, its compressed and not inflated premaxillary dentigerous arms, by its gently sloping and not near-vertically aligned ethmoverine skull region, and by having the opening to the nasal lateral line tubule as large as or larger than the nostril.

From *Haplochromis* (Greenwood, 1979 : 278–81), by not having the major cusp in the outer teeth drawn-out, compressed, expanded, and disproportionately larger than the minor cusp. It also differs in having no elements of the inner tooth rows similar in size or cusp form to teeth in the outer series, and in its nasal opening as large as, or larger than the nostril.

DESCRIPTION

Habitus and anatomy (Fig. 25). In most respects *Enterochromis* closely resembles *Astatotilapia*, and only those features distinguishing the two taxa (or which are developed to a different degree in *Enterochromis*) will be noted.

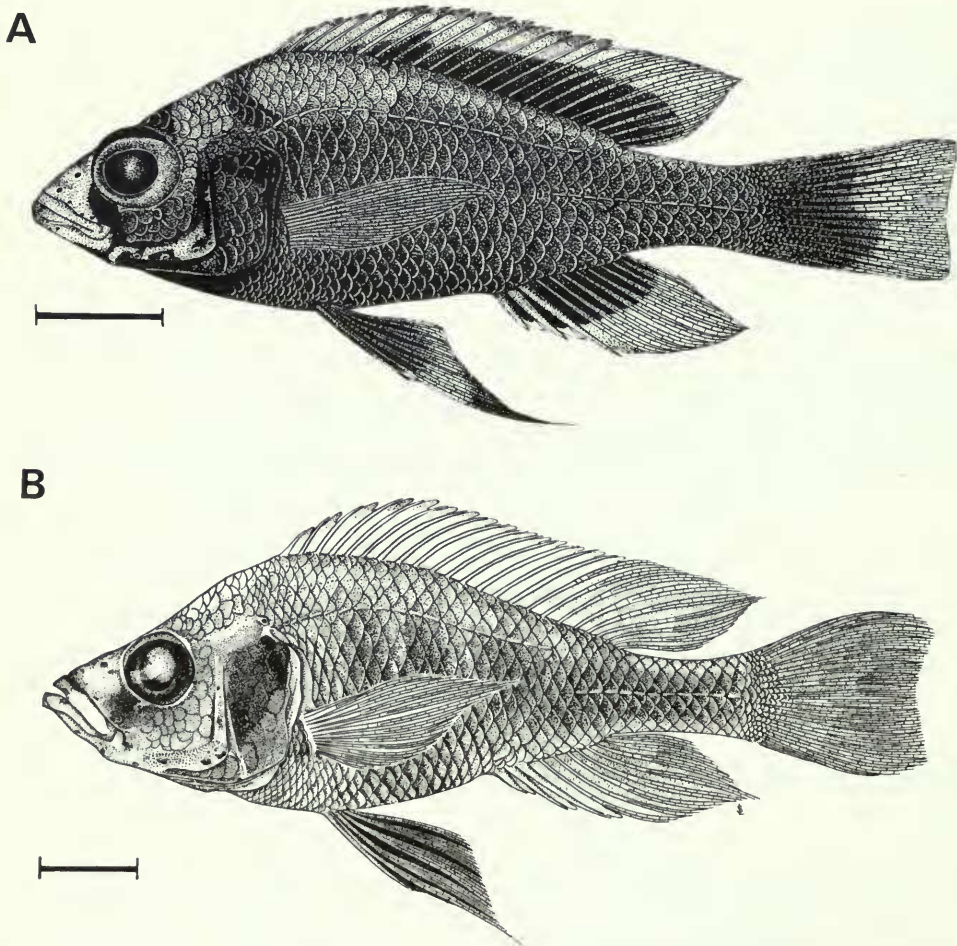


Fig. 25 A. *Enterochromis nigripinnis*. Lake George. B. *Enterochromis erythrocephalus*. Lake Victoria. Scale = 1 cm.

Neurocranium. One species (*E. erythrocephalus*) has a low preorbital skull depth (ca 24% neurocranial length), and the skull is narrow (otic width 50–51% neurocranial length); in the other three taxa these particular measurements are modal for the generalized skull type. (It should be noted that the skull is also narrow [ca 50% neurocranial width] in the otherwise generalized skull of some *Astatotilapia* species, but none has such a shallow preorbital depth as has *E. erythrocephalus*.)

Dentition. Compared with the modal condition in *Astatotilapia*, the teeth in *E. erythrocephalus* and *E. nigripinnis* are somewhat finer. Teeth in the other *Enterochromis* species, however, are of the typical *Astatotilapia* type. One or more outer teeth posteriorly in the premaxilla are enlarged and, generally, unicuspid, as they are in most *Astatotilapia* species. Also, as in that genus, some of the posterior outer teeth in both the premaxilla and the dentary are tricuspid.

No unicuspid teeth have been recorded from an anterior or anterolateral position in either jaw; possibly this is a consequence of the small adult size reached by members of the various species (see Greenwood, 1974 : 106).

There are 40–74 (modal range 50–56) teeth in the outer premaxillary row; the modal range for *Enterochromis* lies in the upper half of that for *Astatotilapia*, and the upper extremes of the *Enterochromis* range are rarely encountered in that genus.

Jaws. One *Enterochromis* species (*E. erythrocephalus*) has an oblique mouth, sloping upwards at an angle of 30°–35° (occasionally 40°) to the horizontal; the mouth in the remaining species is almost horizontally aligned.

Cephalic lateral line pores. All *Enterochromis* species, as far as I can determine, are outstanding amongst at least the Victoria–Edward–Kivu haplochromines in having the anterior opening to the nasal lateral line tubule as large (or almost as large) as the nostril. In other lineages the canal opening is much smaller.

Gut. The intestine in *Enterochromis* is long (ca 3–4 times the standard length) and much coiled. The folding is mostly in a horizontal plane, with 3 or 4 coils arranged below the elongate, greatly distensible stomach; posteriorly the intestine appears to be thrown into at least one vertical loop.

Lower pharyngeal bone and dentition (see also Greenwood & Gee, 1969 : 12–13, 21; and Greenwood, 1973 : 157). The bone is slender, with a triangular and equilateral dentigerous surface. Except for one species, all the teeth are fine, strongly compressed and of approximately the same size; even the posterior transverse row is made up of teeth only a little stouter than the others. In the exceptional species (*E. cinctus*), the teeth are somewhat coarser, and those in the two median rows are slightly stouter than the others. But, even in *E. cinctus* all the pharyngeal teeth are relatively finer and more compressed than those in any *Astatotilapia* species.

Again with the exception of *E. cinctus*, the teeth are numerous and close set, producing a coarse dental felt (coarse that is, compared with the dental felt in most tilapiine species of the genera *Tilapia* and *Sarotherodon*, but fine in comparison with the majority of haplochromine species).

In *E. cinctus* the teeth are more widely spaced and the dental felt is, as a result, coarser.

Contained species

The taxa are listed in approximately the order of their increasing derivation from the generalized condition.

Enterochromis cinctus (Greenwood & Gee), 1969. Lake Victoria; see Greenwood & Gee (1969 : 15–19).

Enterochromis paropiis (Greenwood & Gee), 1969. Lake Victoria; see Greenwood & Gee (1969 : 10–15).

Enterochromis nigripinnis (Regan), 1921. Lakes Edward and George; see Greenwood (1973 : 151–9).

Enterochromis erythrocephalus (Greenwood & Gee), 1969. Lake Victoria; see Greenwood & Gee (1969 : 19–24).

DISCUSSION

The long, much coiled intestine of *Enterochromis* may indicate a somewhat distant common ancestry with the other phytophagous genera, namely, *Haplochromis*, *Xystichromis* and *Neochromis*. This question is discussed on p. 48.

Earlier attempts to relate *E. erythrocephalus* with the *Gaurochromis* lineage, in particular with *G. (G.) empodisma* (see Greenwood, 1974 : 66–7 and fig. 70; also Greenwood & Gee, 1969 : 23) can no longer be substantiated. The two taxa share no unequivocally derived features, and each has its own apomorph features which suggest relationships with other lineages (see p. 37).

Within the genus, *E. erythrocephalus* is the most derived species. Its narrow and pre-orbitally shallow skull, the fine and densely toothed lower pharyngeal bone, and the oblique mouth, are all characters contributing to that status, as are the high number (12) and fine shape of the gill-rakers (see Greenwood & Gee, 1969 : 20). Otherwise, little else can be said about intragroup relationships.

XYSTICHROMIS gen. nov.

TYPE SPECIES: *Chromis nuchisquamulatus* Hilgend., 1888. Lake Victoria; see Greenwood (1956b : 241).

ETYMOLOGY. From the Greek 'xyster', one who scrapes, + *chromis*, alluding to the grazing habits of its member species.

DIAGNOSIS. Small haplochromines with a maximum adult size range of 85–105 mm SL, a much coiled and long intestine (ca 3–4 times SL), and the broad bands (4–6 rows deep) of inner teeth anteriorly and anterolaterally in both jaws, narrowly, if at all separated from the outer tooth row.

Neurocranium of the generalized type except that the preorbital skull profile slopes more steeply and the supraoccipital crest is deeper and more pyramidal in shape.

Teeth in the outer row of each jaw very close set (usually contiguous), moveably implanted, tall, and slender but strong, showing only a slight antero–posterior decline in their height and size. All (except for a few unicuspid posteriorly in the upper jaw) are unequally bicuspid, the minor cusp prominent but clearly smaller than the major one; the crown is not distinctly broader than the neck.

Inner row teeth are tricuspid, those of the outermost one or two rows almost as large as their counterparts in the outer row.

Lower pharyngeal bone without molariform or submolariform teeth; in some specimens the teeth of the median rows are enlarged and coarser than those of the lateral rows.

From other genera with long and coiled intestines, *Xystichromis* is distinguished as follows:

From *Neochromis*, by its gently sloping, not strongly decurved dorsal head profile, its unequally as opposed to equally or subequally bicuspid teeth, its elongate and not fore-shortened dentary (which also is not bullate laterally), and by the ethmovomerine region of the skull sloping at an angle of 40°–50° to the horizontal and not almost vertically aligned.

From *Haplochromis*, particularly by its unequally bicuspid teeth, as compared with the very unequally bicuspid teeth in which the major cusp is protracted and compressed, and the minor cusp is virtually or entirely suppressed.

From *Enterochromis* it is distinguished by the characters listed on p. 43.

DESCRIPTION

Habitus (Fig. 26). There is little to differentiate members of this genus from *Astatotilapia* species. Maximum adult size range is 86–105 mm SL; no information is available on the size at which sexual maturity is reached.

Neurocranium. Skull form in *Xystichromis* is essentially like that in *Astatotilapia* except that the preorbital skull region slopes more steeply, and the supraoccipital crest is relatively deeper and more pyramidal in outline.

Dentition. It is the dentition of *Xystichromis* which provides the greatest number of derived features and, indeed, the synapomorphies uniting members of the lineage.

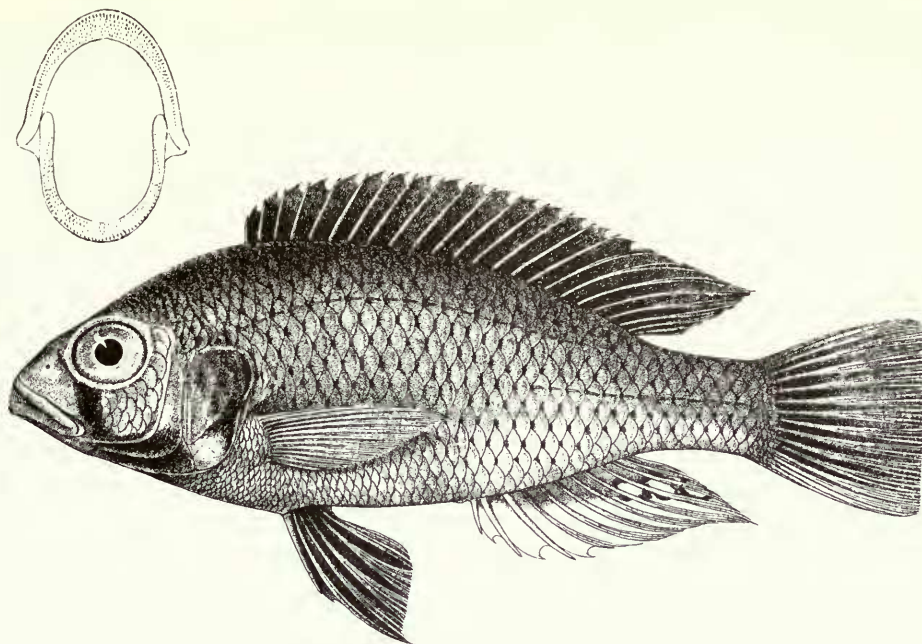


Fig. 26 *Xystichromis bayoni* Lake Victoria. About 1.3× natural size. Inset: the dental pattern of the upper and lower jaws (about 2.5× natural size).

Outer row teeth in both jaws are very close-set (contiguous or partially contiguous), moveably implanted and tall, with only a slight antero-posterior decline in their height and overall size. Apart from one to three enlarged caniniform teeth posteriorly in the premaxilla, and the occasional intercalation of a tricuspid tooth posterolaterally, the teeth are all unequally bicuspids. The acutely pointed minor cusp is prominent but distinctly smaller than the major cusp, which has a somewhat obliquely slanting posterior margin and a broadly acute tip. Many teeth have this posterior margin produced into a low flange over part of its length; such flanges are known from members of other lineages as well (eg *Astatotilapia macropsoides*, *A. elegans* and *A. aeneocolor*, from Lake George (Greenwood, 1973), and *Gaurochromis empodisma* in Lake Victoria); their significance is not known.

Although relatively slender, the outer teeth in *Xystichromis* are robust and but slightly recurved. They also differ from the generalized bicuspid tooth in not having the crown distinctly broader than the neck and body of the tooth; as a result, the anterior and posterior margins of the entire tooth are almost parallel. The crown is also somewhat more compressed than in the generalized bicuspid tooth, although it could not be described as flattened.

There are 36–70 (modal range 50–65) teeth in the outer premaxillary series.

Because the insertion line of the outer teeth is lower than that of the inner teeth, the crowns of the teeth in both series are, effectively, at the same level. Presumably this is a feature associated with the algal-grazing habits of the known species.

Although the modal number of inner tooth rows in any one species is elevated in comparison with the generalized condition, the lower end of the total range (2–8) does overlap that for *Astatotilapia*, but *Xystichromis* individuals with only 2 or 3 inner rows are uncommon.

Upper jaw. Compared with the generalized type of premaxilla, that in *Xystichromis* has a

broader alveolar surface and the dentigerous arms are slightly inflated anteriorly and antero-laterally.

Lower jaw. The dentary is not deep and foreshortened (as in *Neochromis*, see p. 51), but neither is it as slender as the dentary in *Astatotilapia*.

Lower pharyngeal bone and dentition. Both the bone and its teeth are of the generalized type. There is some intrageneric variation in the relative width of the dentigerous surface, with one species, *X. phytophagus*, having a distinctly broad and stout bone (see Greenwood, 1966 : 304-6). Some of the median teeth are coarse, and may even be enlarged posteriorly in *X. bayoni*.

Gut. The intestine in *Xystichromis* is long (at least 3 to 4 times the standard length) and much coiled; the stomach is large and greatly distensible.

Contained species

Since no intralineage relationships can be determined the species are listed alphabetically.

Xystichromis bayoni (Blgr.), 1911. Victoria Nile.

This species was given the replacement trivial name 'niloticus' by Greenwood (1960 : 243) who, disagreeing with Regan's (1922 : 169) idea that the taxon was synonymous with *Haplochromis humilior*, resurrected it to full specific status within the genus *Haplochromis* as then defined.

At that time the name 'bayoni' was preoccupied by *Haplochromis bayoni* (Blgr.), 1909, and so a new trivial name was required for Boulenger's (1911) 'bayoni'. Hence the introduction of 'niloticus' as a replacement (see Greenwood, 1960 : 243-5). Since Boulenger's 1909 'bayoni' is now placed in the genus *Prognathochromis* (see p. 19 above), Boulenger's 1911 name is again available for the species listed here.

Xystichromis nuchisquamulatus (Hilgendorf), 1888. Lake Victoria and the Victoria Nile; see Greenwood (1956b : 241-3).

Xystichromis phytophagus (Greenwood), 1966. Lake Victoria; see Greenwood (1966 : 303-9).

DISCUSSION

Apart from its dental specializations and long, coiled intestine, *Xystichromis* is, anatomically speaking, a generalized haplochromine.

However, the dental pattern, the tall and slender but robust teeth, and the enlarged, broad-banded inner teeth do resemble those of *Neochromis*, a lineage with which *Xystichromis* also shares the derived feature of an elongate and much coiled gut (see p. 52).

It is possible, therefore, that these two genera share a common ancestor in which such dental and alimentary features are present, and that they should be ranked as sister taxa (but see also p. 52).

A long coiled gut is also present in *Haplochromis* and in *Enterochromis* (see p. 45) but neither genus shares all the dental synapomorphies common to *Xystichromis* and *Neochromis*. *Haplochromis* has a uniquely derived crown form in its outer jaw teeth (see Greenwood, 1979 : 278-9), but also has broad bands of teeth anteriorly and anterolaterally in the jaw. In that latter feature it shares an apomorph character with both *Neochromis* and *Xystichromis*. *Enterochromis* has an essentially plesiomorph haplochromine dentition (see p. 45).

If the shared apomorphy of a long, much coiled gut really does indicate a common ancestry for all four genera, then the various dental specializations suggest that *Xystichromis*, *Neochromis* and *Haplochromis* are more closely related to one another than any one is to *Enterochromis*. In other words, *Haplochromis*, because of its greater dental specializations, is the sister taxon of *Xystichromis* and *Neochromis* combined, and *Enterochromis*, because of its relatively generalized dentition is the plesiomorph sister group to all three.

An acceptance of this solution is complicated by various derived syncranial features which *Neochromis* alone shares with a number of other lineages, and which might therefore indicate its relationship to them (the dental features being then taken as parallelisms). However,

the first set of relationships proposed above is the more parsimonious since its resolution involves fewer and less profound dental and anatomical changes (see discussion p. 52).

Intragenetic species grouping within *Xystichromis* is not possible on the basis of available data; no two species appear more closely related to one another than either does to the third member of the lineage.

NEOCHROMIS Regan, 1920

TYPE SPECIES: *Tilapia simotes* Blgr., 1911 (see Regan, 1920 : 45), now considered a junior subjective synonym of *Tilapia nigricans* Blgr., 1906 (see Greenwood, 1956b : 237).

DIAGNOSIS. Small haplochromines (maximum adult size 95 mm SL), with a very strongly decurved dorsal head profile (sloping at 70°–80° to the horizontal), a long, much coiled intestine (ca 3–4 times SL), broad bands of inner teeth anteriorly and anterolaterally in both jaws, not separated from the outer row, and equally or subequally bicuspid outer teeth.

Neurocranium with a strongly decurved preorbital face, the ethmovomerine region almost vertically aligned.

Dentary markedly foreshortened, deep and stout, its anterior margin strongly curved medially so that the anterior outline of the lower jaw is almost rectangular. The region of the dentary surrounding its posterior division into coronoid and horizontal limbs is markedly bullate. Length of lower jaw 30–38% head length, modal range 34–36%.

The anguloarticular complex of the lower jaw is stout, the anterior point of its anteroventral arm blunt or rectangular (never acute).

Premaxilla with noticeably inflated dentigerous arms, almost cylindrical in cross section, the alveolar surfaces broad; its ascending processes as long as the dentigerous arms.

Outer jaw teeth tall, slender but robust, and without any marked antero-posterior decline in height; moveably implanted and very close set (contiguous). Cusp form characteristic, the minor (*ie* posterior) cusp well-developed and only a little smaller than the major (*ie* anterior) cusp, from which it is separated by a narrow notch; the points of each cusp are almost spatulate. The crown is compressed relative to the cylindrical neck and body of the tooth (but is not flattened), and is broader than the body.

Inner tooth rows numerous (3–8, usually 5 or 6), the teeth in a row contiguous, and the rows close set; there is no discrete interspace between the outermost row and the outer row of teeth. Inner teeth tricuspid (with all cusps of about the same height), the teeth in the two outermost rows distinctly larger than those of the innermost rows.

Teeth in the median rows on the lower pharyngeal bone relatively stout in two species, not so in the remainder.

Features distinguishing *Neochromis* from the other taxa with long, coiled, intestines are listed on p. 44 for *Enterochromis*, and p. 46 for *Xystichromis*.

DESCRIPTION

Habitus (Fig. 27). The strongly decurved and steep dorsal head profile, and the near-horizontal mouth, combine to give the pug-headed appearance which is so characteristic a feature of all *Neochromis* species. None reaches a large adult size (ca 95 mm SL).

Neurocranium. The preorbital face of the skull is very strongly decurved (sloping at an angle of ca 70°–80° to the horizontal), the ethmovomerine region is aligned almost vertically and its tip extends ventrally to a point below a horizontal through the anterior part of the parasphenoid (see Fig. 28). The supraoccipital crest is of variable outline and relative height, but it is always somewhat deeper and less wedge-shaped than in a generalized skull.

Dentition. Teeth in the outer row of both jaws are tall (and without any marked antero-posterior decline in height), slender but strong, are moveably implanted and so close-set as to be contiguous. There are 40–70 teeth (modal range 50–56) in the outer premaxillary row.

One species (*N. nigricans*) has the last, or sometimes the last two teeth in the premaxillary row enlarged and unicuspid, but usually in that species, and in the other two *Neochromis* species, the posterior teeth are like the others.

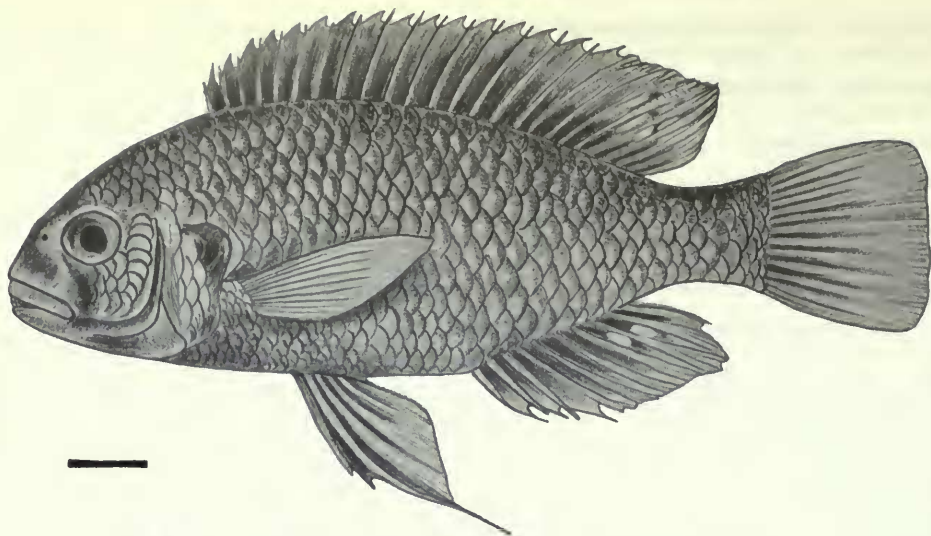


Fig. 27 *Neochromis nigricans*. Lake Victoria. Scale = 1 cm.

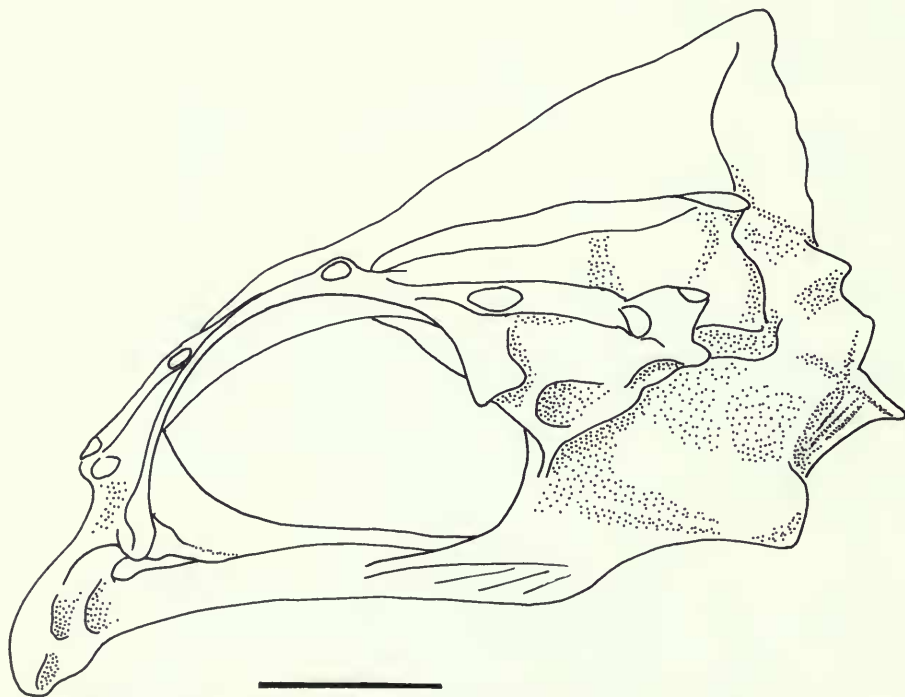


Fig. 28 Neurocranium of *Neochromis nigricans*; left lateral view. Scale = 3 mm.

Cusp form in *Neochromis* is very characteristic (Fig. 29). The inner (*ie* posterior) cusp is well-developed, often only a little smaller than the major (*ie* anterior cusp), and is directed obliquely backwards (rather than vertically upwards). The points of both cusps are spatulate or somewhat acutely spatulate (but never acute). The crown is compressed (relative to the cylindrical neck and body of the tooth) but is by no means flattened; it is also broader than the neck so that the margins of the tooth are not parallel (*cf.* *Xystichromis* p. 47).

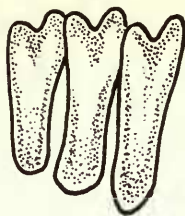


Fig. 29 Outer row teeth from the dentary of *Neochromis nigricans*, viewed labially. Scale = 1 mm.

Inner tooth rows are composed of moveably implanted tricuspoid teeth in which the two lateral cusps are of almost the same height and width as the median one. Those teeth forming the two outermost rows in each jaw are enlarged, and even those in the remaining rows are relatively larger than their counterparts in other lineages except *Xystichromis*; all, however, are shorter than the outer row teeth. There are 3–8 (modes 5 or 6) rows of inner teeth anteriorly and anterolaterally in each jaw, and one or two rows laterally. Teeth in these rows are contiguous, and the rows themselves are close set so that only a very narrow interspace separates them; the interspace between the outermost row of the inner series and the outer tooth row is barely discernible. Thus, as compared with *Xystichromis*, although the area covered by the inner tooth rows is almost the same, there are more rows of teeth in *Neochromis*, and the rows are set much closer together (see p. 47). As in *Xystichromis*, tooth insertion levels are such that the crowns of the inner and outer row teeth are at the same level despite the inner teeth being slightly shorter.

Mouth. The mouth is horizontal and the jaws equal anteriorly; the lower jaw is broad and its anterior outline, when viewed from below, is almost rectangular.

Upper jaw. The premaxilla has notably inflated dentigerous arms, oval to near-circular in cross section anteriorly and anterolaterally, but somewhat more compressed posteriorly. Compared with the generalized premaxilla, that in *Neochromis* has a broader alveolar surface, and the ascending processes are longer (as long as the dentigerous arms).

Lower jaw. The dentary is deep relative to its length, and has the appearance of being a stout, foreshortened bone (Fig. 30). Anterolaterally, each ramus curves inwards rather abruptly so that the anterior margin of the entire jaw is rectangular.

The anguloarticular complex is stout, with the anterior point of its anteroventral arm blunt or rectangular in outline.

The crown of the coronoid process (the ascending arm) on the dentary has a slight but definite medial inflection.

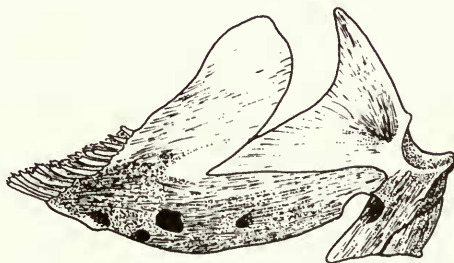


Fig. 30 Dentary of *Neochromis nigricans*, left lateral view. Scale = 3 mm.

Lower jaw length in *Neochromis* (30–38% head length, modal range 34–36%) broadly overlaps that in the majority of non-piscivore lineages with small-sized adults (*ie* < 110 mm SL), although the modal length in several of these species is higher (40–44%) than in *Neochromis*. Lower jaw width in *Neochromis* (1.0–1.4, mode 1.2 times longer than broad) also overlaps that in lineages with a generalized syncranial morphology, but modally it is distinctly greater in *Neochromis*.

Lower pharyngeal bone and dentition. The dentigerous surface is triangular and as broad as it is long. In *Neochromis nigricans* and *N. serridens* the teeth are fine and compressed bicuspid, densely arranged on the bone, with only the posterior transverse row composed of stouter teeth; *N. fuscus*, however, has all the pharyngeal teeth relatively coarser, less closely set and with the two median rows composed of somewhat enlarged (but cuspidate) teeth.

Gut. The intestine is long (at least 3–4 times longer than the standard length) and much coiled; the stomach is large and distensible.

Contained species

For the possible interrelationships of these taxa, see below.

Neochromis nigricans (Blgr.), 1906. Lake Victoria and the Victoria Nile (*Tilapia simotes* Blgr., 1911, the type species of *Neochromis*, is currently considered to be a junior synonym of this species; see Greenwood, 1956b : 237–40).

Neochromis serridens (Regan), 1925. Lake Edward; see Trewavas (1933 : 327–8).

Neochromis fuscus (Regan), 1925. Lake Edward; see Trewavas (1933 : 329).

DISCUSSION

In all *Neochromis* species certain derived syncranial features, such as the strongly decurved preorbital skull, the deep, foreshortened dentary, the stout anguloarticular complex, the laterally bullate dentary, and the inflation of the premaxillary arms, are shared either *in toto*, in part or in varying degrees of expression, with several lineages (*Macrolepodus*, *Ptyochromis*, *Hoplotilapia*, *Platytaeniodus*, *Paralabidochromis*, *Lipochromis*, *Schubotzia* and *Allochromis*).

It is difficult to assess the significance of this situation. Other synapomorphies occurring in these taxa, but not in *Neochromis*, point to further groupings that can be made amongst them (see discussions on pp. 92–94) and suggest that the syncranial features shared with *Neochromis* are, at most, an indication of distant (rather than recent) common ancestry. Alternatively, the syncranial synapomorphies could be parallelisms associated with the independent evolution of strong jaws and dentition (often multiseriate), or of a multiseriate dentition alone.

The latter interpretation must be invoked if the hypothesized relationship between *Neochromis*, *Haplochromis*, *Enterochromis* and *Xystichromis*, put forward on p. 48, is accepted. It should be stressed that this relationship, unlike that associating *Neochromis* with *Macrolepodus*, *Ptyochromis* etc, does not require the independent evolution of a long gut (and presumably associated physiological changes) in *Neochromis*, nor the unique development of its dental type within a 'lineage' having totally different dental specializations and a simple gut form.

Thus, it is more parsimonious to propose that *Neochromis* is related to the other species with long, coiled intestines and bicuspid teeth, modified though the teeth may be in some species, than to the eight other genera with which it shares some syncranial specializations (see pp 48–49).

Unfortunately there are few available specimens of *Neochromis serridens* and *N. fuscus*, the Lake Edward representatives of the genus. As a result, little is known about the range of variation in critical characters in these species, but it would seem that the dentition of *N. nigricans*, the Lake Victoria representative, is less specialized than that in the Edward species. Since *Neochromis nigricans* has teeth which are more unequally bicuspid than in the others, and its inner rows are generally fewer in number, the Edward taxa would seem to be more closely interrelated than either is to *N. nigricans*.

HAPLOCHROMIS Hilgendorf, 1888

TYPE SPECIES: *Chromis (Haplochromis) obliquidens* Hilgendorf, 1888. This now much impoverished genus is redescribed in the first part of this paper (see Greenwood, 1979 : 278–81).

Contained species

The taxa are grouped and listed in order of their increasing derivation.

Haplochromis limax Trewavas, 1933. Lakes Edward and George; see Greenwood (1973 : 167–72).

Haplochromis annectidens Trewavas, 1933. Lake Nabugabo; see Greenwood (1965 : 329–35).

Haplochromis lividus Greenwood, 1956. Lake Victoria; see Greenwood (1956*b* : 232–7).

Haplochromis astatodon (part) Regan, 1921. Lake Kivu; see Greenwood (1979 : 280).

Haplochromis obliquidens Hilgendorf, 1888. Lake Victoria; see Greenwood (1956*b* : 226–32).

PSAMMOCHROMIS gen. nov.

TYPE SPECIES: *Pelmatochromis riponianus* Blgr., 1911 (as redefined by Greenwood, 1960 : 252–6). Lake Victoria.

ETYMOLOGY. From the Greek '*psammos*', sand, + *chromis*, referring to the sandy substrata seemingly preferred by most members of the genus.

DIAGNOSIS. Haplochromines reaching a maximum adult size of 100–123 mm SL, the body relatively slender to moderately deep (31–43% SL, modal range 36–38%); lips thickened in all species, the lower lobate in one.

Neurocranium of a near-generalized type but *shallower in the otico-occipital region (40–46% neurocranial length)*.

Outer jaw teeth tall and slender, their crowns recurved and either compressed or finely acuminate and cylindrical in cross-section. Very unequally bicuspid teeth present in specimens of all sizes, but unicuspid predominate in fishes > 80–90 mm SL; 24–68 teeth in the outer premaxillary row.

Inner teeth tall and slender, tri- or unicuspid, and usually implanted so as to lie almost horizontally; commonly arranged in 2–4 rows anteriorly.

Premaxilla with a definite anterior beak, its ascending processes longer than the dentigerous arms, which have a slight ventral decurvature over the posterior half (more marked in some species than in others).

Dentary with a very distinctive form, each ramus noticeably inflated anteriorly and antero-laterally, this circumscribed swelling extending almost to the bone's ventral profile. Over this region (and slightly behind it) the narrow outer margin of the alveolar surface dips distinctly downward so that the outer tooth row also has a ventral inflection (see Fig. 32).

Lower pharyngeal bone in some species moderately stout, its median teeth enlarged and submolariform, but the bone slender and without enlarged teeth in others.

DESCRIPTION

Habitus (Fig. 31). There are few outstanding features in the habitus of most *Psammochromis* species. The body varies from relatively slender to moderately deep (31–43% SL, modal range 36–38%), the dorsal head profile is straight or gently curved, and slopes fairly steeply. All species have thickened lips, and the lower lip may be lobate in *P. aelocephalus*, which species also has a highly variable snout form (noticeably protracted in some individuals; see Greenwood, 1959*b* : 214–17).

Maximum adult size ranges from 100–123 mm SL; individuals reach sexual maturity at a length of 80–85 mm in those species attaining the larger maximum sizes.

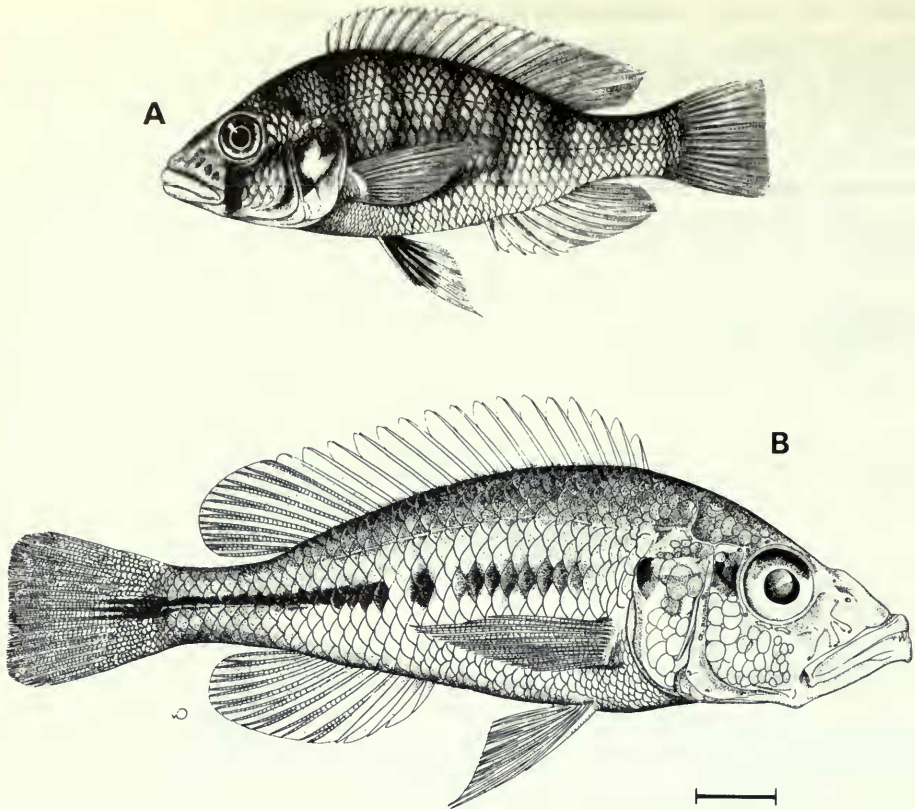


Fig. 31 A. *Psammochromis riponianus*. Lake Victoria. About two-thirds natural size. B. *Psammochromis cassius*. Lake Victoria. Scale = 1 cm.

Neurocranium. The skull is of a near-generalized type but has a lower otico-occipital region (depth 40–46% neurocranial length) so that the preotic dorsal profile slopes downwards and forwards fairly gently; the supraoccipital crest is relatively low and is wedge-shaped in profile.

Although in one species (*P. riponianus*) some individuals have the pharyngeal mill enlarged to a degree comparable with that in *Gaurochromis* (*Mylacochromis*) *obtusidens* (see p. 34), there is no corresponding enlargement of the pharyngeal apophysis on the skull base. As compared with those congeneric species not having an enlarged pharyngeal mill, the parasphenoid contribution to the apophysis in *P. riponianus* is slightly more expansive, but the basioccipital facets are barely larger.

Dentition. The outer row jaw teeth are slender and tall, the body and recurved crowns either relatively compressed (only the lower part of the tooth cylindrical in cross-section) or the crown is finely acuminate and the whole tooth cylindrical in cross-section and very slender. Species with the latter type of teeth have the teeth widely spaced, especially in the lower jaw.

When bicuspid, the coarser type of tooth has the minor cusp greatly reduced, the major cusp vertically protracted and pointed; bicuspid forms of the finely acuminate unicuspid are as yet unknown.

Some bicuspid teeth are present in most specimens of all other species, but predominate only in fishes <90 mm SL; above that size, unicuspid and, or, weakly bicuspid teeth are more frequent. *Psammochromis cassius* is unusual in having only unicuspid teeth present in specimens as small as 70 mm SL, and, apparently, in having some lower teeth lying outside, or even penetrating into, the upper lips (see Greenwood & Barel, 1978 : 162).

A characteristic feature of two species from Lake Victoria (*P. riponianus* and *P. saxicola*), is the very abraded crowns on most outer teeth, which then appear bluntly incisiform.

Inner teeth are also slender and tall, tricuspid in small individuals but unicuspid in larger fish, implanted so as to lie almost horizontally, and generally embedded deeply in the oral mucosa (Greenwood, 1960 : 254). There may be as many as 5 rows of inner teeth anteriorly in each jaw; the modal numbers are, however, 2-4.

Mouth. Lips are clearly and equally thickened, but in one species (*P. aelocephalus*) the lower lip may be produced anteriorly into a small but definite mental lobe. The mouth is horizontal or but slightly oblique; this, combined with the thickened lips and particular head profile, impart to the members of this lineage a very characteristic but undefineable physiognomy (see Fig. 31; also figs 13 & 14 in Greenwood, 1960; and figs 20 & 21 in Greenwood, 1973).

Upper jaw. The premaxilla is somewhat expanded and protracted anteriorly and anteromedially into a definite beak or peak. Its ascending processes are longer than the dentigerous arms, which have a slight but distinct ventral curvature over their posterior halves (the curve more marked in some species than in others).

The maxilla is elongate and slender in *P. saxicola* but relatively foreshortened and deep in the other species. In none is the medial face of the posterior arm strongly concave (and thus the lateral aspect is but slightly bullate), and none has a marked medial curvature of its articular head.

Lower jaw. The most trenchant and diagnostic synapomorphy linking members of this lineage lies in the morphology of the dentary (Fig. 32).

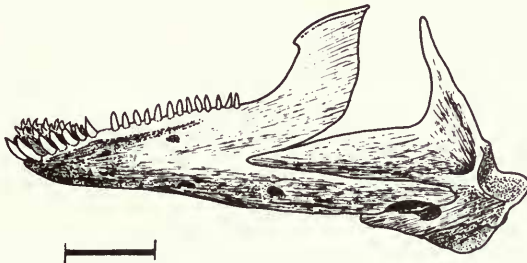


Fig. 32 Dentary of *Psammochromis saxicola* in left lateral view. Scale = 3 mm.

Anteriorly and anterolaterally the bone immediately below the alveolar surface is distinctly inflated, the well-circumscribed swelling extending almost to the ventral margin of each ramus. Over this swollen region, and a little behind it as well, the narrow outer margin of the alveolar surface dips downwards so that the line of outer teeth also dips ventrally in that region of the jaw. Consequently the tips of the outer teeth are on a level with those of the much smaller inner teeth.

The dentary also departs from the generalized type in being relatively shallower. Thus, although the length of the entire lower jaw (dentary + anguloarticular) is within the 'generalized' range (33-49% head length) it gives the impression of being much more slender and attenuated.

No mental protuberance is developed at the dentary symphysis. Indeed, the ventral symphyseal profile slopes backwards so that the jaw appears 'chinless', except for a slight vertically directed ventral projection at the symphyseal base.

Lower pharyngeal bone and teeth. There is considerable inter- and some intraspecific variation in the stoutness of the bone, and there are correlated differences in the nature of its dentition (see Greenwood, 1959 : 216; 1960 : 254 & 258, and figs 4 & 5).

All or some of the teeth in the four median rows may be enlarged and are often molariform or submolariform. The remaining teeth, and sometimes those of the median rows as well, are weakly cuspidate and compressed (except, as is usual, for the robust teeth in the posterior transverse row).

Squamation. Except in two species, the scales anteriorly and ventrally on the chest region are distinctly smaller than those on the ventral flanks and belly, and appear to be more deeply embedded. There is, however, no abrupt size change between the scales of the two regions, which grade imperceptibly into one another (see Greenwood, 1979 : 270–2).

In the exceptional taxa (*P. acidens* and *P. cassius*) the chest scales are not obviously smaller than the belly scales, and do not give the appearance of being deeply embedded.

Contained species

The taxa are listed in order of their increasing apomorphy.

Psammochromis graueri (Blgr.), 1914. Lake Kivu.

Amongst the BM(NH) material identified as *graueri*, only three specimens (BMNH reg. nos: 1914.4.8 : 16, 19 & 20) are apparently conspecific. The concept of *graueri* used in this paper is thus based on those specimens, of which one, reg. no. 1914.4.8 : 20, a fish 99.0 mm SL, is chosen as the lectotype of the species.

Psammochromis schubotzi (Blgr.), 1914. Lakes Edward and George; see Greenwood (1973 : 183–8).

The possible relationship between *P. schubotzi* and *A. schubotziella* (see p. 9) suggested in that paper can no longer be upheld since the latter taxon shares none of the derived features shown by *P. schubotzi*.

Psammochromis riponianus (Blgr.), Lake Victoria and probably the Victoria Nile; see Greenwood (1960 : 252–6)

Psammochromis saxicola (Greenwood), 1960. Lake Victoria, and probably the Victoria Nile; see Greenwood (1960 : 256–9).

Psammochromis aelocephalus (Greenwood), 1959. Lake Victoria; see Greenwood (1959b : 214–17).

Psammochromis acidens (Greenwood), 1967. Lake Victoria, and probably the Victoria Nile; see Greenwood (1967 : 73–7).

Psammochromis cassius (Greenwood & Barel), 1978. Lake Victoria; see Greenwood & Barel (1978 : 161–4).

DISCUSSION

Previously (Greenwood, 1974 : fig. 70), most of the species included in *Psammochromis* were thought to be related to a lineage comprising, amongst other taxa, those now divided between the genera *Harpagochromis* and *Prognathochromis* (including its subgenus *Tridontochromis*); the *Psammochromis* species were considered to be most closely related to the latter group (the so-called *tridens* complex). In turn, the '*tridens* complex' and *Psammochromis* (then the '*riponianus* complex') were ranked as the sister group of a species (*H. welcommei*) here classified as the monotypic genus *Allochromis* (see p. 57).

Anatomical and osteological information now available for all these various taxa renders that hypothesis, based chiefly on neurocranial architecture, untenable in its entirety but not in part.

Skull form in *Psammochromis* is of a near-generalized type, and its derived dental features are unlike those in either subgenus of *Prognathochromis*.

The form of the dentary in *Psammochromis* exhibits apomorphies not shared with *Prognathochromis*, and there are no obvious synapomorphies linking *Psammochromis* with the dentally specialized *Allochromis* (the former *H. welcommei*).

However, there are certain derived features in the morphology of the dentary in *Psammochromis* which might still indicate its relationship with *Allochromis*, an argument which is taken up later (p. 60). These same features may also indicate a shared common ancestry with *Macrolepurodus*, *Paralabidochromis* and *Ptyochromis* (see p. 66). In other words, *Psammochromis* and *Allochromis* together may constitute the sister group of the three other genera (see also pp 92–94).

Psammochromis acidens previously was given, tentatively, the status of sister group to the '*empodisma-obtusidens*' lineage, that is, the genus *Gaurochromis*; p. 32 (Greenwood, 1974).

Now that skeletal material of *P. acidens* is available it is clear that the lower jaw morphology in this species is far removed from that in *Gaurochromis*. Likewise, a possible relationship of *P. cassius* with the 'serranus group' (that is, *Harpagochromis*), as suggested by Greenwood & Barel (1978: 164), is not supported by the peculiar morphology of its lower jaw; both *P. acidens* and *P. cassius* have the distinctive and derived type of dentary characterizing the genus. *Psammochromis cassius* and *P. acidens* do, however, depart from other members of the lineage in having both a very different tooth form (see p. 54), and chest scales which are not noticeably smaller than those on the ventrolateral flanks and belly. The latter feature must be ranked as plesiomorphic, the dental one as derived. Possibly the two species together represent a subgroup within the lineage, but more material must be studied before they are formally recognized as such.

ALLOCHROMIS gen. nov.

TYPE SPECIES: *Haplochromis welcommei* Greenwood, 1966. Lake Victoria.

ETYMOLOGY. From the Greek 'allos', different, strange + *chromis*, alluding to the unusual tooth shape and dental pattern, as well as to the lepidophagous habits of the type species.

DIAGNOSIS. Haplochromine fishes having an adult size range of ca 80–105 mm SL, a shallow, streamlined body (depth 30–33% SL), a gently decurved dorsal head profile (sloping at ca 35°–40°), a horizontal mouth and slightly thickened lips (Fig. 33). In general, the habitus is like that of many *Prognathochromis* species. *Allochromis* is, however, immediately distinguished by its dental morphology and the wide, broadly crescentic bands of fine teeth.

Teeth in the outer row of both jaws are close set and have a very slender, tall and near-cylindrical neck which expands abruptly into a compressed, bicuspid crown which is about twice as broad as the neck; the crown and upper third of the neck are strongly recurved and lie almost at right angles to the rest of the tooth (see Fig. 34). Inner row teeth are mostly tricuspid, the cusps of approximately equal size, and the whole crown strongly recurved.

Both jaws have the teeth arranged in a broad, almost crescentic band extending nearly to the posterior limits of the dentigerous surfaces involved (Fig. 35).

DESCRIPTION

Habitus (Fig. 33). A shallow, streamlined body combined with the gently curved and sloping head profile give this taxon a very *Prognathochromis*-like appearance (cf. Fig. 8). The mouth is horizontal and the lips are slightly thickened.

Adult size range for the few specimens known is ca 80–105 mm SL.

Neurocranium. Overall skull shape closely approaches that in species of the *Psammochromis* lineage; that is, a near-generalized neurocranium but with somewhat shallower otico-occipital and pre-orbital regions (ca 25% and 45% of neurocranial length, respectively). The supraoccipital crest is relatively low and wedge-shaped in profile.

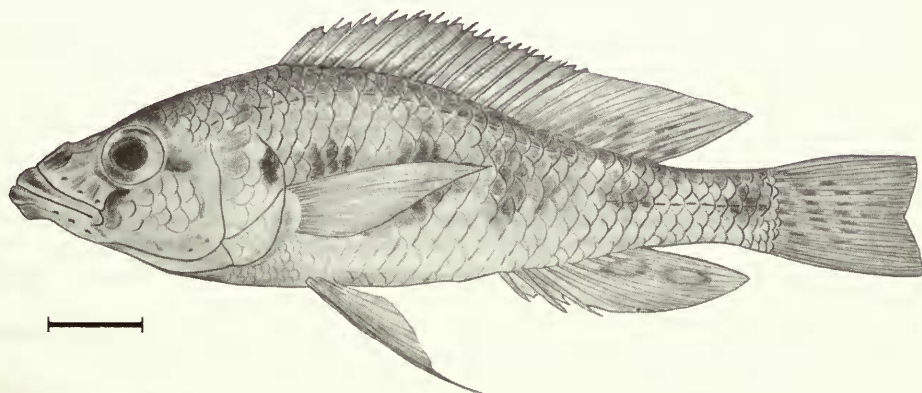


Fig. 33 *Allochromis welcommei*. Lake Victoria. Scale = 1 cm.

Dentition. Outer row teeth have a very characteristic shape and cusp form (see Fig. 34). In lateral view the tooth has a very slender, nearly cylindrical and tall neck which expands rather abruptly, but equally on either side, into a compressed bicuspid crown. The crown is almost twice as wide as the body of the tooth, its outline resembling a stylized drawing of a tulip. Both the crown and the upper third of the neck are strongly recurved.

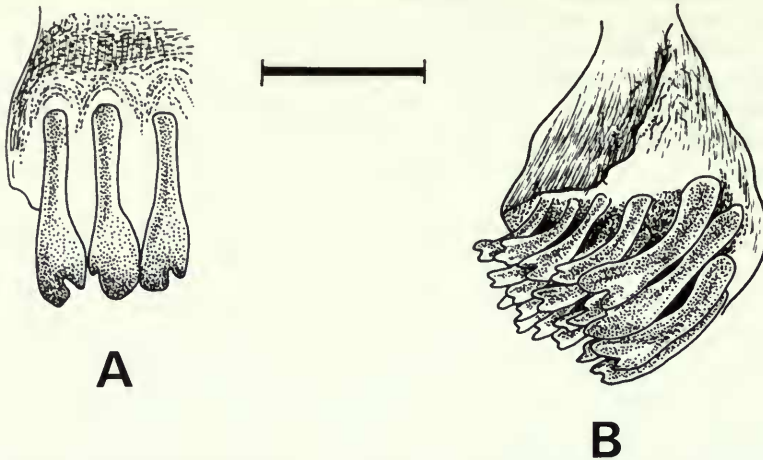


Fig. 34 Teeth from the left premaxilla of *Allochromis welcommei*. A. Labial aspect, viewed anteriorly. B. Ventromedial aspect viewed somewhat anteriorly. Scale = 1 mm.

Most outer teeth are unequally bicuspid, but there are a few tricuspids posteriorly in the row. The major cusp has a sub-acuminate, almost rounded distal margin; the minor cusp is more acute but is by no means pointed. In life these teeth, and those of the inner series, are moveably attached to the jaw.

Teeth in the inner series have the same overall shape as the outer ones but the crown is generally tricuspid, although bicuspids do occur frequently in the outermost row. There is little difference in the size of the three cusps, but the middle one is slightly higher and broader; their distal margins are sub-acuminate. All inner teeth are strongly recurved.

A very gradual size gradient exists across the inner rows; teeth in the outermost row are almost as tall as those in the outer series.

There are 70–80 close-set teeth in the outer premaxillary row, the margins of their cusps contiguous or slightly overlapping.

The dental pattern in both jaws is of a highly derived and distinctive type (see Fig. 35). The teeth are set out in broad crescentic bands which are not confined to the anterolateral parts of the jaw, but extend almost to the posterior limits of their respective dentigerous surfaces. Each arm of the crescent decreases gradually in width so that the inner tooth bands are multi-seriate to their posterior limits in the dentary, and almost to those limits in the premaxilla (Fig. 35).

At its broadest point there are 7–11 rows in the upper, and 6–11 in the lower jaw, the numbers decreasing posterolaterally to *ca* 3 or 4 in the latter and a single or double row in the former. The rows are very closely spaced and there is no gap between the inner and outer tooth rows in either jaw.

Upper jaw. The premaxilla has the greater part of its dentigerous arms inflated and ovoid in cross section; the posterior quarter of each arm, however, is less enlarged and is more compressed.

The ascending processes are only about half as long as the horizontal dentigerous arms, which are produced anteriorly and anterolaterally into a slight but broad beak.

The maxilla is elongate and relatively shallow, its articular head with only a slight medial curvature.

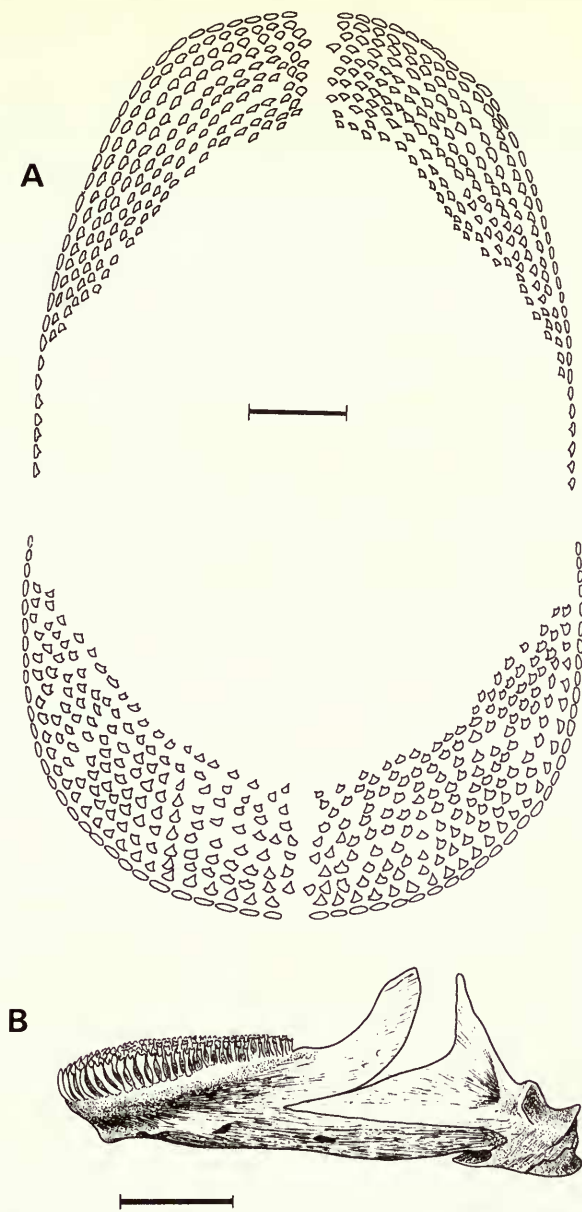


Fig. 35 A. Dental pattern of *Allochromis welcommei*. Scale = 1 mm. B. Dentary of *Allochromis welcommei*, in lateral view. Scale = 3 mm.

Lower jaw. The dentary is elongate and relatively shallow. Its alveolar surface, however, is inflated and broad, forming a deep bullation extending beyond, and overhanging, the lateral wall of each ramus. Anterolaterally, the inflated region extends almost to the ventral margin of the ramus.

Each alveolar surface has a decided anteroventral inclination, sloping forwards and downwards from a point immediately in front of the ascending dentary arm to the superficially shallow symphyseal area. The symphysis itself extends vertically through the bullation so that it is both deep vertically and, since it incorporates the bullate part of the bone, also wide dorsally.

The anguloarticular is of the generalized type, with an acute tip to its horizontally aligned ventral limb.

Lower jaw length is 41–46% of head length, and the jaw is clearly longer (1.3–2.0 times) than broad.

Lower pharyngeal bone and teeth. The bone is slender and relatively elongate, its triangular dentigerous surface slightly broader than long (see Greenwood, 1966 : fig. 6). Apart from the transverse posterior row, none of the pharyngeal teeth is noticeably enlarged; all are small, compressed and weakly cuspidate.

Contained species

Allochromis welcommei (Greenwood), 1966. Lake Victoria; see Greenwood (1966 : 309–18).

DISCUSSION

There are no synapomorphic features which allow the sister taxon of *Allochromis* to be identified precisely.

The outer row jaw teeth in *Allochromis* are unique and thus autapomorphic, but the multiseriate dental pattern does occur in several lineages (*Hoplotilapia*, *Platytaeniodus*, *Neochromis* and *Ptyochromis*, especially *P. xenognathus*). However, *Allochromis* does not exhibit other characteristics which can be considered unequivocally synapomorphic with those in any of these taxa, and each, including *Allochromis*, has its own distinctive dental pattern when these are compared in detail. One apparent synapomorphy, the inflated premaxillary dentigerous arms, would seem to be a parallelism associated either with the presence of enlarged teeth, a multiseriate dentition, or a combination of both (see discussion on p. 52).

Allochromis also differs from most of the taxa mentioned above in the gross morphology of its neurocranium, which does, however, resemble that in *Psammochromis*. In both genera the skull deviates from the generalized condition towards that found in the least derived species of the *Prognathochromis* lineage. It was this similarity in skull architecture which previously led me (Greenwood, 1974) to suggest that *Allochromis* was the sister group of the 'tridens complex' (now recognized as the subgenus *Tridontochromis* of *Prognathochromis*; p. 20). A reconsideration of other derived features in both *Allochromis* and *Prognathochromis*, *sensu lato*, now renders that hypothesis untenable.

In that paper, I also suggested that *A. welcommei* (plus the 'tridens complex') might be the sister group of three taxa which, together with others, now constitute the genus *Psammochromis*; see above, p. 56.

Certain neurocranial similarities existing between *Allochromis* and *Psammochromis* have already been noted (p. 57), but more significant (particularly considering the very different tooth form and patterns in the genera) are their similarities in lower jaw morphology, which is undeniably derived in both taxa.

Both genera have a pronounced anteroventral inclination to the outer tooth row of the dentary (itself a slender, elongate bone), whose anterior and anterolateral aspects are markedly inflated below the alveolar surface. The tooth rows in *Psammochromis* are neither as numerous nor as spatially extensive as they are in *Allochromis* so that those shared derived features cannot be ascribed to that cause, and thus be dismissed as parallelisms.

If these apparent synapomorphies in the morphology of the dentary can be accepted as truly synapomorphic, *Allochromis* could be the derived sister taxon of *Psammochromis*. If, in turn, one can accept the arguments put forward for a common ancestry shared by *Psammochromis* on the one hand and *Paralabidochromis*, *Ptyochromis* and *Macropleurodus* on the other (see p. 66), then *Psammochromis* and *Allochromis* together should comprise the sister group of the other three genera combined. Another possible member of this lineage *sensu lato*, *Schubotzia eduardiana*, is discussed on pp. 87–88 & 94.

PTYOCHROMIS gen. nov.

TYPE SPECIES: *Ctenochromis sauvagei* Pfeffer, 1896. Lake Victoria (see Greenwood, 1957 : 76–81, plate 4, upper figure).

ETYMOLOGY. From the Greek 'pyto', to spit out, + *chromis*, alluding to the way in which these fishes crush mollusc shells orally and then spit out the fragments.

DIAGNOSIS. Haplochromine fishes with a maximum adult size range of 105–130 mm SL, a dorsal head profile ranging from straight and steeply sloping to strongly decurved, a small,

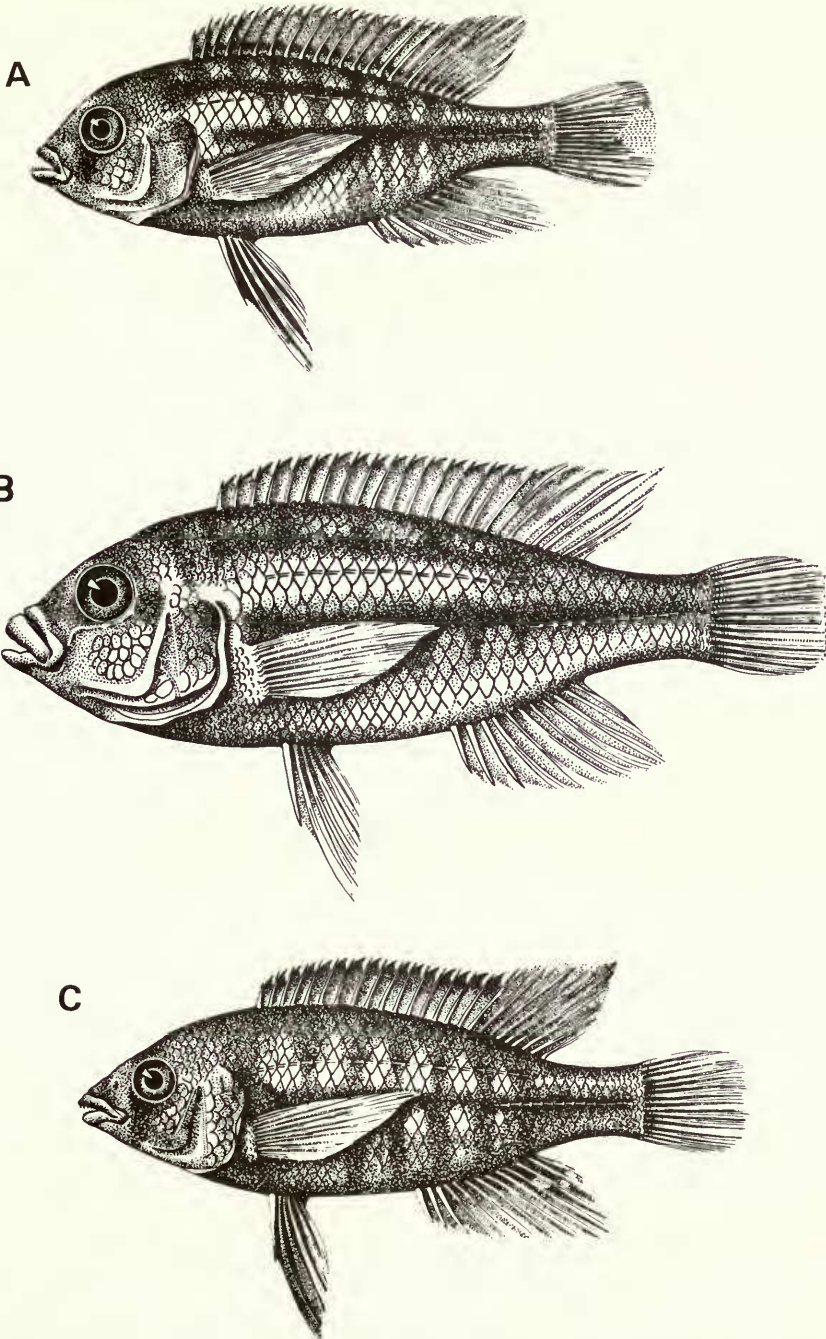


Fig. 36 A. *Ptyochromis sauvagei*. Lake Victoria. About natural size. B. *Ptyochromis granti*. Lake Victoria. About two-thirds natural size. C. *Ptyochromis xenognathus*. Lake Victoria. About natural size.

horizontal mouth with thickened lips, and a lower jaw that is usually shorter than the upper. The slender teeth are very strongly recurved, those of the inner series arranged in a broad band across the anterior part of each jaw.

Neurocranium with the preorbital face sloping fairly steeply (ca. 60° – 65° , but 70° – 75° in one species), its preorbital depth 30–33% of neurocranial length.

Premaxilla with somewhat inflated dentigerous arms which, anteriorly, are produced into a broad, shelf-like 'beak'. Twenty-six to 56 teeth in the outer premaxillary row (modal range 40–44).

Dentary deep posteriorly but shallowing rapidly over the anterior two-thirds of its length, the lateral walls curving abruptly medially from a level immediately below the alveolar surface. The outer margin of this surface, over its anterior half, dips downwards and slightly outwards so that the insertions of the outer row of teeth lie below those of the inner series.

Lower jaw length 22–38% of head length (modal range 34–35%).

Lower pharyngeal bone stout and broad, the median rows with coarser teeth, but none is submolariform or molariform.

DESCRIPTION

Habitus (Fig. 36). The dorsal head profile is variable, both inter- and intraspecifically, and ranges from strongly decurved to straight but steeply sloping. The mouth is horizontal, or less commonly, slightly oblique. There is a tendency for the lower jaw to be slightly shorter than the upper one; the lips are thickened, more so in some species than in others.

Body form shows no outstanding features, and is of the generalized type.

Maximum adult size ranges from 105–130 mm SL; sexual maturity is reached at lengths between 70 and 100 mm.

Neurocranium. Skull form in this genus combines features seen in *Macropleurodus* and *Paralabidochromis* (see pp. 81 & 68) but with most species and individuals approximating more closely to the latter condition (Fig. 37). Generally, the preorbital face slopes fairly steeply (ca 60° – 65° to the horizontal) but in one species (*P. annectens*) the slope may reach 70° – 75° ; preorbital skull depth ranges from 30–33% of neurocranial length. The tip of the vomer lies distinctly below the level of the parasphenoid.

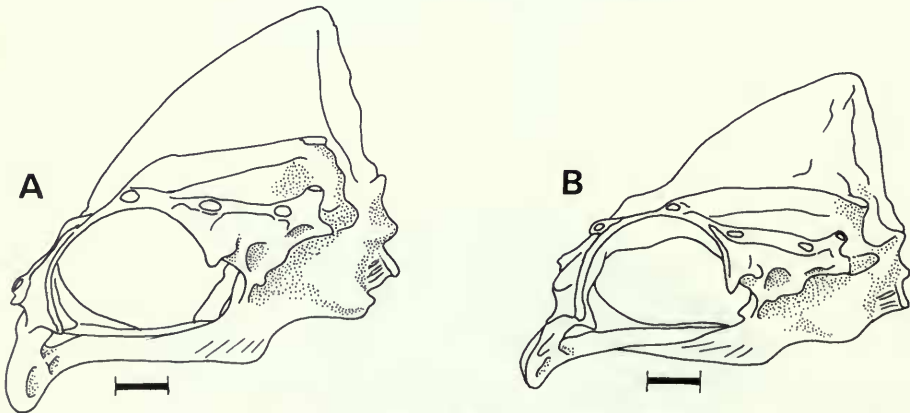


Fig. 37 Neurocranium (in left lateral view) of A. *Ptyochromis annectens*, and B. *Ptyochromis xenognathus*. Scale = 3 mm.

Supraoccipital crest outline varies from near pyramidal to a deep wedge-shape, with a corresponding variation in the height of its posterior margin.

Dentition. In both jaws the teeth in the outer row are slender but strong, with markedly recurved crowns (Fig. 38); the angle formed between the buccal face of the crown and the neck is ca 130° . The crown is neither expanded nor noticeably compressed, and joins imperceptibly the cylindrical neck.

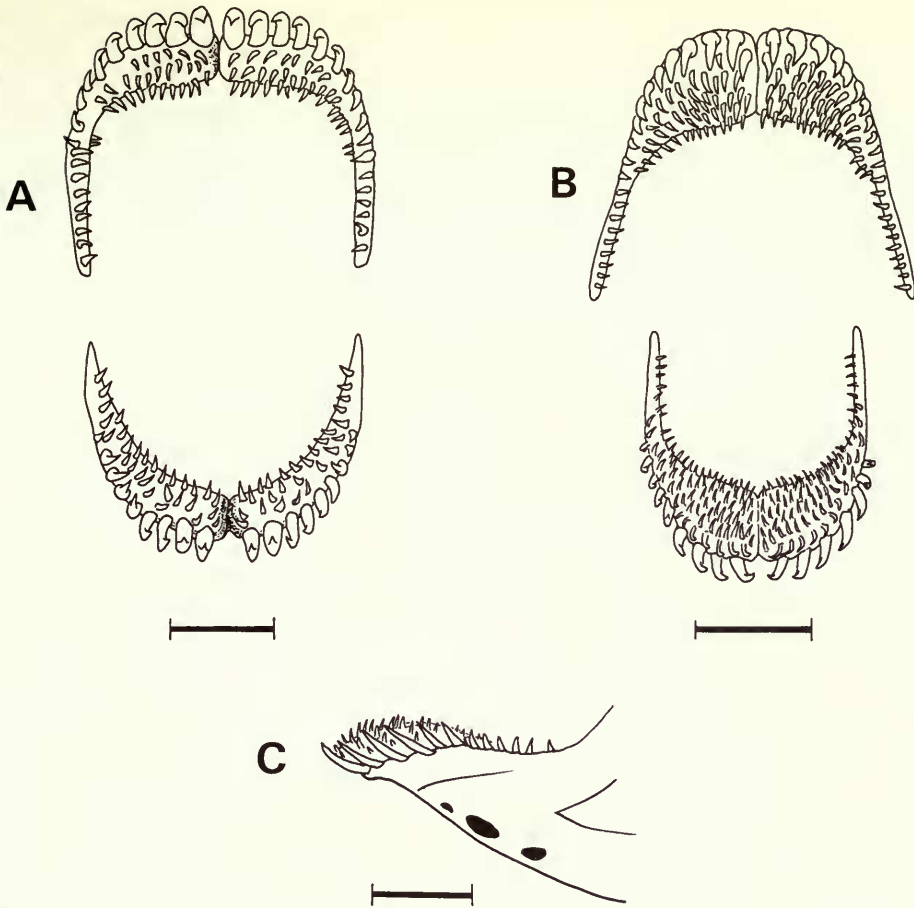


Fig. 38 Dental pattern in: A. *Ptyochromis annectens*, B. & C. *P. xenognathus* (entire pattern, and as seen laterally in dentary respectively). Scale = 3 mm.

Unequally bicuspid crowns predominate in the dentition of fishes < 80 mm SL; a mixture of bi- and unicuspid occurs in fishes between 80 and 100 mm long (with unicuspid first appearing anteriorly in the jaws). In larger individuals the teeth are all or predominantly unicuspid.

Anteriorly and anterolaterally in the lower jaw the teeth are implanted almost procumbently and below the level of those situated laterally (see also the description of the dentary, p. 64). As a result, their crowns are on about the same level as those of the inner teeth. Tooth insertion on the premaxilla is nearly vertical or very slightly procumbent.

There are 26–56 (modal range 40–42) teeth in the outer premaxillary row.

Teeth forming the inner rows are small and arranged in a characteristic pattern, namely a wide anteromedial band lying transversely across the front of each jaw, but narrowing abruptly to a single or double row laterally, and a single row posterolaterally (see Fig. 38A). Modally, there are 4 or 5 rows in the upper jaw and 3 or 4 in the lower; *Ptyochromis xenognathus* (Fig. 38B) is exceptional in having modes of 7 and 5 rows in the jaws respectively. The total range of tooth row numbers is from 3–9 (rarely 2) in the premaxilla and 2–9 in the dentary (see Greenwood, 1957 : 83 for comments on the aberrant tooth pattern in the holotype of *P. annectens*; also Regan, 1922 : fig. 14).

Most inner teeth in fishes less than 80 mm SL are tricuspid, but are predominantly unicuspid in fishes > 90 mm SL.

Upper jaw. Three of the four *Ptyochromis* species have the dentigerous arms of the premaxilla somewhat inflated, especially anteriorly and anterolaterally where the tooth rows are broadest. The fourth species (*P. xenognathus*), has little or no inflation of the arms, but anteriorly (in the region below the ascending processes) the bone is extended forward as a shallow but broad shelf corresponding with the area of maximum tooth row width. (This species, it will be recalled, has the highest number of inner tooth rows.) Because this shelf extends forwards as a plateau beneath the ascending processes, the premaxilla in *P. xenognathus* has very characteristic lateral and dorsal profiles (Fig. 39).

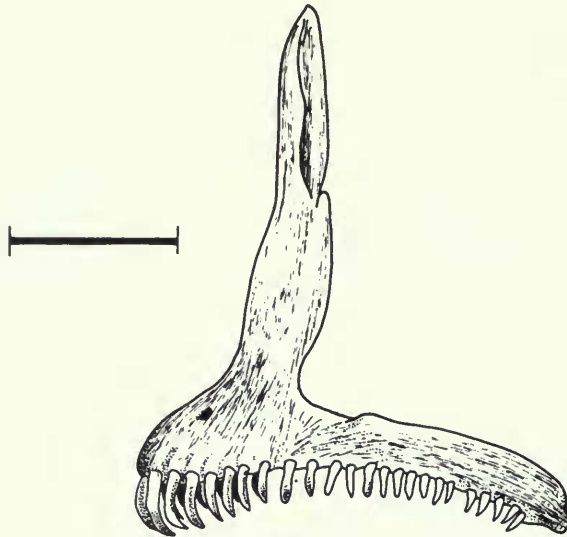


Fig. 39 Premaxilla (left) of *Ptyochromis xenognathus*. Scale = 3 mm.

Anterolaterally, each dentigerous arm of the premaxilla curves rather sharply mediad so that in occlusal view the entire structure has the outline of a broad-based U; the base is narrowest in *P. xenognathus*.

Premaxillary ascending processes are shorter than the dentigerous arms in all species except *P. xenognathus*, where they are equal.

Each maxilla is foreshortened, its posterior arm relatively deep, with a strongly concave median face (and a corresponding bullation of its lateral face). There is some variation in the extent to which the articulatory head is curved medially; curvature is strong in *P. granti* and *P. annectens*, but only moderate in *P. sauvagei* and *P. xenognathus*.

Dentary. There are several outstanding, and derived, features in this bone. In all species it is deep posteriorly but shallows rapidly forward from the region near the point where the ascending (coronoid) arm begins to rise. Consequently, in lateral view the ventral profile of the dentary appears to slope steeply upwards into a shallow symphyseal region (Fig. 40). Anteriorly, when compared with the condition seen in both generalized and differently derived dentaries, the side wall of the dentary in *Ptyochromis* species does not descend vertically for some distance before it begins to curve inwards. Instead, its medially directed curvature begins only a short distance below the alveolar surface, and the curvature is unusually abrupt. This pattern of curvature, coupled with the relatively deep coronoid region of the bone, gives the dentary a very characteristic appearance (Fig. 38C). The appearance is most extreme in *P. xenognathus* and is least marked in *P. sauvagei* and *P. granti*. Parenthetically it should be noted here that the dentary of *P. annectens* figured in Greenwood (1974 : 70, fig. 40, captioned *Haplochromis prodromus*, but see p. 66 below for nomenclature) was in fact drawn from a misidentified skeleton of a *Paralabidochromis* species (see p. 67), probably *Paralabidochromis crassilabris*.

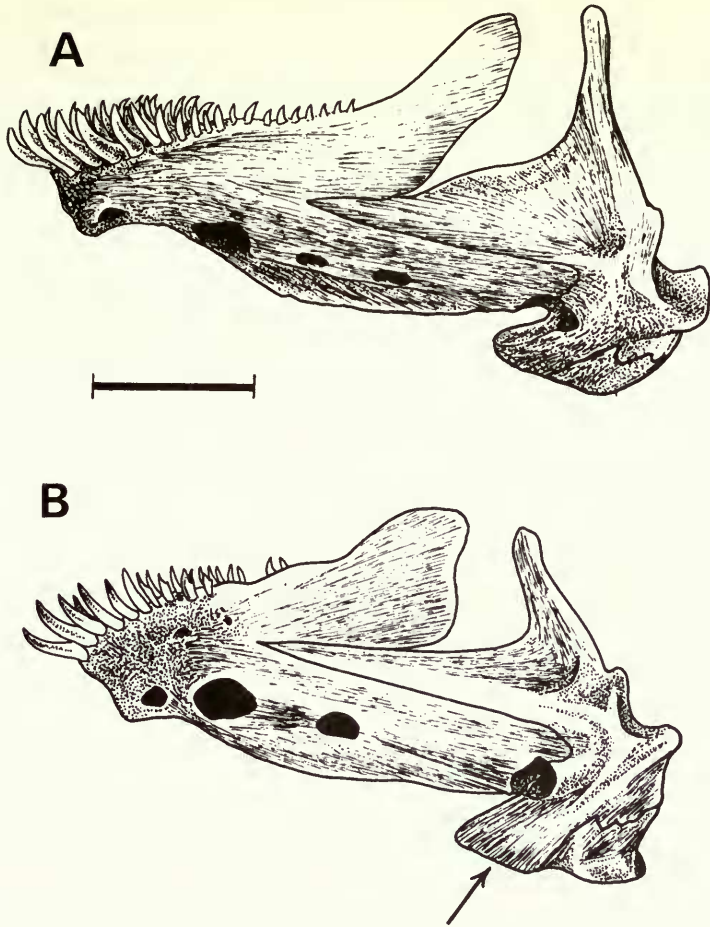


Fig. 40 Left dentary of: A. *Ptyochromis sauvagei* seen in lateral view. B. *Ptyochromis xenognathus*, viewed somewhat ventrolaterally, from the left, to show the shape of the anterior margin to the anguloarticular (arrowed). Scale = 3 mm.

Anteriorly and anteromedially the alveolar surface of the dentary has a noticeable fore-and-aft expansion (corresponding, as in the premaxilla, to the greatest width of the inner tooth rows), and a correlated antero-posterior lengthening of the symphyseal surface.

About halfway along its length the alveolar surface for the outer tooth row in the dentary dips downwards and forward to occupy a position below the alveolar surface for the inner tooth rows. Immediately below the somewhat ventrolaterally displaced anterior outer teeth, the dentary is thickened and a little bullate. A similar swelling, associated with a displaced outer tooth row, occurs in *Psammochromis* (see p. 55 and further discussion on p. 66).

The anguloarticular is deep and stout. Its anteroventral arm, which barely underlies the posteroventral edge of the dentary, has a blunt anterior margin (Fig. 40).

Lower jaw length is 22–38% head length (modal range 34–35%) and is thus shorter than in a generalized syncranium but comparable with that in some derived lineages (eg *Paralabidochromis* and *Macropleurodus*). Usually the lower jaw is longer than broad (1.3–1.4 times longer).

Contained species

The taxa are listed in order of their increasing derivation.

Ptyochromis sauvagei (Pfeffer), 1896. Lake Victoria; see Greenwood (1957 : 76–81).

Ptyochromis annectens (Regan), 1922. Lake Victoria; see Greenwood (1957 : 82–6) where the species is referred to as *Haplochromis prodromus* Trewavas, 1935. *Ptyochromis annectens* was originally described by Regan (1922) as *Haplochromis annectens* but when Trewavas (1935) transferred the Lake Malawi species *Cyrtocara annectens* Regan, 1921 to the genus *Haplochromis*, she proposed the replacement name *prodromus* for the then homonymous Victoria taxon. With the removal of Regan's 1922 species from the genus *Haplochromis*, his original specific epithet again becomes available.

Ptyochromis granti (Blgr.), 1906. Lake Victoria; see Greenwood (1957 : 86–90).

Ptyochromis xenognathus (Greenwood), 1957. Lake Victoria; see Greenwood (1957 : 90–5).

DISCUSSION

In an earlier review of relationships amongst Lake Victoria haplochromine species (Greenwood, 1974, fig. 70), the four species now referred to *Ptyochromis* were also grouped together, and with the addition of two species currently placed in *Paralabidochromis* (p. 71), were considered to be the sister group of *Macrolepurodus*.

Both *Ptyochromis* and *Macrolepurodus* share certain derived features in the morphology of the lower jaw, namely an outer tooth row dipping ventrally over the anterior half of its length, a deep and stout anguloarticular complex whose anteroventral arm has an obtuse anterior margin, and a dentary whose lateral walls, at least anteriorly, are abruptly curved inwards from almost the level of the alveolar surface, so that they are aligned more nearly horizontally than vertically.

Dentally, there is little in common between the two lineages (cf. pp. 62 & 82), except for the strongly recurved tooth form in both. Certainly the teeth in two *Paralabidochromis* species (see p. 69) more closely resemble those of juvenile *Macrolepurodus* than do the teeth in any *Ptyochromis* species.

All the derived jaw features shared by *Ptyochromis* and *Macrolepurodus* are also present in *Paralabidochromis* (see pp. 64, 70 & 83) although the inward slope of the dentary wall is less well-developed in that lineage.

Trophically, both *Ptyochromis* and *Macrolepurodus* share a derived feeding habit, that is, the oral removal of a snail's shell before its soft parts are ingested (see Greenwood, 1974 : 69 *et seq.*). *Paralabidochromis* species, on the other hand, are all insectivores with some taxa known to be specialized in their ability to remove insect larvae and pupae from burrows in wood or rock (Greenwood, 1959b : 210).

In brief, *Ptyochromis*, *Macrolepurodus* and *Paralabidochromis* all share a number of derived features in the jaws and detailed morphology of their jaw bones (especially the lower jaw), and in the way the outer row of teeth is inserted on the dentary. All have a similar and derived neurocranial form. The teeth and the dental pattern are derived in all three genera, with those of *Ptyochromis* and *Paralabidochromis* more alike than either is to *Macrolepurodus* which has the most derived tooth morphology and dental pattern (see p. 82).

From the evidence available it is impossible to indicate precise interrelationships between the three genera, although the original concept of their being more closely related to one another than to any other lineage (Greenwood, 1974) does seem to be corroborated by the characters discussed above and on p. 84. (See also p. 95).

The peculiar alignment of the outer tooth row in the dentary in these genera resembles closely that of *Psammochromis* (see p. 55). There is a further resemblance in the way the anterior wall of the dentary immediately below the displaced section of the tooth row is thickened and bullate. In other respects, however, the morphology of the dentary (and its anguloarticular bone) in *Psammochromis* is near the elongate and shallow generalized type, and not like the relatively deep, short and stout bone in *Macrolepurodus*, *Paralabidochromis* and some *Ptyochromis* species. But, in two *Ptyochromis* (*P. sauvagei* and *P. xenognathus*) the proportions of the dentary are intermediate between those of *Psammochromis* and the dentary in the other *Ptyochromis* species. In turn, these other *Ptyochromis* species intergrade with the *Paralabidochromis* and *Macrolepurodus* conditions, so that there is, in effect, a

morphocline in dentary proportions running from *Psammochromis* to *Macropleurodus* (as representatives of the two extreme conditions).

The slender but strong, tall and recurved outer jaw teeth in *Psammochromis* must be ranked as derived in relation to the unequally bicuspid, slightly recurved and stout teeth characterizing many lineages. Basically, the *Psammochromis* tooth-form approaches that of *Ptyochromis*, albeit one less strongly recurved and with the crown more obviously compressed. They could, however, be considered the plesiomorph 'sister form' of the *Ptyochromis* type.

Neurocranial shape in *Psammochromis* differs quite markedly from that in the other three genera under consideration (see p. 54); it represents a slight departure from the generalized type towards that of the predatory piscivorous lineage *Prognathochromis*. That is, a slight overall elongation and streamlining of the basic form, as compared with the foreshortening and elevation of that type manifest in *Ptyochromis*, *Paralabidochromis* and *Macropleurodus*.

Considering the various synapomorphies discussed above, their range of expression and their differences, *Psammochromis* could be included as a member of an assemblage forming the sister group of *Ptyochromis*, *Paralabidochromis* and *Macropleurodus* combined. In most respects the level of derivation (from their hypothetical common ancestor) which *Psammochromis* has reached, appears to be much less marked than that shown by any other member of the total assemblage.

***PARALABIDOCHROMIS* Greenwood, 1956**

TYPE SPECIES: *Paralabidochromis victoriae* Greenwood, 1956. Lake Victoria.

Note. Regan (1920:45) erected the genus *Clinodon* for the species *Hemitilapia bayoni* Blgr, 1908. The paratype of that species, which Regan examined, was later chosen as the holotype for *Haplochromis plagiodon* Regan & Trewavas (1928:224-5), a species which I now include in the genus *Paralabidochromis*. Since the holotype of *Hemitilapia bayoni* Blgr., (see Boulenger, 1915: 491, fig. 340) the designated type species of Regan's *Clinodon* is, however, referable to *Haplochromis obliquidens* (see Greenwood, 1956b: 226-232, and 1979:278), the older name *Clinodon* is not available for the taxon here called *Paralabidochromis*.

DIAGNOSIS. Haplochromines with a maximum adult size range of 70-150 mm SL, a forceps-like dentition (lower teeth implanted procumbently), lips somewhat thickened (hypertrophied and lobate in one species), mouth horizontal, dorsal head profile straight, or slightly concave, and sloping fairly steeply.

Neurocranium with a deep preorbital region (33-37% neurocranial length cf. 25-30%, modal range 26-27% in the generalized skull); entire preorbital gently curved and sloping at an angle of 45°-50°. Supraoccipital crest of variable outline, from near pyramidal to deeply wedge-shaped.

Dentary foreshortened and deep, with a marked lateral bullation in the region of its division into coronoid and horizontal arms. *Profile of the symphyseal region with a pronounced posteroventral slope giving the jaw a distinctly chinless appearance.* Lower jaw length 30-49% head length (modal range 33-35%).

Premaxilla with slightly inflated dentigerous arms (oval in cross-section), its ascending processes as long as, or slightly longer than dentigerous arms. *Maxilla foreshortened,* its posterior arm deep but not markedly bullate.

Outer jaw teeth strong, slender, recurved and cylindrical in cross-section, the crown somewhat compressed when bicuspid, otherwise cylindrical. Teeth anteriorly and anterolaterally in the lower jaw implanted procumbently, sloping forwards and upward at an angle of ca 45°-50°. Upper jaw teeth implanted almost vertically, but when the premaxilla is *in situ* they are inclined forwards to form, with the procumbent lower teeth, a forceps-like dentition. *Relatively few outer teeth in both jaws, 16-48 (modal range 30-35) in the*

premaxillary outer row. Cusp form variable but usually bicuspid in fishes <65–70 mm SL, and unicuspid, near conical in larger individuals.

Inner teeth arranged in 2 or 3 (rarely 1 or 4) rows, separated from the outer row by a distinct interspace.

Lower pharyngeal bone short and broad, the median row teeth coarse but rarely submolariform.

DESCRIPTION

Habitus (Fig. 41). Body form departs but slightly from the generalized *Astatotilapia* shape, with the dorsal head profile straight or slightly concave and sloping fairly steeply. The lips are somewhat thickened in all species and are hypertrophied, even lobate, in *P. chilotes*.

Maximum adult size range is from ca 70–150 mm SL.

Neurocranium. Skull form departs somewhat from the generalized condition in that the preorbital region is relatively deeper (33–37% neurocranial length, cf. 25–30%, modal range 26–27%) and in consequence the preorbital profile slopes more steeply (ca 45°–50°) and is slightly curved (Fig. 42). The supraoccipital crest is a little higher relative to the generalized condition, and varies in profile from pyramidal to deeply wedge-shaped.

Dentition. The outer jaw teeth are strong and robustly slender, recurved, and cylindrical in cross-section, the crown slightly compressed when bicuspid. Teeth anteriorly in the lower jaw are implanted procumbently so that they slope forward and upward at an angle of ca 45°–50° to the horizontal. All species have the anterior and immediately anterolateral

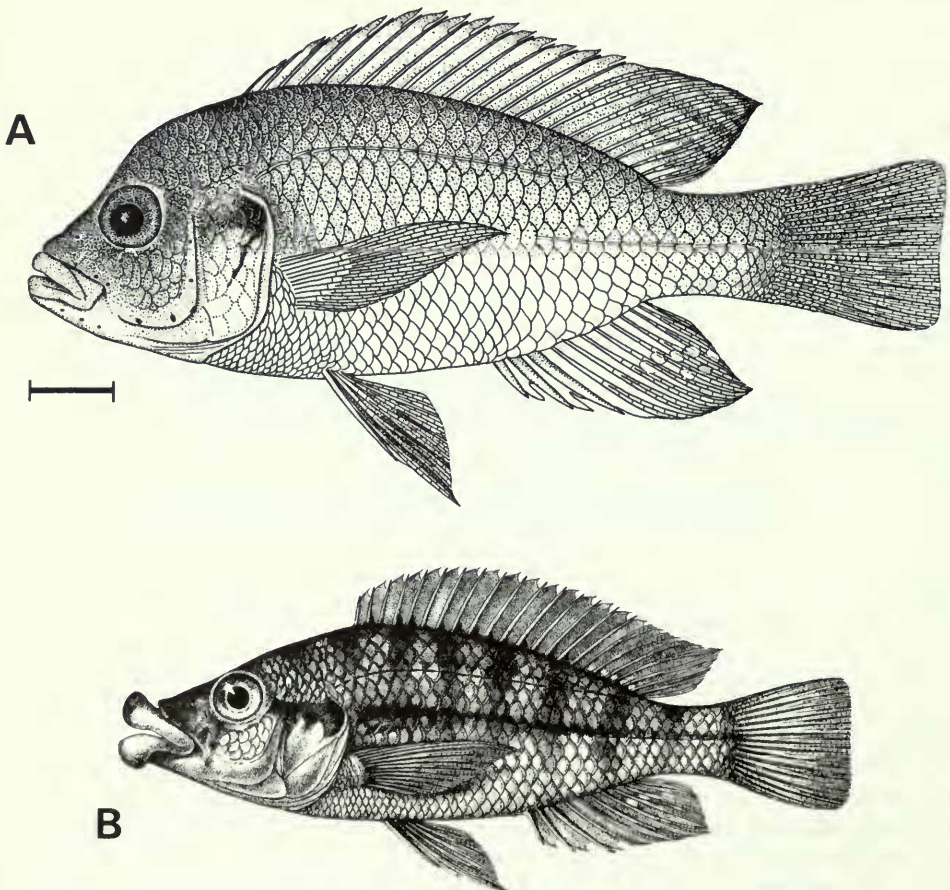


Fig. 41 A. *Paralabidochromis labiatus*. Lake George. Scale = 1 cm. B. *Paralabidochromis chilotes*. Lake Victoria. About two-thirds natural size.

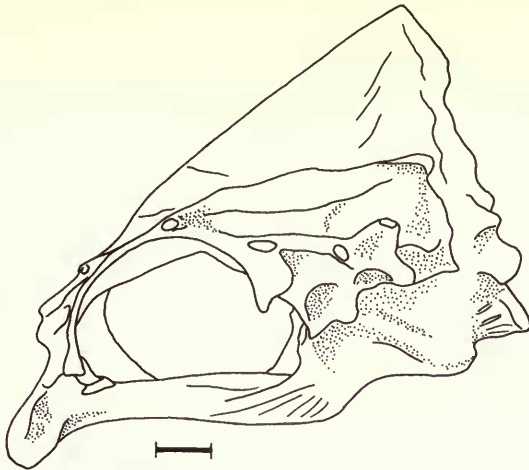


Fig. 42 Neurocranium (left lateral view) of *Paralabidochromis chilotes*. Scale = 3 mm.

teeth longer than the lateral ones; the size discrepancy being more marked in some species than in others. Since anteriorly the line of insertion for these outer teeth has a distinctly ventral direction, their tips lie at about the same level as those of the inner rows.

The upper teeth are inserted almost vertically on the premaxilla, but when that bone is *in situ* it slopes at an angle such that the anterior upper teeth are directed procumbently, and they occlude with their counterparts in the lower jaw to provide a forceps-like dental arrangement.

In most species the dental arcade in both jaws, but particularly that in the premaxilla, narrows anteriorly to give it a narrow-based 'U'-shaped outline.

There are relatively few teeth in the outer row of either jaw, the premaxillary series having 16–48 (modal range 30–35).

Cusp form is interspecifically variable, but is predominantly bicuspid in most specimens of all species at a standard length of less than 65–70 mm.

Species in which the definitive outer dentition is unicuspid have a near-conical tip to the crown, which is thus more robust than in the typical unicuspid teeth in such lineages as *Harpagochromis* and *Prognathochromis*.

In one species, *P. victoriae*, the anterior teeth in both jaws are more slender and are relatively longer than those in other members of the genus, thus enhancing the forceps-like nature of the dentition (see Greenwood, 1956a : 328, and fig. 10).

Two types of bicuspid teeth occur in *Paralabidochromis*. The commoner is close to the generalized kind but has the cusps of markedly unequal size, the major one approximately equilateral in outline and less compressed than in the generalized tooth; the minor cusp may be relatively smaller in *Paralabidochromis* teeth. The second cusp type has so far been recorded, as the predominant form, in only one species, *P. plagiodon*. Here the minor cusp is aligned at a slight angle so that it resembles a weak spur, and the posterior margin of the major cusp slopes obliquely forward to meet its near vertical anterior margin at a somewhat obtuse angle; the entire cusp is also more compressed than in the other type of tooth (Fig. 43). In other words, cusp form in *P. plagiodon* resembles that in *Haplochromis lividus* (Greenwood, 1956b : fig. 2B; 1959 : 206; and 1979 : 278), although it is stouter overall and the anterior angle of the major cusp lies in the same vertical as the neck of the tooth (not outside it as in *Haplochromis*).

Unlike the generalized bicuspid, where the crown is expanded relative to the neck, in neither type of *Paralabidochromis* tooth is the crown much wider than the neck.

Inner teeth are tricuspid (sometimes weakly so) or, in specimens > 90 mm SL, a mixture of tri- and unicuspids. They are arranged in 2 or 3 rows (rarely in 1 or 4 rows), and are always

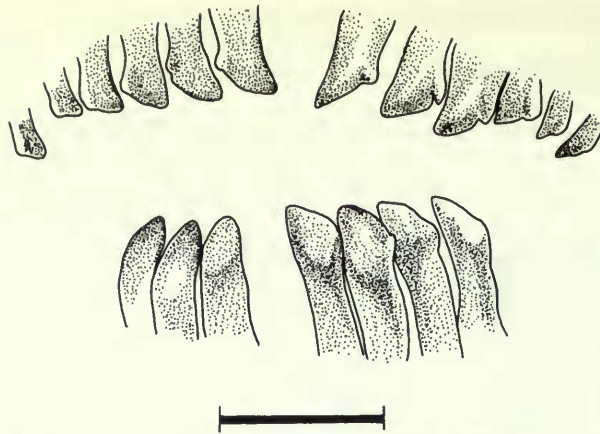


Fig. 43 Outer jaw teeth of *Paralabidochromis plagiodon*, viewed *in situ* and from in front, to show the nature of the crowns. Since the lips are not fully reflected, the bases of the teeth are not visible. Scale = 1 mm.

separated from the outer teeth by a distinct interspace; in some individuals the outermost inner row is composed, anteriorly, of teeth slightly larger than those of the other inner rows, but still distinctly smaller than the outer row teeth.

Mouth. The lips are thickened in all *Paralabidochromis* species and are hypertrophied in *P. chilotes*; some individuals of that species have both lips produced into prominent medial lobes, but in others the lobes may be represented only by a slight bulbous swelling (see Greenwood, 1959b : 208, and fig. 11). The mouth is horizontal, and both jaws are equal anteriorly.

Upper jaw. The dentigerous arms of the premaxillae are somewhat inflated, especially anteriorly and anterolaterally (where the bone is a compressed oval in cross section). Inflation is more marked in some species than in others. The ascending processes are as long as, or slightly longer than the dentigerous arms.

The maxilla is foreshortened and its posterior arm is relatively deep; the medial face of the latter is not markedly concave and thus there is no strong bullation of its lateral aspect. The articular head of the bone curves gently mediad.

Lower jaw. The dentary is short and deep, giving the entire lower jaw a foreshortened appearance (Fig. 44). This impression is enhanced by the bullation of each ramus near its

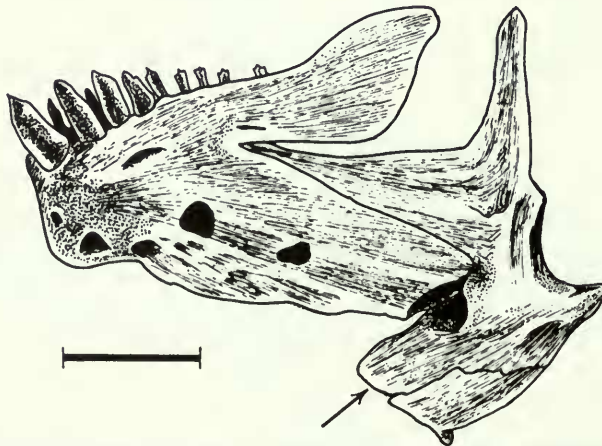


Fig. 44 Lower jaw of *Paralabidochromis crassilabris*, seen ventrolaterally from the left, to show the anterior margin of the anguloarticular (arrowed). Scale = 2 mm.

division into ascending (coronoid) and horizontal limbs. In these respects the dentary resembles that found in some other lineages (eg *Lipochromis*, *Neochromis* and *Macrolepurodus*).

Its anterior profile, both in lateral and in ventral views, is most characteristic. The symphyseal region of the bone has a pronounced posteroventral slope which gives it a rather 'chinless' look in lateral view. This area is also slightly expanded horizontally and the bone hereabouts is noticeably thickened. Anteriorly, each ramus has only a gently curved mediad inclination so that the entire jaw, when viewed from above, has a bluntly apexed V-shaped outline. In all these respects the dentary of *Paralabidochromis* is unlike that in *Lipochromis* and *Neochromis*, and in most respects that of *Macrolepurodus* as well; see above.

In three species (*P. crassilabris*, *P. plagiodon* and *P. beadlei*) the lateral wall of each ramus has, anteriorly, a fairly marked mediad curvature so that it slopes inwards rather than almost vertically downwards (see also *Ptyochromis* and *Macrolepurodus*, pp. 64 & 84 respectively).

The anguloarticular is deep and robust, the anterior point of its anteroventral arm blunt or rectangular in outline (Fig. 44).

Lower jaw length ranges from 30–49% of head length (modal range 33–35%); the jaw is always narrower than it is long. In both these features *Paralabidochromis* broadly overlaps the majority of non-piscivorous lineages whose adults have a maximum length of less than 115 mm, but its modal lower jaw length is slightly lower.

Lower pharyngeal bone and dentition. The bone is short and broad, its triangular dentigerous area always broader than it is long. All but two species have the median tooth rows composed of coarse teeth, and in some individuals of certain species these teeth (especially the posterior few) have submolariform crowns; otherwise the crown is bicuspid and compressed.

Contained species

The taxa are grouped, approximately, in order of their related and increasing derivation.

Paralabidochromis beadlei (Trewavas), 1933. Lake Nabugabo; see Greenwood (1965: 335–41).

Paralabidochromis paucidens (Regan), 1921. Lake Kivu; see Regan (1921: 638).

Paralabidochromis crassilabris (Blgr.), 1906. Lake Victoria; I have not yet published a revised description of this species; the information used here is derived from the specimens used by Regan (1922: 167–8) in his previous revision, supplemented by new material and osteological preparations.

Paralabidochromis labiatus (Trewavas), 1933. Lakes Edward and George; see Greenwood (1973: 196–9).

Paralabidochromis plagiodon (Regan & Trewavas), 1928. Lake Victoria; see Greenwood (1959b: 205–7); and note on p. 67 above.

Paralabidochromis chromogynos (Greenwood), 1959. Lake Victoria; see Greenwood (1959b: 212–4).

Paralabidochromis chilotes (Blgr.), 1911. Lake Victoria and probably, the Victoria Nile; see Greenwood (1959b: 207–12).

Paralabidochromis victoriae Greenwood, 1956. Lake Victoria; see Greenwood (1956a: 328–9).

DISCUSSION

Paralabidochromis victoriae has the most derived and forceps-like dentition of all the species, yet morphologically speaking, the various stages in its evolution are represented in

other members of the lineage. The least derived conditions are those seen in *P. beadlei* (Lake Nabugabo), *P. paucidens* (Lake Kivu) and *P. labiatus* (Lake Edward and George) and *P. crassilabris* (Lake Victoria). Two Lake Victoria species *P. chromogynos* and *P. chilotes*, in that order, most closely approach *P. victoriae*.

Paralabidochromis plagiodon, although retaining a basically plesiomorph tooth form for a member of this lineage (but a distinctly apomorph one relative to the basic bicuspid tooth) does exhibit certain autapomorphic features in the crown shape of these teeth (see p. 69 above). The expansive, obliquely margined major cusp, the small spur-like minor cusp, and the somewhat buccally orientated crown (Fig. 43) set *P. plagiodon* apart from other members of the lineage (with which it nevertheless shares several synapomorphies).

Its distinctive dental features, however, do approach those seen in small specimens (< 90 mm SL) of *Macrolepurodus*, a genus which differs from *Paralabidochromis* in several autapomorphic dental characters and some osteological ones as well. The *Macrolepurodus*-like features in the dentition of *P. plagiodon*, together with certain derived features in the morphology of the lower jaw shared by *Macrolepurodus* and all species of *Paralabidochromis*, suggest that the lineages could have shared a relatively recent common ancestry. This, and other possible interrelationships of *Paralabidochromis*, are discussed further on pages 66, 84 & 93.

HOPLOTILAPIA Hilgendorf, 1888

TYPE SPECIES (*Paratilapia?*) *retrodens* Hilgendorf, 1888. Lake Victoria; see Greenwood (1956a: 319 & 321) for detailed synonymy.

DIAGNOSIS. Haplochromines with an adult size range of ca 96–145 mm SL, characterized by a number of dental and syncranial specializations.

The dentary has an almost square anterior outline, is very shallow over most of its length, is 'chinless' and has a marked lateral bullation of the area surrounding its bifurcation into ascending (coronoid) and horizontal arms. In the entire fish it has a very shovel-like appearance.

Premaxilla with very strongly inflated dentigerous arms, the broad alveolar surface extending almost to their posterior tips, and virtually circular in cross-section.

Teeth in both jaws are arranged in broad bands (5–10 rows deep) of almost uniform width over their entire length; those of the outer row not separated by a distinct interspace from the inner rows, and, at least in fishes > 75 mm SL, continuing almost to the crown of the coronoid process (and often accompanied by one or more inner rows). Unicuspid teeth predominate in both the inner and outer rows of specimens in the known size range (ca 55–145 mm SL), but some bi- and tricuspid teeth occur amongst the inner rows in fishes < 100 mm SL.

DESCRIPTION

Habitus (Fig. 45). The straight or weakly concave, steeply sloping dorsal head profile, coupled with the broad, horizontal mouth and shallow, square-ended lower jaw give *Hoplotilapia* a very characteristic appearance. In other respects it is a typical, moderately deep-bodied haplochromine (depth of body 31–42% of SL, mean 38%).

The adult size range is from 96–145 mm SL.

Neurocranium. The skull has a moderately steep (50°–55°) and straight or very gently curved preorbital profile (see Greenwood, 1956a: fig. 8A; and 1974: fig. 76). Its preorbital depth is 34–35% of neurocranial length (*ie* deeper than the generalized type).

The supraoccipital crest is relatively high and expansive, with a near-pyramidal outline.

Dentition (See also Greenwood, 1956a: 322, fig. 8B; and 1974: fig. 74). In both jaws the outer row teeth are slender but strong, cylindrical in cross-section, strongly recurved, and with the crown but slightly, if at all, compressed.

Outer teeth in the lower jaw (Fig. 46) are implanted procumbently (the neck almost horizontal); those situated anteriorly in the upper jaw are effectively procumbent because the

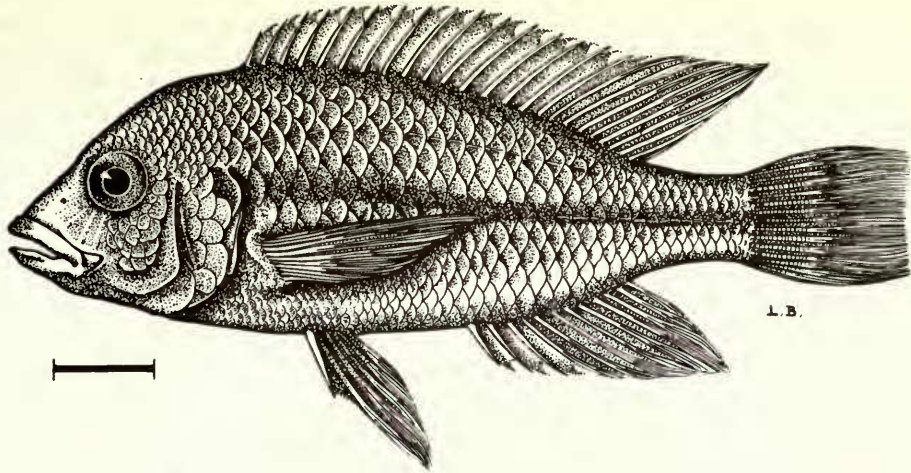


Fig. 45 *Hoplotilapia retrodens*. Lake Victoria. Scale = 2 cm.

premaxillary alveolar surface slopes forward and upward at an appreciable angle. Because of their strong recurvature, the crowns of the anterior teeth in the lower jaw are directed almost vertically, despite the near-horizontal alignment of their necks.

Most fishes > 75 mm SL have the outer row of dentary teeth continuing onto the coronoid process of the bone, and ending near the coronoid crest (see below).

Unicuspid teeth predominate in the outer row of most specimens in the size range available for study (*ie* 55–144 mm SL), but a few lateral and posterolateral teeth may show faint traces of a minor cusp.

There are 40–68 teeth in the outer premaxillary row.

Unicuspid teeth also predominate in the inner tooth rows, with some bi- and tricuspid teeth present, especially in smaller fishes.

This predominance of unicuspid teeth in fishes < 90 mm SL can be considered a derived characteristic.

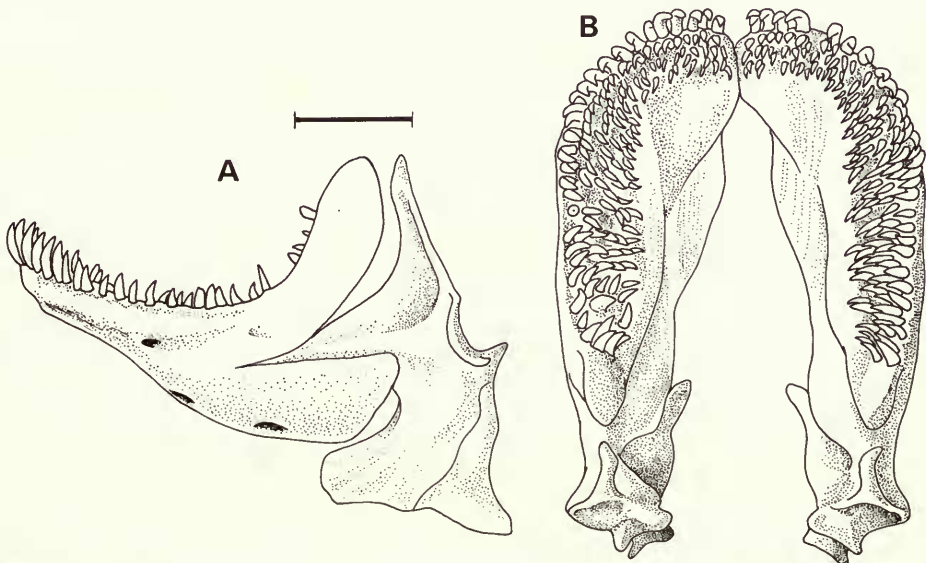


Fig. 46 Lower jaw of *Hoplotilapia retrodens* in: A. Lateral view, and B. occlusal view. Scale = 3 mm.

The most outstanding dental feature in *Hoplotilapia* is the great and almost uniform breadth of the tooth bands over the entire length of the dentigerous surface in both jaws (Figs 46 & 47). It will be recalled that the outer row of teeth in the lower jaw usually extends to near the apex of the coronoid process; the inner rows (here somewhat reduced in width) also extend onto the coronoid process, but stop short of the outer row by a distance of two or three outer teeth.

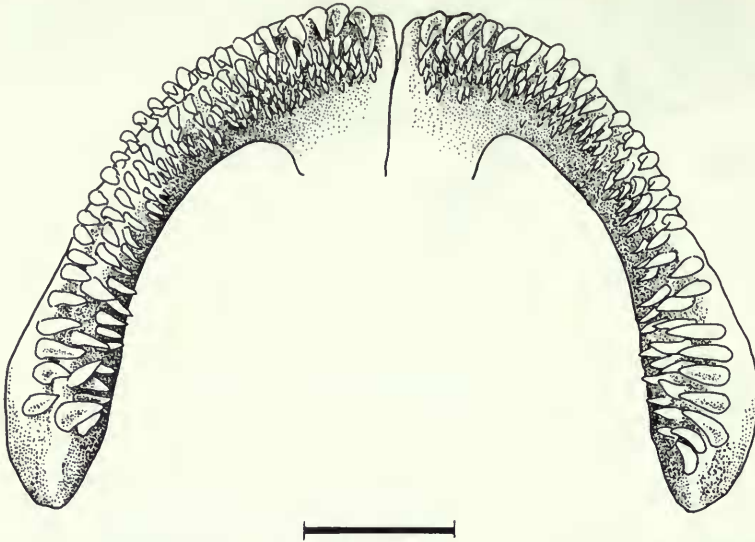


Fig. 47 Dentigerous surface of the premaxilla in *Hoplotilapia retrodens*, to show dental pattern. Scale = 3 mm.

Teeth forming the inner rows are not particularly close set, but are inserted across the entire width of the alveolar surfaces involved. There are 5–8 rows of teeth anteriorly, and 4–5 rows posteriorly on the premaxilla, with 5–10 anteriorly and 3–5 posteriorly on the dentary (see also Greenwood, 1956a: 322).

Upper jaw. The premaxilla is a robust bone with very strongly inflated dentigerous arms that are virtually cylindrical in cross-section, each widest over the posterior quarter of its length. The posterior fifth of each arm is bulbous (Fig. 47).

The ascending processes are much shorter than the dentigerous arms (half to two-thirds the length), and the articular processes are stout and anteroposteriorly expanded.

The maxilla is somewhat foreshortened and relatively deep, with a deeply concave medial face to its posterior arm (and a correspondingly bullate lateral face). Its articular head is strongly curved mediad.

Lower jaw. The dentary is a most distinctive bone, unlikely to be confused with the dentary in any other haplochromine from the Victoria–Edward–Kivu flock.

It is stout, with an almost vertical ascending (coronoid) arm which is, relative to the depth of the ramus, markedly elevated (Fig. 46A). This apparent shallowness of the dentigerous ramus is attributable to the way in which its lateral wall curves abruptly mediad from a level just below the alveolar surface. As a result of this curvature, the greater part of the ramus is almost horizontally (and not vertically) aligned and underlies the very broad alveolar surface (see Fig. 46B) beyond which it extends medially.

In lateral view the dentary is devoid of a 'chin', its anterior profile sloping steeply backwards and downwards. Whereas in other haplochromines the symphyseal surface is either vertical or is inclined posteriorly, in *Hoplotilapia* it lies at an angle of ca 45° to the horizontal. The actual articular surface of the symphysis is relatively narrow in the vertical plane, but it is extensive in the near horizontal plane.

The region surrounding the dentary's bifurcation into ascending and horizontal arms is inflated, the lateral bullation emphasized by the shallowness of the ramus in that area.

About the anterior half of each ramus curves strongly medially so that the anterior margin of the entire lower jaw is subrectangular when viewed dorsally.

The anguloarticular is deep and stout, the anterior margin of its anteroventral arm deep and rectangular in outline.

Lower jaw length is 34–41% of head length; the length/breadth ratio of the jaw varies intraspecifically from broader than long to 1.3 times longer than broad.

Lower pharyngeal bone and dentition. The bone is short and broad, its triangular dentigerous area equilateral in outline. All the teeth are cuspidate and relatively coarse, with those of the median rows stouter than the others (except for the posterior transverse row).

Contained species

Hoplotilapia retrodens Hilgendorf, 1888. Lake Victoria and, probably, the Victoria Nile; see Greenwood (1956a: 319–326).

DISCUSSION

Although many of the derived features characterizing *Hoplotilapia* are autapomorphies (e.g. the gross morphology of the lower jaw, the form of the premaxilla, and the dental pattern in both jaws), most would seem to be foreshadowed in the *Pytochromis* lineage, especially in *Pytochromis xenognathus* and *P. annectens* (see pp. 62–65 above).

For example, in *Pytochromis* the tooth bands are broad in both jaws (but particularly in the dentary), there is a distinct tendency for the lateral wall of the dentary to curve sharply medially, the teeth in the lower jaw are procumbent, the outer teeth in both jaws of larger specimens are strong but slender unicuspid and have markedly recurved crowns.

There are other resemblances too; for instance in overall neurocranial architecture, the robust lower jaw, the morphology of the anguloarticular bone, and the inflated dentigerous arms of the premaxilla. These could, however, be the products of convergence associated with the evolution of strong jaws since some or all of the features occur in *Neochromis* and *Lipochromis*, lineages that share no other derived characters with *Hoplotilapia* (see p. 52).

Those characters apart, the other synapomorphies do seem to suggest that *Hoplotilapia* may share a common ancestry with *Pytochromis*, and by an extension of that relationship, with *Paralabidochromis* and *Macropleurodus* as well (see pp. 66–67). This argument will be elaborated and evaluated when the possible relationships of *Hoplotilapia* and *Platytaeniodus* have been considered (see p. 80 below).

PLATYTAENIODUS Boulenger, 1906

TYPE SPECIES: *Platytaeniodus degeni* Blgr., 1906. Lake Victoria; see Greenwood (1956a: 312 & 315) for detailed synonymy.

DIAGNOSIS. Haplochromine fishes with an adult size range of ca 70–155 mm SL, readily diagnosed by their peculiar dental pattern.

Teeth in the dentary are grouped into two broad pyriform patches, contiguous anteriorly. In the premaxilla the teeth are arranged in a broad, inverted U-shaped band, whose arms and base are of almost uniform width in fishes < 100 mm SL, but in larger fishes the posterior parts of the arms are expanded medially so that they approach one another closely in the midline (Fig. 51). There are corresponding modifications to the shape of the premaxilla and dentary, the latter having a near-circular outline when viewed occlusally (Fig. 50).

DESCRIPTION

Habitus (Fig. 48). The gently curved, moderately steeply sloping dorsal head profile, coupled with the thickened, broad, beak-like projection of the premaxilla and the rounded anterior margin of the dentary, give to *Platytaeniodus* a most unusual physiognomy. This distinction is enhanced by the thickened lips (the lower often lying outside the upper lip), and by the almost completely hidden maxilla.

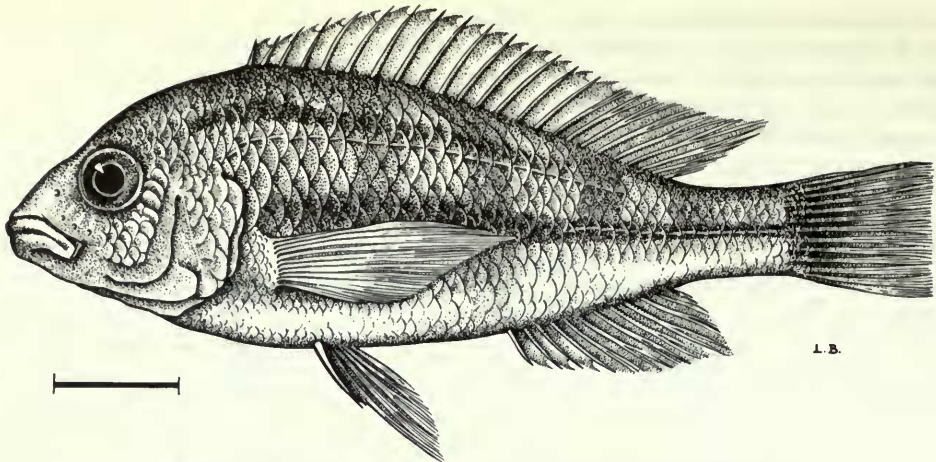


Fig. 48 *Platytaniodus degeni*. Lake Victoria. Scale = 2 cm.

Adult size range is from 71–154 mm SL.

Neurocranium. Skull morphology in *Platytaniodus* is close to that of *Paralabidochromis* (Fig. 49); that is, an anteriorly deepened variant of the generalized form (preorbital skull depth 36–37% of neurocranial length), with the preorbital region fairly strongly decurved and sloping at an angle of *ca* 55°–60° to the horizontal. The supraoccipital crest is moderately high, its outline near-pyramidal, and the anterior margin straight or gently curved.

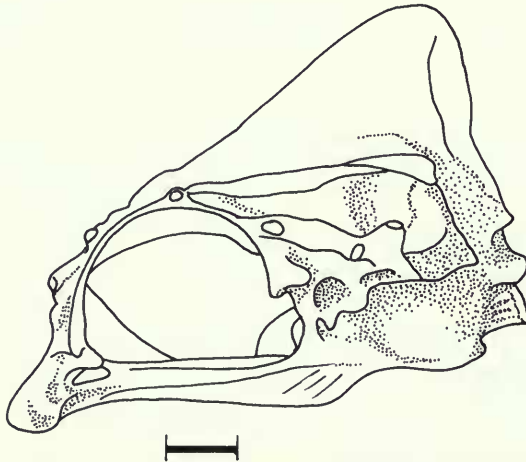


Fig. 49 Neurocranium (left lateral view) of *Platytaniodus degeni*. Scale = 3 mm.

Dentition (See also Greenwood, 1956a: 312–3, 316 & fig. 6; 1974: fig. 73). The outer row teeth in both jaws are moderately slender but strong, are implanted vertically and are close-set. An admixture of uni- and unequally bicuspid teeth occurs in fishes of all sizes (smallest seen 67 mm SL), with unicuspid teeth predominating in fishes > 90 mm SL. Unicuspid teeth have slender, conical crowns that are slightly broader than the near-cylindrical neck of the tooth; bicuspids have the crown a little compressed. In neither form is the crown strongly recurved; usually it is straight.

There are 36–50 teeth in the outer row of the premaxilla.

Inner teeth are either unicuspid or tricuspid, or there may be an admixture of both kinds with tricuspids predominating in fishes < 100 mm SL (particularly in the innermost rows).

There is a very gentle size-gradient between the outer row teeth and those of the inner rows. Virtually no interspace separates the two series. Like the outer teeth, those of the inner series are tall, slender and strong. Teeth in the innermost 2 or 3 rows are more compressed than the others. Implantation is vertical, and the crowns are slightly recurved.

It is in the arrangement of its jaw teeth that *Platytaeniodus* departs most markedly from the other lineages (Figs 50 & 51).

In both jaws the teeth are arranged in broad bands composed of 5–9 rows in the premaxilla and 5–7 in the dentary. There is no obvious anteroposterior decrease in the number of premaxillary rows but there is a size-correlated change in the dental pattern (Figs 50 & 51).

Small fishes (< 100 mm SL) have the bands either of uniform width over the entire length of the premaxillary alveolar surface, or there is a slight medial expansion of the rows on the posterior third of that surface (Fig. 50A). In larger fishes this medial expansion is continued

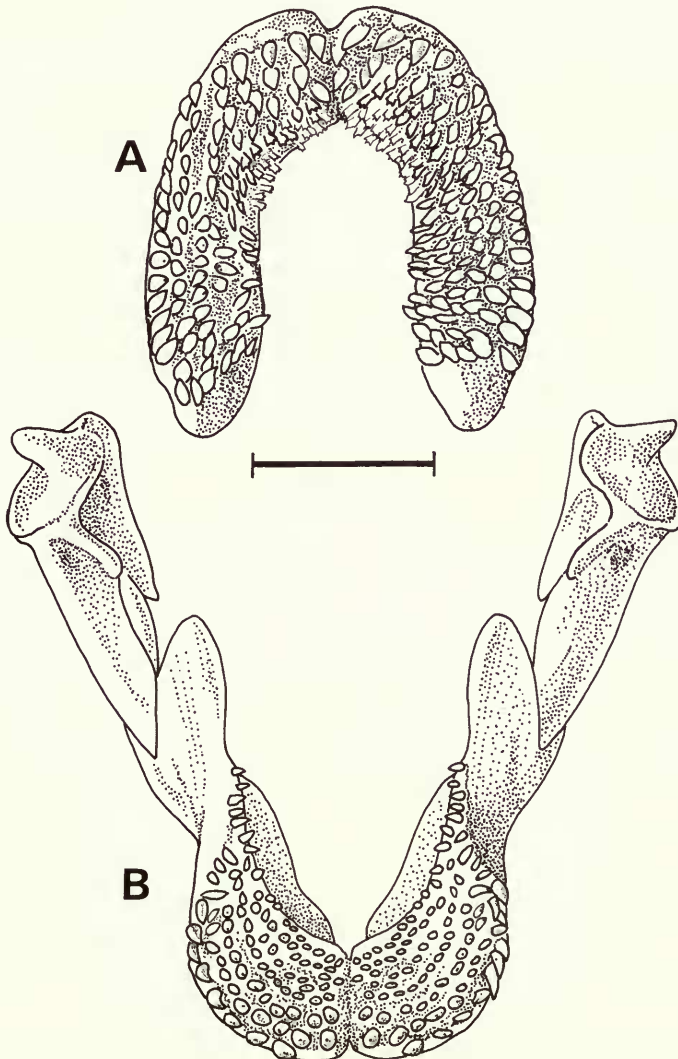


Fig. 50 *Platytaeniodus degeni*. A. Occlusal view of premaxillary dental surface. B. Lower jaw, in occlusal view.

From a small specimen (80 mm SL) to show dental pattern of premaxilla (cf. Fig. 51). Scale = 3 mm.

until, in fishes > 120 mm SL, the inner aspects of each arm are narrowly separated from one another (Fig. 51).

It should be stressed that this local expansion of the alveolar surface is not correlated with any increase in the number of tooth rows carried on it; these are always equal in number, or at most slightly fewer than those on the anterior and anterolateral regions of the bone.

Tooth bands on the lower jaw are less subject to variation in shape with body size. The teeth are confined to the anterior and anterolateral regions of the jaw, and are grouped into two broad patches roughly pyriform in outline and contiguous at the symphysis. Posteriorly on each side there is a short, single row of up to seven teeth lying between the main dental concentration and the base of the ascending arm of the dentary; these teeth are apparently a posterior extension of the outer tooth row.

Each pyriform patch is broadest anteriorly, narrowing rather abruptly over about its posterior sixth (Fig. 50B); before that point there is no decrease in the number of tooth rows.

The teeth in both jaws are so arranged that the tips of their crowns all lie in the same plane (and not, as is usual, with those of the outer row above the others).

As might be expected with a tooth pattern of this sort, the supporting bones, especially the dentary, are considerably modified even when compared with those in *Macrolepurodus* and *Hoplotilapia*.

Mouth. The unusual, almost 'duck-billed' appearance of the mouth has already been noted. In most specimens the lower jaw is shorter than the upper, and laterally its well-developed, deep, lip usually lies outside the upper lip, hiding its lower margin posteriorly. The lips are not only thickened, but their free margins are also produced so as to extend above, or as in the case of the upper jaw, below the tips of the teeth.

Upper jaw. The maxilla is foreshortened and deep, with no appreciable mediad curvature of its articular head.

The premaxilla has its dentigerous arms gently inflated, even anterior to the origin of the ascending processes. Here the bone is drawn out into a narrow but deep, shelf-like expansion. The entire dentigerous part of the bone posterior to the shelf is virtually cylindrical in cross-section; it ends, on each side, as a short blunt projection formed

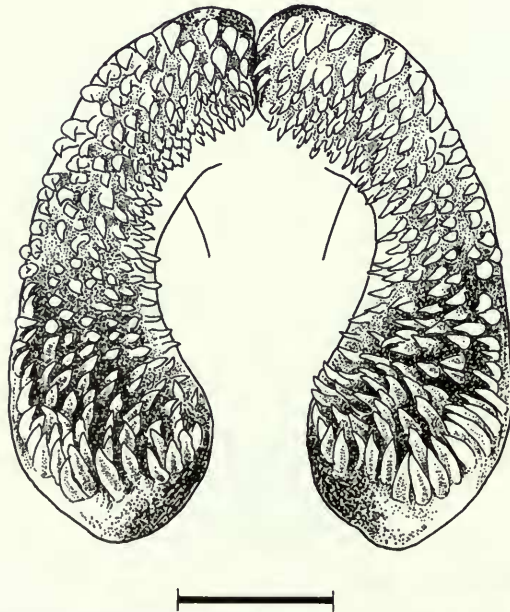


Fig. 51 *Platytaeniodus degeni*. Premaxillary dental surface (in occlusal view); from a specimen 120 mm SL. Scale = 3 mm.

immediately behind the last teeth (Fig. 51). Each arm of the bone has a marked downward curvature over almost the posterior third of its length (Fig. 52).

Both the ascending and the articular processes of the premaxilla are moderately stout; the length of the former is greater than that of the dentigerous arms.

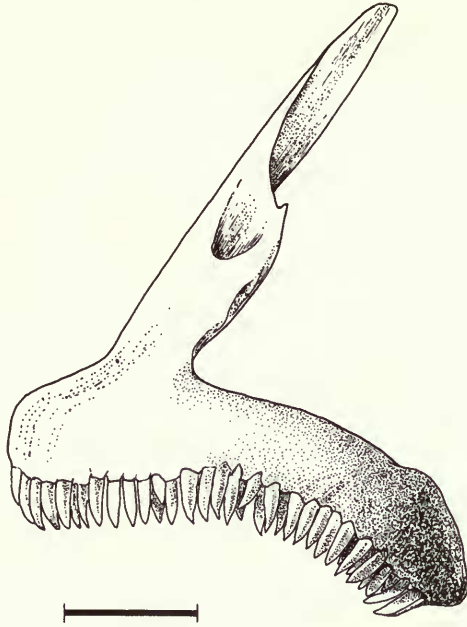


Fig. 52 *Platytaeniodus degeni*. Premaxilla in left lateral view; from a specimen 120 mm SL. Scale = 3 mm.

Lower jaw. In addition to being stout and foreshortened, the dentary has a most extraordinary overall appearance. Posteriorly, in the region of its division into ascending and horizontal arms, it is distinctly inflated, but the greatest departure from the generalized condition is seen anteriorly. The very broad and pyriform alveolar surface, and the bone supporting it, are produced outwards (almost to the ventral margin of the ramus) as an inflated, ovoid swelling. This projects laterally well beyond the rest of the bone (Fig. 50B). Below the swollen area, the ramus continues ventrally in almost the vertical plane; posteriorly, however, it curves sharply mediad, thus further emphasizing the swollen anterior region of the jaw.

As a result of this anterior swelling, the symphyseal area on each ramus is both deep and wide anteroposteriorly, and the dentary has a very characteristic bulbous semicircular anterior outline.

The anguloarticular bone is deep and stout, the anterior margin of its anteroventral arm deep and subrectangular in outline.

Lower jaw length is from 32–40% of head length (mean 37%); the jaw is clearly longer than it is broad (1.2–1.7 times longer).

Lower pharyngeal bone and dentition. The bone is short and broad, its triangular dentigerous surface equilateral in outline. The teeth are coarse and cuspidate, those of the two median rows and the posterior transverse row stouter than the others.

Contained species

Platytaeniodus degeni Blgr., 1906. Lake Victoria; see Greenwood (1956a: 312–318).

DISCUSSION

Most of the derived features characterizing *Platytaeniodus* are autapomorphies (eg the

peculiar dental pattern and shape of the lower jaw; the medial expansion of the premaxillary alveolar surfaces and the overall morphology of that bone). As such they give no indication of the taxon's interrelationships with other haplochromines in or outside the lakes under review.

Only the uniformly broad premaxillary tooth bands extending along the entire length of each premaxillary arm appear at first sight to be a synapomorphic feature shared with *Hoplotilapia* (see p. 74).

In other derived dental features, *Hoplotilapia* and *Platytaeniodus* have little in common, unless it be argued that fundamentally both taxa do have uniformly broad bands of teeth in the lower jaw as well. Those in *Hoplotilapia*, however, extend far onto the ascending process of the dentary, whereas in *Platytaeniodus* they are confined to the horizontal part of the bone, and have a very different arrangement anteriorly (cf Figs 46 & 50B). If the basic pattern is synapomorphic, then each taxon has departed from that basic condition along differently derived pathways.

Another possible synapomorphy lies in the nature of the dentary immediately below the anterior and anterolateral portions of its alveolar surface. In *Platytaeniodus* this region is hypertrophied to form the characteristically bulbous bow of the dentary. In *Hoplotilapia* this region of the dentary is inflated to form a deepened shelf of bone overhanging, laterally, the anteroventral aspects of the ramus; the shelf so formed resembles, albeit in an embryonic way, the peculiar stage-like development of the jaw in *Platytaeniodus*.

The sum of the various apparent synapomorphies shared by *Platytaeniodus* and *Hoplotilapia* would suggest that each taxon is the other's nearest living relative. That *Hoplotilapia* shows some synapomorphic similarities with, ultimately, the *Pytochromis* lineage, could indicate a shared common ancestry for that lineage (that is *Paralabidochromis*, *Macrolepurodus*, *Hoplotilapia* and *Platytaeniodus*). The precise sequence of dichotomies interrelating the different taxa has, however, still to be resolved (see also p. 93).

MACROLEURODUS Regan, 1922

TYPE SPECIES: *Haplochromis bicolor* Blgr., 1906 (type specimen only; see Greenwood, 1956a: 299–301). Lake Victoria.

DIAGNOSIS. Haplochromine fishes reaching a maximum adult size of ca 150 mm SL, usually with a very strongly decurved dorsal head profile (dorsum of snout sloping at ca 70°–80° to the horizontal), a small mouth and thickened lips, *the upper lip displaced laterally by the hypertrophied outer premaxillary teeth which, consequently, are exposed when the mouth is shut.*

Teeth in the outer row of both jaws are stout, with an inwardly directed, strongly recurved major cusp (lying at almost right angles to the neck) and a greatly reduced minor cusp (often merely a slight protruberance on the crown). The minor cusp is vertical and, because of the extreme curvature of the major cusp, lies labially to the tip of that cusp. Fishes > 80 mm SL have, laterally on the premaxilla, one or more inner tooth rows composed of enlarged teeth morphologically similar to those in the outer series.

DESCRIPTION

Habitus (Fig. 53). *Macrolepurodus* has a very distinctive head and mouth, at least in specimens over 60 mm SL (smaller individuals are unknown). The dorsal head profile is generally very strongly decurved, the dorsum of the snout sloping steeply at an angle of 70°–80°; less commonly the profile is slightly curved (and may be straight). Annectant forms link the two extremes (see Greenwood, 1956a: 304–5, fig. 3).

The mouth appears to be relatively small, and has fairly well-developed lips. On one or both sides the upper lip is displaced dorsally by the hyperdeveloped lateral dentition. As a result, the teeth in that region are exposed, and the fish could be described as having a permanent leer on one or both sides of its face.

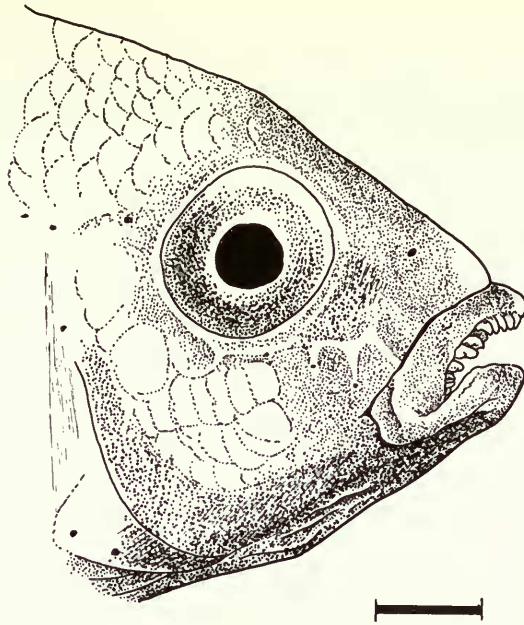


Fig. 53 Head of *Macrolepurodus bicolor* to show naturally displaced upper lip and exposed dentition. Scale = 5 mm.

Adult size range for the only species, *M. bicolor*, is 80–150 mm SL; most specimens are sexually mature at lengths of between 90 and 100 mm.

Neurocranium. Despite some variation in the superficial dorsal outline of the head, the underlying preorbital profile of the skull is invariably steep and curved, the ethmovomerine region sloping at an angle of 80°–85°, its tip clearly reaching a level below that of the parasphenoid (Fig. 54; also Greenwood, 1956a: fig. 4A; and 1974: figs 66 & 76).

As would be expected in a skull of this shape, the preorbital depth of the neurocranium is high (34–37% of neurocranial length), particularly when compared with a generalized skull (24–30%, modal range 26–27%).

The supraoccipital crest is tall and expansive, with a near-pyramidal lateral profile.

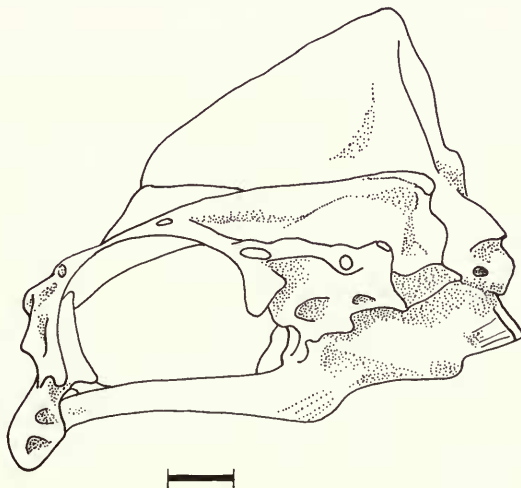


Fig. 54 Neurocranium (left lateral view) of *Macrolepurodus bicolor*. Scale = 3 mm.

Dentition (see also Greenwood, 1956a: 299–301, and 304–5; 1974, fig. 75). The most derived features of *Macrolepurodus* are to be found in its dentition, especially in the morphology of the upper jaw teeth and their arrangement on the premaxilla.

In both jaws, the outer teeth are stout, with a cylindrical to subcylindrical neck which merges gradually into a protracted, conical major cusp aligned almost at right angles to the neck.

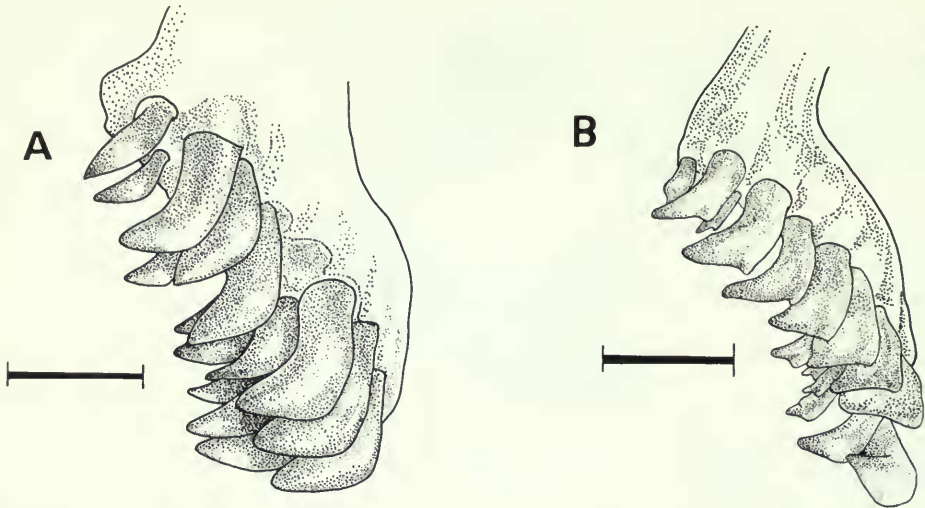


Fig. 55 *Macrolepurodus bicolor*. Left premaxilla; the occlusal surface viewed medially and from somewhat below. A. Large fish (115 mm SL); the minor cusp is absent from all teeth; and B. Smaller individual (88 mm SL), to show the prominent minor cusp on all teeth (cf. Figs 43 & 57).

Superficially, the teeth in fishes > 100 mm SL appear to be unicuspid, but closer examination usually discloses a low bump on one side of the crown near the region of its juncture with the neck (Fig. 55A). In smaller fishes this swelling is discernible as a discrete, spur-like cusp inclined labially (Figs 55B & 57).

The major cusp is directed buccally, the arrangement of the teeth being such that in those situated laterally in the jaws, the crown lies at right angles to the anteroposterior axis of the row.

There is a clear-cut anteroposterior size gradient amongst the outer teeth, better marked in the lower than the upper jaw. Posteriorly in the lower jaw a few teeth barely show the characteristic morphology of the rostral elements in the row, and are little more than stout, incurved, uni- or weakly bicuspid teeth.

Anteriorly and anterolaterally, the outer dentary teeth are implanted somewhat prominently, with the result that the morphologically 'outer' aspect of the crown forms a sloping occlusal surface. This unusual condition is emphasized because the line of tooth insertion dips distinctly ventrad over the anterior half of the dentary.

Premaxillary outer row teeth are, in contrast, vertically implanted; there are 24–40 (modally 34–36) teeth in this row.

Two kinds of inner teeth are present in the premaxilla, at least in fishes > 90 mm SL. Those in the first, or first and second inner rows, are stout, and in shape closely approximate to their counterparts in the outer row. Anterolaterally and laterally these teeth are larger than elsewhere in the row and are crowded together. Teeth forming the innermost row or rows of the series are weakly tricuspid (almost unicuspid) and small (but coarser than equivalent-sized tricuspid teeth of the generalized type).

Such coarse, weakly tricuspid teeth are present in all the inner rows of fishes less than 90 mm SL.

There are 2–4 inner tooth rows anteriorly in the premaxilla, and 1 or 2 posterolaterally. Most of the specimens examined have the dextral tooth band a little wider than the sinistral one, and composed of slightly larger teeth. Symmetrical or sinistral hypertrophy has, however, been recorded.

A somewhat similar morphological differentiation is apparent amongst the inner teeth of the dentary. Here the outermost row is composed of relatively large, strongly recurved and uni- or bicuspid teeth that are both smaller and more refined than their counterparts of the outer row, but have essentially similar gross morphology. Teeth in the second and third rows are small, compressed tricuspids (occasionally bicuspids). The serial arrangement of inner row dentary teeth is regular, with 2 or 3 (sometimes 4) rows anteriorly and a single row posteriorly.

An infrequent variant of the basic tricuspid form in *Macrolepurodus* is known. The lateral cusps are displaced behind and slightly medial to the central cusp, so that the tooth has a triangular crown with a cusp in each angle. Such teeth generally occur only in the outermost row of the inner premaxillary series.

What little information there is on the ontogeny of tooth form and pattern shows that buccal larvae (*ca* 9 mm total length) have slender, conical outer teeth indistinguishable from those in like-sized larvae of *Astatotilapia* (Greenwood: 1956a: 308). During later ontogenetic stages these teeth must be replaced by others having the characteristic *Macrolepurodus* form and pattern. At a standard length of *ca* 85–95 mm it is known that certain lateral inner teeth on the premaxilla are replaced by enlarged teeth closely resembling their counterparts in the outer row.

Upper jaw. The dentigerous arms of the premaxilla are greatly inflated (especially anterolaterally), are cylindrical or nearly cylindrical in cross section, and have an expansive alveolar surface over the greater part of their length. This arm of the bone is distinctly arched at about its midpoint, the degree of curvature being greater on that side of the maxilla with the most enlarged teeth; see above (Greenwood, 1956a: fig. 4C).

The ascending premaxillary processes, as compared with the dentigerous arm, are slender and as long or longer than those arms.

The maxilla is foreshortened, its posterior portion relatively deep and with a pronounced median concavity (and thus a correspondingly strong bullation of the lateral face). Its articular head has a pronounced medial curvature.

Lower jaw (Fig. 56). The robust lower jaw (dentary + anguloarticular) is deep relative to its length, thus appearing foreshortened and massive.

Each ramus of the dentary is much inflated in the region surrounding its division into ascending and horizontal arms. Anteriorly the bone has a pronounced median curvature so that the entire jaw, viewed from above, has the outline of a broad-based U.

Anteriorly, the upper part of the dentary is greatly thickened, and has a broad superficial surface extending from the symphysis anteriorly to the base of the ascending arm posteriorly.

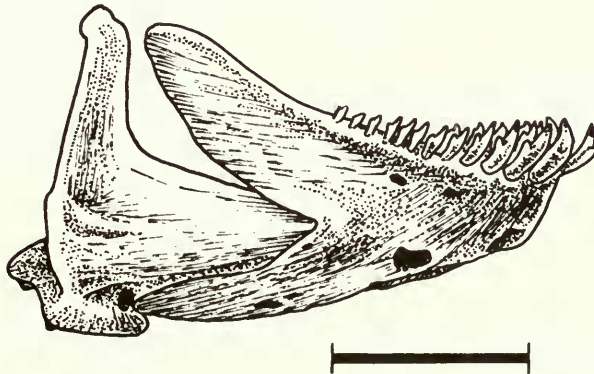


Fig. 56. *Macrolepurodus bicolor*. Right dentary in lateral view. Scale = 3 mm.

Only about the outer half of this surface is dentigerous. Laterally, the ramus wall curves abruptly towards the midline so that it lies more nearly horizontally than vertically.

Each aspect of the symphyseal surface is wide anteroposteriorly, and runs almost vertically (cf. the backwardly sloping symphysis and resultant 'chinless' outline in *Paralabidochromis* p. 71).

The anguloarticular is massive and carries a broad and deep articular surface for the head of the quadrate. Its anteroventral prolongation has a near rectangular anterior margin and is so aligned that it runs downward in parallel with the posterior margin of the dentary (not ventral to that margin as it does in most other lineages).

Lower jaw length is from 28–36% of head length (mean 32%), that is somewhat shorter than in the generalized syncranium, but similar to that in most species of the *Paralabidochromis* and *Ptyochromis* lineages. Usually the lower jaw is as broad as it is long, but in some specimens it may be slightly longer than broad.

Lower pharyngeal bone and dentition. The relatively stout bone is short and broad, its triangular dentigerous surface broader than long. The teeth are cuspidate and compressed, but not noticeably fine; those in the two median series usually are coarser than the others (except those in the transverse posterior row).

Contained species

Macroleuroodus bicolor (Blgr.), 1906. Lake Victoria; see Greenwood (1956a : 299–312)

DISCUSSION

Some of the derived features seen in *Macroleuroodus* appear to be an intensification or elaboration of those found in *Paralabidochromis*. This is particularly apparent when the jaw skeletons and dentition of the two genera are compared. The skeletal modifications could, at least in part, be associated with the more massive teeth and expansive dental pattern characterizing *Macroleuroodus*.

Neurocranial form in *Macroleuroodus* also seems to represent a modification of the derivative trend manifest in the majority of *Paralabidochromis* species. Namely, an increase

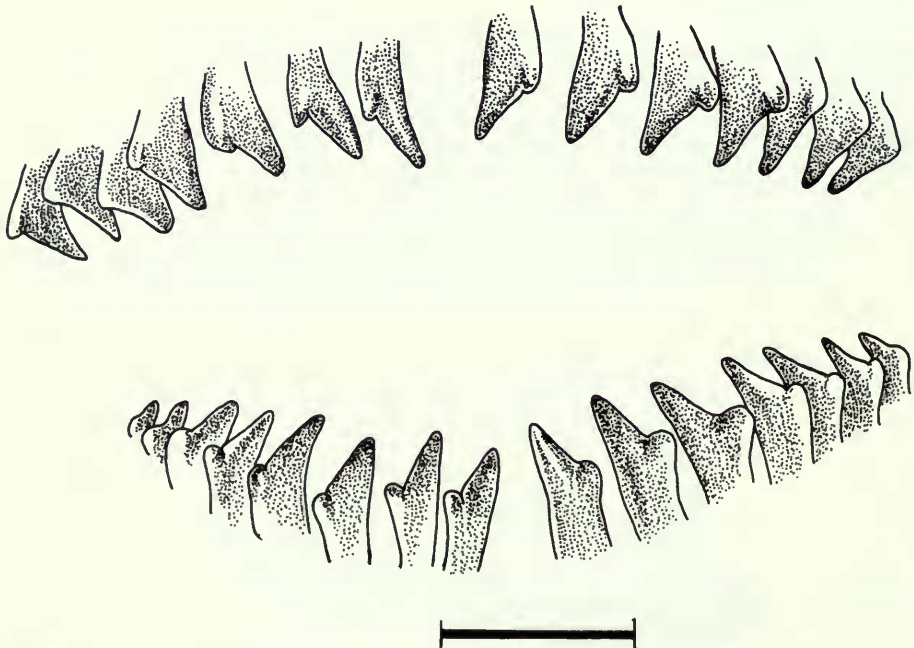


Fig. 57 Dentition of a juvenile *Macroleuroodus bicolor*, viewed *in situ* and from in front, to show the nature of the crowns. Since the lips are not fully reflected, the bases of the teeth are not visible. (For comparison with Fig. 43.) Scale = 1 mm.

in the slope of the preorbital skull face, especially in the ethmovomerine region (cf the neurocranial descriptions for the two taxa, p. 81 and p. 68 respectively).

An apparently similar trend of apomorphic intensification could be invoked to explain the evolution of the peculiar outer tooth form in *Macropleurodus*. That is to say, from the unequally bicuspid teeth of a type seen in *P. beadlei* or *P. plagiodon*, the *Macropleurodus* type could develop by an increase in stoutness, the differential elongation of the major cusp, and an increase in its curvature towards the midline (cf. Figs 43 & 57). As noted before (p. 72), the outer teeth in small *Macropleurodus* do resemble those of adult *P. plagiodon*. It is also known that in *Macropleurodus* the peculiar inner teeth are developed relatively late in ontogeny, when the fish is between 85 and 95 mm long. Smaller individuals have inner teeth like those of comparable-sized, and larger, *Paralabidochromis*.

In the absence of other and more clear-cut synapomorphies it is possible to reach only a tentative conclusion about the relationships of *Macropleurodus*; namely, that *Macropleurodus* could share a fairly recent common ancestor with *Paralabidochromis*. The possible further relationships of *Paralabidochromis* are discussed on p. 93.

SCHUBOTZIA Boulenger, 1914

TYPE SPECIES: *Schubotzia eduardiana* Blgr., 1914. Lake Edward; for synonymy see Greenwood (1973 : 215–21).

Note. In my paper on the haplochromine species from Lake George (Greenwood, 1973), I placed this monotypic taxon in the genus *Haplochromis* (as then recognized), mainly on the grounds that '... To retain *Schubotzia eduardiana* in a separate and monotypic genus serves only to hide its close phyletic relationship with *Haplochromis*'. That sentiment was certainly valid when the genus *Haplochromis* had such a broad and non-monophyletic interpretation. However, the redefinition of *Haplochromis* (*sensu stricto*) and other elements of the old *Haplochromis* concept (Greenwood, 1979), negates my action and the reasons I gave for it. Following the methodology applied in the latter paper, this species must be given generic rank, and thus it returns to its former name, *Schubotzia*.

DIAGNOSIS. Small haplochromines (adult size range ca 55–80 mm SL), with a relatively shallow body (30–37% SL, mean 34%), thickened lips, a horizontal mouth in which the lower jaw (29–35% head length, mean 33%) is shorter than the upper, and jaw teeth of a distinctive type.

These teeth have an expanded crown that is markedly compressed and strongly recurved, and which constitutes almost half the length of the tooth; the overall appearance is one of a paddle with its blade bent at right angles to the shaft. Most teeth are unicuspid and the distal margin of the crown is rounded.

All outer teeth are moveably implanted and close-set, those of the dentary extending almost to the crest of the low ascending arm (coronoid) of the bone.

Inner teeth are small and tricuspid, with strongly compressed and recurved crowns; virtually no interspace separates the outer row of teeth from the 2 or 3 inner series in the upper jaw, or the single (rarely double) series in the lower jaw.

DESCRIPTION

Habitus (Fig. 58). The body is relatively slender (30–37% SL, mean 34%), the dorsal head profile straight or gently curved, sloping at an angle of 30°–35°. The thickened lips and the shorter lower jaw give the head a distinctive profile.

Neurocranium. Apart from its moderately decurved preorbital profile and more steeply sloping ethmovomerine region (which projects distinctly below the level of the parasphenoid), the skull is of a generalized type. Its preorbital depth is ca 30% of the neurocranial length, and the supraoccipital crest is low and wedge-shaped in outline.

Dentition. Outer teeth in both jaws have the crown greatly expanded relative to the slender subcylindrical neck and body, the much compressed crown constituting about half the height of the tooth (Fig. 59). Except for a few weakly bicuspid teeth in the smallest specimen

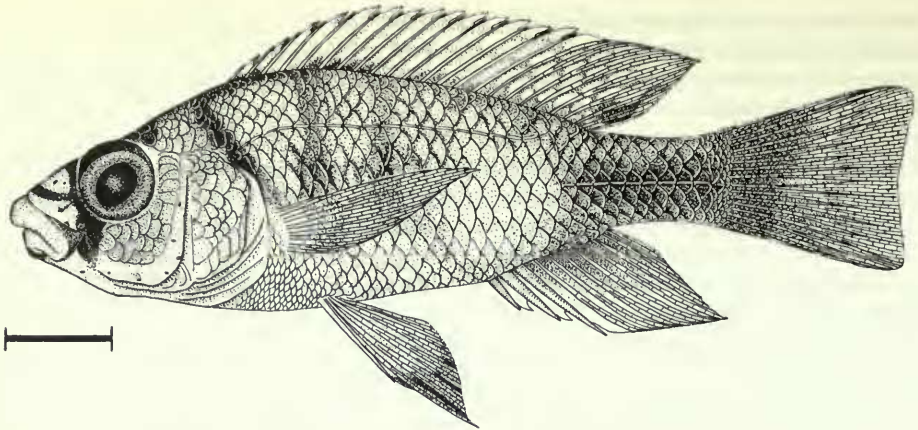


Fig. 58 *Schubotzia eduardiana*. Lake George. Scale = 1 cm.

examined (35 mm SL), the crown is unicuspid and its distal margin rounded. If the tooth were flattened out, it would have the shape of a paddle.

In bicuspid teeth, the minor cusp is not separated from the major one by a distinct gap, but merely by a narrow, V-shaped, groove.

The teeth are implanted vertically, but the strong buccal curvature of the crown results in that part of the tooth being aligned almost horizontally. In the lower jaw, the outer row is continued posteriorly almost to the tip of the low coronoid arm of the dentary. Rarely, a few small tricuspid teeth are intercalated, posteriorly, amongst the unicuspid outer teeth of the lower jaw. There is a slight anteroposterior size gradient in the height of the premaxillary teeth, and a more marked gradient in the lower jaw.

Both jaws have the teeth fairly close-set (but never with the crowns contiguous); in fresh material the teeth are moveably implanted.

There are 40–52 (mean 48) teeth in the outer premaxillary row. Teeth forming the inner rows are tricuspid and small, and have strongly compressed, recurved crowns. Almost no

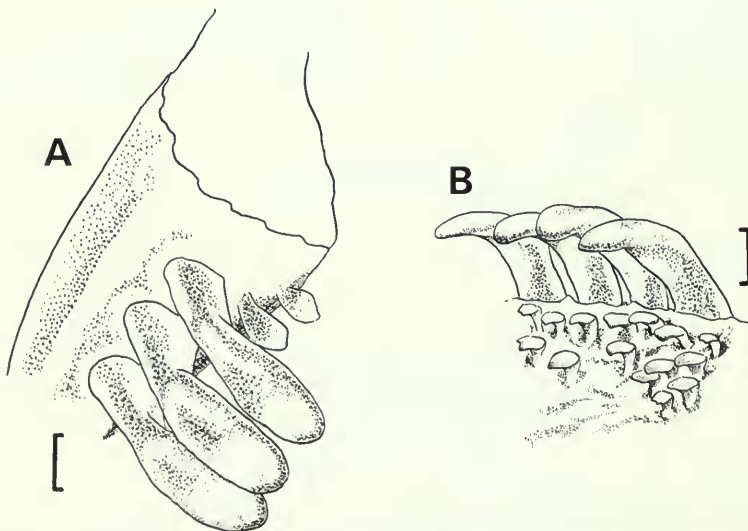


Fig. 59 *Schubotzia eduardiana*. A. Right premaxilla (in part), viewed medially and from below to show lateral aspect of the outer teeth. B. Teeth from the left dentary (anterolateral in position) viewed medially to show lingual aspect of the teeth. Scale = 0.25 mm.

space separates the outer teeth from those of the inner rows, of which there are 2 (rarely) or 3 in the upper jaw and a single (rarely double) row in the lower jaw.

Upper jaw. The maxilla is moderately foreshortened and deep; its articular head curved gently mediad.

The premaxilla is inflated and almost cylindrical in cross-section; its ascending processes are almost half the length of the dentigerous arms which, when viewed from below, have a broadly rounded U-shaped outline.

Lower jaw. The dentary is stout, deep (especially posteriorly) and foreshortened in appearance, with a low ascending (coronoid) arm; it is not noticeably inflated in the region around its bifurcation into ascending and horizontal arms (Fig. 60). The alveolar surface, at

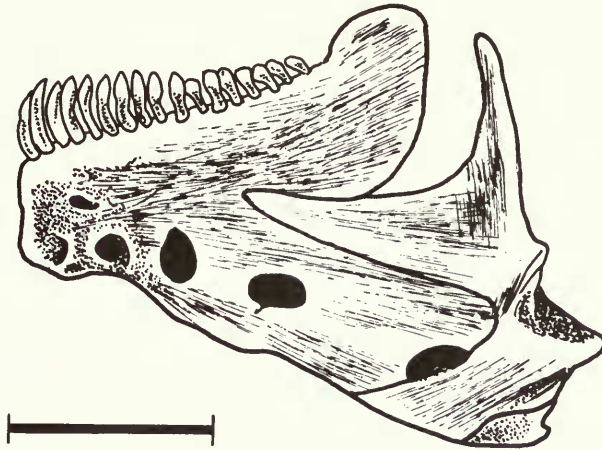


Fig. 60 *Schubotzia eduardiana*. Left ramus of lower jaw, seen from a somewhat ventrolateral position. Scale = 3 mm.

least anteriorly and laterally, is somewhat broadened, the inflation extending a little below the alveolar surface as a shallow dorsal bullation of the ramus wall. This bullation, like the overlying alveolar surface, clearly slopes forward and downward from a point near the upward curve leading into the coronoid arm (onto the greater part of which the outer tooth row is continued posteriorly and upwards).

The anguloarticular is a little stouter than in the generalized type of jaw but, as in the latter, its anteroventral arm has an acute anterior angle; the arm itself lies almost horizontally beneath the posterior part of the dentary's ventral margin.

Length of the lower jaw is 29–35% (mean 33%) of head length; the length/breadth ratio of the jaw ranges from unity to 1.4 times longer than broad (mode 1.1 times).

Lower pharyngeal bone and teeth. The bone is relatively elongate and narrow; none of its teeth is enlarged (except, as usual, those in the transverse posterior row and, in larger fishes, a few posterior teeth in the median rows as well). The triangular dentigerous surface is about 1.3 times longer than it is broad.

Contained species

Schubotzia eduardiana Blgr., 1914. Lakes Edward and George; see Greenwood (1973 : 215–21).

DISCUSSION

Like the monotypic genera in Lake Victoria, *Schubotzia* is readily distinguished by its autapomorphic characters. But, it is extremely difficult to find its sister group amongst potentially related taxa because few of its derived features are shared ones.

The subalveolar bullation of the dentary in *Schubotzia* suggests a relationship with the Victoria lineages *Psammochromis* and *Allochromis* (see pp 55 & 59), as does the antero-

ventral slope to the outer tooth row on that bone; but, neither of the latter genera has the foreshortened and deep dentary of *Schubotzia*, and the actual dentition is distinctive in the three taxa (each being derived in its own way). The gross and detailed morphology of the dentary in *Schubotzia* also shares some features with that bone in the *Ptyochromis-Macroleurodus* assemblage, the possible sister group of *Psammochromis* and *Allochromis*. Thus there is a suggestion that *Schubotzia* is related to this lineage in its broadest sense, but it cannot be placed with certainty in either of the supposed sister divisions (see p. 94). On balance, the nature or degree of expression of its apparently synapomorphic features indicate closer relationship with the *Ptyochromis* assemblage.

Lake Victoria haplochromines of uncertain generic relationship

The status of the three species considered below will probably be resolved when studies on several newly discovered taxa are completed. Only one of the species treated here is represented by adequate study material, another factor hampering their full inclusion in the present revision.

'HAPLOCHROMIS' *CRONUS* Greenwood, 1959

When first described (Greenwood, 1959b : 180–2), and in a later publication (Greenwood, 1974), '*H. cronus*' was thought to be a relative of species now placed in the nominate subgenus of *Lipochromis* (see p. 29 above). This assignment was based on the paedophagous habits of the few *cronus* specimens with food remains in the gut, and on some osteological features of the jaws. Superficially at least, and in its dentition, *cronus* appears to be more like the generalized species now placed in *Astatotilapia* (see p. 6) although it reaches a larger adult size (135 mm SL) than any member of that genus.

In one feature, an almost completely scaled caudal fin, *cronus* differs from all known haplochromines in the Victoria–Edward–Kivu assemblage; a completely scaled caudal is, indeed, generally considered to be the 'hall-mark' of haplochromines from Lake Malawi (see Regan, 1922 : 158). The value of this character as a phylogenetic marker, however, has still to be tested, and for the moment I shall disregard its presence in *cronus*.

Since the original description of *cronus* was prepared I have been able to examine one rather damaged and incomplete cranial skeleton, and thus gain more data on its osteological characteristics.

The morphology of the premaxilla and maxilla is very like that in members of the nominate subgenus of *Lipochromis*, as is the morphology of the lower jaw (dentary and anguloarticular bones), see p. 30. Other elements of the syncranium too are like those in *Lipochromis*, but all the resemblances involve either plesiomorph (*ie* non-derived) characters or those suspected of repeated and convergent origins.

The outer row jaw teeth in *cronus* are unlike those in either subgenus of *Lipochromis*, being large, relatively stout and caniniform unicuspid with recurved tips; none is embedded in the oral mucosa, which is not noticeably thickened.

In recently dead specimens the jaws are neither so markedly distensible nor so protractile as those in *Lipochromis*, even when compared with species of the nominate subgenus (see p. 30 above).

Thus, there are no clear-cut apomorphies shared by *cronus* and *Lipochromis*; the few apparent synapomorphies in jaw morphology also occur in lineages not thought to share a recent common ancestry with *Lipochromis* (see discussion on p. 52).

Dentally, '*H. cronus*' resembles members of the genus *Harpagochromis*, but its inclusion in that lineage is precluded by the morphology of its skull and jaws, features which, together with its large adult size, also exclude it from *Astatotilapia*.

Amongst the haplochromine material recently collected by members of the Leiden University research team there is at least one undescribed species which appears to resemble *cronus* both superficially and anatomically. When this taxon has been studied (especially in

relation to other newly discovered paedophages) it may be possible to reconsider the status of '*H. cronus*'.

Until that time and until more material of '*H. cronus*' is available, little purpose would be served by giving the species any formal supraspecific grouping.

'*HAPLOCHROMIS*' *APOGONOIDES* Greenwood, 1967

I suggested originally (Greenwood, 1967 : 108), on the basis of its dentition and strongly decurved snout, that '*H. apogonoides*' could be related to species now placed in the genus *Ptyochromis* (see p. 60).

The dental resemblance, however, is actually confined to the morphology of the teeth (stout, very strongly recurved unicuspid), and does not include the dental pattern or other details.

In *apogonoides*, unlike *Ptyochromis*, the anterior outer teeth of the lower jaw are not implanted procumbently, there is no pronounced anteroventral dip in their line of insertion, there is a decided gap between the inner and outer series of both jaws, and the number of tooth rows anteriorly and anterolaterally is not increased above the generalized number (hence the tooth bands, compared with those in *Ptyochromis*, are narrower).

'*Haplochromis*' *apogonoides* also lacks the foreshortened and deep dentary and the stout, anteriorly obtuse ventral arm to the angulo-articular, derived features found in *Ptyochromis*. In fact the lower jaw of *apogonoides* is, in one respect, derived along the opposite morphocline from that manifest in *Ptyochromis*. It is, relatively speaking, longer than in the generalized type and much longer than that in *Ptyochromis* (45–51% of head length in *apogonoides*, cf. 22–38%, mode 35%, in *Ptyochromis*).

The two taxa do share certain apomorph jaw features (posteriorly bullate dentary, inflated dentigerous arms in the premaxilla) but, as noted for '*H. cronus*', these are of doubtful validity when establishing interlineage relationships.

Thus there seem to be no grounds for assuming that '*H. apogonoides*' and *Ptyochromis* shared a recent common ancestor. Nor is it yet possible to find other characters indicating a close relationship of *apogonoides* with any other lineage in the Victoria–Edward–Kivu flock.

The extreme recurvature of the teeth in *apogonoides*, coupled with the morphology of its dentary, would seem to preclude any close relationship with *Astatotilapia*, *Harpagochromis*, *Gaurochromis* or *Lipochromis* (see pp. 7, 10, 32, & 27 respectively), some of whose species do have a superficial likeness to *apogonoides* (see Greenwood, 1967). Furthermore, *apogonoides* shares no apomorph features with any of these taxa, except perhaps with *Harpagochromis* an increased relative lower jaw length.

As with '*H. cronus*', the situation may be clarified when certain newly discovered species have been studied more closely.

'*HAPLOCHROMIS*' *THELIODON* Greenwood, 1960

The few specimens of '*H. theliodon*' available for study (seven in all) are remarkably uniform in appearance (see Greenwood, 1960 : fig. 15) and all have two features which, when taken in combination, are very distinctive. Namely, a stout lower pharyngeal bone with numerous molariform teeth, and very small, deeply embedded scales on the thoracic region of the body. (The upper pharyngeal bones of the specimen prepared as an alizarin transparency are enlarged, but have only a few molariform teeth.)

The extent to which the lower pharyngeal bone and its dentition are hypertrophied is comparable with that in one species of *Labrochromis* (*L. humilior*) and that in *Gaurochromis* (*Mylacochromis obtusidens*); the bone's outline is nearer that of *L. humilior*.

Rather surprisingly, the neurocranial apophysis for the upper pharyngeal bones in *theliodon* is not developed to a degree comparable with the apophysis in *L. humilior* or *Gaurochromis* (*M. obtusidens*). It has only a slight expansion of the parasphenoid facet, and the basioccipital facets are no larger than those in the generalized type.

From both *L. humilior* and *G. (Mylacochromis) obtusidens*, '*H.*' *theliodon* is immediately distinguished by the very small chest scales, a derived feature found in the lineage *Thoracochromis* (see Greenwood, 1979:290-5). In its hypertrophied pharyngeal mill, *theliodon* closely resembles *Thoracochromis pharyngalis* (Poll, 1939) of the Lake Edward drainage system. However, the small chest scales in '*H.*' *theliodon* do not have an abrupt size demarcation with the scales on the lateral and anterolateral aspects of the body (as is the case in all *Thoracochromis* species). Again, unlike *Thoracochromis*, there are more scales between the posterior part of the upper lateral line and the dorsal fin insertion (see Greenwood, 1979:291). Thus there are no grounds for placing *theliodon* in the *Thoracochromis* lineage, especially since it also lacks another *Thoracochromis* apomorphy, an incompletely scaled cheek.

Returning for the moment to those haplochromine lineages in Lake Victoria with which '*H.*' *theliodon* shares some derived features, *Labrochromis* and *Gaurochromis*.

The lower pharyngeal bone, as noted before, is like that in *Labrochromis humilior* but the apomorph chest scale pattern in *theliodon*, coupled with its lower, more streamlined skull, caution against supposing a sister-group relationship between these taxa on the basis of the pharyngeal mill alone. Also, an enlarged pharyngeal mill has evolved independently in lineages other than *Labrochromis* (eg in *Gaurochromis*, *Astatoreochromis* and *Thoracochromis*), and so its value as a phyletic marker in this context must be ranked rather low (see also p. 42).

The fine and numerous jaw teeth in all *Gaurochromis* are a derived feature (see p. 32), and are not shared with '*H.*' *theliodon*. An hypertrophied pharyngeal mill is also a derived feature but it is not possible to suggest that *theliodon* is the plesiomorph sister group to *Gaurochromis* on that basis because only one taxon in the *Gaurochromis* lineage has enlarged pharyngeal bones and teeth. The other species have fine pharyngeal bones and teeth, and since in other lineages this is the plesiomorph condition, it seems unlikely that the trend would be reversed in *Gaurochromis* (and that apart from the problems of convergence already noted).

Certain species of the genus *Psammochromis* do have small chest scales and a slight hypertrophy of the lower pharyngeal bone and dentition (see pp 54 & 56). But, all *Psammochromis* share derived features in the morphology of the lower jaw and its dental arrangement, (see p. 55). None of these features is present in '*H.*' *theliodon*, and the greater hypertrophy of its pharyngeal mill would also preclude it from plesiomorph sister-group status with *Psammochromis*. Likewise, since not all *Psammochromis* species have small chest scales, one cannot use that feature to suggest a close relationship with '*H.*' *theliodon*.

Similar arguments can be ranged against any attempted pairing of '*H.*' *theliodon* with other lineages from Lakes Victoria, Edward and Kivu. The species would, therefore, seem to be the sole representative of a distinct lineage and thus coordinate with those already accorded generic rank (see pp. 55 & 56). However, I hesitate to give '*H.*' *theliodon* that status until more specimens from a wider range of localities are available, and more is known of its syncranial anatomy.

Lake Kivu haplochromines of uncertain generic relationship

'HAPLOCHROMIS' *SCHOUTEDENI* Poll, 1932

This Lake Kivu species probably should be referred to *Paralabidochromis* (see p. 67), but I have not been able to see enough specimens, nor to obtain relevant osteological data, to reach a definite conclusion; see Poll (1932).

'HAPLOCHROMIS' *WITTEI* Poll, 1939

As with '*H.*' *schoutedeni*, a lack of material renders it difficult to place this Kivu species. Again, it would seem to be a member of the *Paralabidochromis* lineage.

Summary and conclusions

Some points of a general nature arising from this revision have been discussed in the introduction (p. 2), and others have been treated in an earlier paper (Greenwood, 1979 : 313–14). They need no repetition, except perhaps to reiterate that no progress has been made in resolving the problem of whether or not the Victoria–Edward–Kivu flock is of mono- or polyphyletic origin.

No unique apomorphy is shared by members of that flock and one cannot therefore erect a satisfactory hypothesis for its monophyletic origin. Equally, one cannot as yet find sister-groups outside the lake area for any of the endemic lineages described here. Thus, any hypothesized polyphyletic origin is also without adequate foundations.

A lack of differentially shared apomorphies has also rendered it virtually impossible to establish sister-group relationships for lineages within the flock. Since, therefore, a complete and sequentially dichotomous cladogram for the flock as a whole cannot be established either, another line of evidence, in this case one indicating a monophyletic origin, is not available.

I say virtually impossible because some lineages do seem to be relatable on the basis of one, or at best a few, synapomorphic features. But, in these instances all that can be achieved is the formulation of the broad hypothesis '... These various lineages are more closely related to one another than to any other lineage (or group of lineages) because they alone share this (or these) synapomorph feature or features'. The 'others' still remain as phyletic isolates.

Again, within a lineage it has proved almost impossible to provide a precise and sequentially ordered series of dichotomies. A few dichotomies can be resolved at a high level of generality for the lineage (or group of related lineages) but beyond that one is usually left with the all too familiar unresolved tri- or polychotomy.

Brundin (1972) has laid great emphasis on the importance of the 'search for the sister-group' when constructing a cladistic phylogeny. In that respect my analysis of the Victoria–Edward–Kivu haplochromines has failed. The search for sister groups will have to be continued.

It cannot be argued, at the interlineage (*ie* intergeneric) level of universality, that the Victoria–Edward–Kivu flock is too young (at most 1my; see Greenwood, 1974) for the synapomorphies identifying sister groups to have evolved (see Brundin, 1972 : 110). The lineages exist and are presumed to be monophyletic on the basis of apomorphies unique to each. Any apparent synapomorphies developed in the future would not be true synapomorphies but convergences. Clearly, if synapomorphies exist they must be present now and are either indeterminable by the techniques applied to the problem, or I have failed to recognize them, or the sister-groups exist elsewhere.

Possibly the sister lineages may yet be identified outside the geographical area encompassing the Victoria–Edward–Kivu flock, for example amongst the '*Haplochromis*' species of Lake Malawi. They certainly cannot be recognized amongst the fluviatile haplochromines of east and central Africa (see Greenwood, 1979).

On the other hand, it has been suggested (Greenwood, 1974) that the Victoria–Edward–Kivu flock is but distantly related to that of Malawi. It would then have evolved from one or even several species more closely related to those now inhabiting the local river systems than to those associated with Lake Malawi. If that is the history of the two flocks, then I can foresee the greatest difficulties in ever constructing a fully sequential cladogram for the Victoria–Edward–Kivu flock.

The morphological equivalents of any hypothetical common ancestor (or ancestors) must be of an *Astatotilapia* type since none of the Victoria–Edward–Kivu taxa shows the derived features characterizing the other fluviatile lineages (see Greenwood, 1979). Because present-day *Astatotilapia* species cannot be sorted into sister species on the basis of anatomical synapomorphies, it is reasonable to suppose that the situation was no different in Pleistocene and pre-lake times. The synapomorphic features identifying a present-day lineage would,

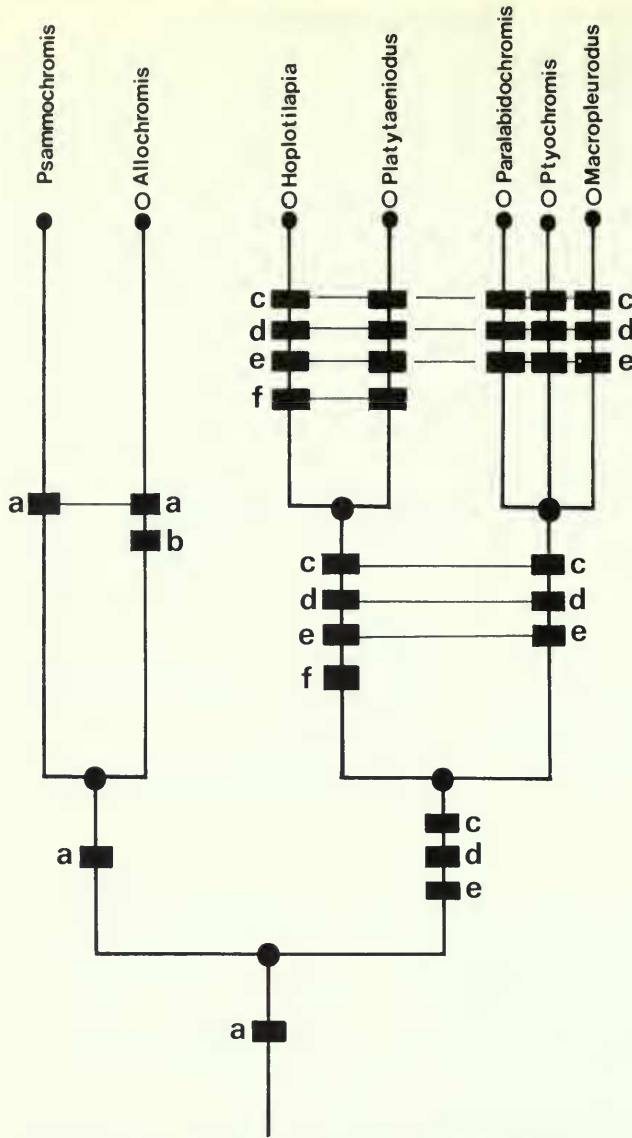


Fig. 61 Tentative cladogram for the *Psammochromis-Macropleurodus* super-lineage; see text pp. 93-94.

● Hypothetical common ancestor

○ Various autapomorphies (see text, pp. 57, 72, 75, 67, 62, & 80 for the taxa respectively).

- a. Dentary slender, with a strong ventrad dip in the line of outer row tooth insertions anteriorly and anterolaterally, a marked lateral bullation of the ramus below that region.
- b. Teeth in both jaws arranged in broad, crescentic bands over most but not all of the alveolar surfaces on the dentary and premaxilla.
- c. Dentary foreshortened and deep, its lateral walls curving abruptly mediad a short distance below the alveolar surface of the bone.
- d. Anterior outer row teeth of the dentary implanted procumbently (except in *Platytaeniodus*; see text p. 79).
- e. Anterior margin to anteroventral limb of anguloarticular rectangular or bluntly rounded.
- f. Teeth in broad bands on entire alveolar surface of the dentary and premaxilla.

therefore, be the apomorphic features evolved at the first (speciational) dichotomy leading to the origin of that lineage, and thereafter carried in it through successive speciation events. Under such circumstances it would be impossible to relate the two taxa resulting from that speciation event because the plesiomorph taxon would not show the diagnostic apomorph features of its derived sister species (and, subsequently, its descendent taxa as well).

Should the flock be of monophyletic origin, then a similar situation would exist if the plesiomorph daughter species of each dichotomy remained, in terms of derived features, indistinguishable from the mother species. In other words, one would have, through time, an anatomically identical line of stem taxa from which a series of primary side branches were split off. Each branch would be characterized by a different set of apomorph characters superimposed on the plesiomorph 'bauplan' common to every branch and to the successive stem species as well.

Clearly, if sister groups are to be identified, no matter how the Victoria-Edward-Kivu flock evolved, there is need for further and more detailed examination of the resultant taxa and, I would suspect, the use of characters other than strictly anatomical ones.

As mentioned earlier, some sister groups have been recognized amongst the lineages of that flock, with the result that two 'super-lineages' can be reconstructed.

The assemblage of species in the genera *Psammochromis*, *Allochromis*, *Paralabidochromis*, *Macrolepurodus*, *Platytaeniodus* and *Hoplotilapia* (with possibly, *Schubotzia* as well) is the larger of the two super-lineages so far delimited (Fig. 61).

These, in many respects dentally diverse taxa are, with one exception, united on the basis of a single synapomorphy, the marked ventrad inclination, anteriorly and anterolaterally, of the outer tooth row in the dentary (see Fig. 61;a). The exceptional taxon, *Hoplotilapia*, has a very highly modified dentary, modified in such a way as to obscure the primary nature of its outer tooth implantation. *Hoplotilapia* is included in the group because of other synapomorphies which are shared with certain taxa having the group synapomorphy (see below).

The first dichotomy within this major assemblage (Fig. 61) is based on the nature of the overall morphology of the dentary.

In one of these primary divisions (*Psammochromis* and *Allochromis*) the dentary retains the slender, elongate facies of a kind not greatly different from the generalized condition, although it is somewhat inflated and bullate on either side of the symphysis. Dental pattern and tooth shape in *Psammochromis* and *Allochromis* are very different, with those of *Allochromis* showing a much derived condition, and those in *Psammochromis* retaining a more nearly generalized one (see pp. 54 & 59).

The other primary division (Fig. 61) is characterized by two, or possibly three, major synapomorphies. The first of these is shared by all members, namely a foreshortened, deep dentary, usually with the rami especially robust in that region occupied by the anterior bullation in *Psammochromis* and *Allochromis*. The second synapomorphy is shared by all but one genus (*Platytaeniodus*, see below) and involves the anterior dentary teeth being implanted procumbently (almost horizontally in two taxa). The third synapomorphy may be only a correlated character associated with the foreshortening, deepening and strengthening of the lower jaw; it concerns the shape and proportions of the anteroventral arm of the anguloarticular bone, which is deep and has a rectangular or rounded anterior margin (shallow and acute in the plesiomorph condition).

Other apparently derived features in the dentary involve the manner in which its lateral walls incline steeply, and in varying degrees abruptly, medially, a condition foreshadowed in *Allochromis* of the other primary division (see above).

Hoplotilapia (see above) is included with the other taxa because of its deep, stout and foreshortened dentary, the shape of its anguloarticular, and because it has horizontally implanted dentary teeth which, in their derived gross morphology, resemble those in two other group members. *Platytaeniodus* (see above) is included, despite the vertical implantation of its teeth, because of the overall shape of its dentary and the anguloarticular.

Within this second primary division there are two further dichotomies, one of which terminates in an unresolved trichotomy (Fig. 61).

Members of one subdivision are characterized by having their oral teeth arranged in broad bands that extend over almost the entire dentigerous surface of both the premaxilla and the dentary. Its constituent taxa, both currently monotypic, are *Hoplotilapia* and *Platytaeniodus*; each is readily distinguished by various autapomorphic features.

Species belonging to the second subdivision (Fig. 61) are characterized by their teeth not occurring in broad bands over the entire dental surface of the jaws. In one genus (*Ptyochromis*) the inner tooth rows are wide anteriorly in the jaw, or even anteriorly and anterolaterally (*P. xenognathus*), but are reduced to a single row laterally and posterolaterally.

Three genera go to make up this subdivision, namely *Paralabidochromis*, *Ptyochromis* and *Macroleurodus*. Each is recognizable on the basis of its autapomorphies, but it is not possible to determine which two of the three taxa is the more closely related. Hence, the existence here of an unresolved trichotomy (Fig. 61).

Schubotzia, as was mentioned earlier, is a possible member of this super-lineage, but it typifies in many ways some of the difficulties encountered when one attempts to interrelate different lineages on a simple dichotomous basis.

The dentary in *Schubotzia* has a typical, downward sloping anterior deflection to the outer tooth row, thus suggesting that the fundamental relationships of the genus lie with the super-lineage. Its overall dentary form is nearest that in members of the *Ptyochromis-Paralabidochromis-Hoplotilapia-etc* primary division (Fig. 61) since it is relatively deep and foreshortened (not elongate and slender) although it does have the generalized type of anguloarticular seen in the *Psammochromis-Allochromis* primary division. The outer jaw teeth in *Schubotzia* have some autapomorphic features (see p. 85) but in their gross morphology (especially the broad spatulate crown strongly recurved on its fine and narrow neck) and in their vertical insertion on the dentary, these teeth closely resemble those of *Allochromis* and thus are of a shape not found elsewhere in the Victoria-Edward-Kivu flock. The dental pattern, however, is of a generalized type.

In brief, *Schubotzia* shares derived features with members in both the primary divisions of this super-lineage. It could be placed in one division or the other only if particular weight was given to a specific apomorphy (*ie* either the jaw shape or the tooth shape), and there are no grounds on which such an action could be based.

The problem created by *Schubotzia*, together with the uncertainties I entertain about the validity of the tooth-line character uniting the two primary divisions, are some of the reasons why I am treating this super-lineage as an informal assemblage of possibly doubtful phyletic significance. Likewise, in the current state of knowledge, I would hesitate to recognize formally the aggregated taxa in any of the three secondary dichotomies (*ie Psammochromis-Allochromis*, *Paralabidochromis-Ptyochromis-Macroleurodus*, and *Platytaeniodus-Hoplotilapia*).

A second super-lineage brings together four genera, *Enterochromis*, *Xystichromis*, *Neochromis* and *Haplochromis*. Here the sole apomorphy uniting the taxa is a long and much coiled intestine (all member species are phytophagous).

The primary dichotomy, based on dental apomorphies, results in one genus, *Enterochromis*, becoming the sister group of the other three genera combined.

Enterochromis retains an essentially underived dental morphotype and pattern, whereas its sister group shows various kinds of derived cusp form, and a trend towards an increase in the number of inner tooth rows with the resulting elimination of the gap between the inner and outer tooth series.

Within the tri-generic sister group, a secondary dichotomy would separate *Xystichromis* as the plesiomorph sister taxon; the specializations seen in the dental morphology of *Haplochromis* and *Neochromis* are very disparate and thus for the moment it is probably best to consider the trio as an unresolved trichotomy.

Apart from the members of the two super-lineages discussed above, none of the other

genera currently recognized can be interrelated. Consequently the general phylogenetic picture remains much as shown in the 'wheel diagram' used in my earlier analysis of the Victoria flock, in which, of course, the lineages were treated as subdivisions of a single genus (Greenwood, 1974).

The detailed picture, on the contrary, is different, with some groupings enlarged and others reduced as a result of redefined specific interrelationships, as well as the incorporation of species from lakes other than Victoria. Also, there would now be many more 'spokes' to the wheel, the result of a more critical assessment of the presumed apomorph or plesiomorph status of the characters (chiefly cranial ones) used to construct that provisional phylogeny.

A noticeable change involves the paedophagous species, which were considered to be a trophic group (or grade) of diphyletic origin (see Greenwood, 1974 : fig. 7, and discussions in the text). These species (with two exceptions, '*H.*' *cronus* [p. 88] and *Astatotilapia barbarae* [p. 32]) are now treated as a single phyletic lineage with two subdivisions (*ie* subgenera); see discussion, p. 31.

This arrangement, too, may come to be altered when a number of newly discovered paedophagous species from Lake Victoria has been studied in greater detail. Preliminary studies indicate that the present nominate subgenus (*Lipochromis*) may have to be given lineage (*ie* generic) status (and itself be subdivided). The phyletic integrity of the total lineage as now conceived, however, will be unaltered, and the paedophages will then become the third super-lineage.

More profound anatomical investigation of the two piscivorous lineages *Harpagochromis* and *Prognathochromis*, particularly the latter, may also lead to rearrangements within the genera and perhaps help to clarify their interrelationships with other members of the flock.

Naturally, any further research on the Victoria-Edward-Kivu flock will help towards clarifying relationships, but any equally important step in that direction must involve the haplochromines of Lake Malawi, if only to establish on more adequate grounds the suggestion that their relationship with the Victoria-Edward-Kivu assemblage is a distant one (Greenwood, 1974 : 99).

Almost 60 years ago, Regan (1922 : 160) concluded his revision of the Lake Victoria Cichlidae by writing '... it will be evident that I do not regard the classification here proposed as entirely satisfactory... at present I am not in a position to improve this arrangement'.

I can but appropriate his statement as an epilogue for my own work.

Acknowledgements

Since, in many respects this paper incorporates all my various '*Haplochromis*' studies, I can thank again all those people who helped me then, and many of whom have helped me again in the preparation of this paper.

In particular I am much indebted to my colleagues in the Fish Section of the British Museum (Natural History), Drs Ethelwynn Trewavas and Keith Banister, Margaret Clarke, Jim Chambers and Gordon Howes. They have contributed in so many ways; as audiences for my ideas, as critics, and as the source of ideas and information (not least in the difficult task of finding suitable names for the new taxa). To them all I proffer my warmest thanks. Especially is it a pleasure to thank Gordon Howes who has done so much for me, particularly in preparing most of the figures illustrating the paper (some taken from earlier work, others newly drawn) and in radiographing innumerable specimens (a job in which he was ably assisted by Margaret Clarke).

From amongst these many people I am, however, particularly beholden to Dr Ethelwynn Trewavas. She it was who introduced me to the fascinations of cichlid taxonomy some thirty years ago, and who has ever since been a source of inspiration and help (as she has been to so many other ichthyologists and fishery workers throughout the world). Thus, I would dedicate this paper to her on the occasion of her 80th birthday in November this year, with affection and gratitude.

A guide to the identification of haplochromine genera in Lakes Victoria, Kioga, Nabugabo, Edward, George and Kivu

Because few of the haplochromine genera from these lakes are recognizable on superficial characters alone, it is impossible to construct a simple key for their identification.

Instead, I have tried to produce a set of introductory pointers as a guide to generic identification using only features that can be ascertained readily. Any tentative identification made on this basis can then be checked against the relevant generic diagnoses, descriptions and figures. That step will be particularly important in those cases where the characters used in the guide are more applicable to groups of genera than to a single genus.

All haplochromines so far recorded from these lakes have a gradual size transition between the scales of the chest and those covering the ventral and ventrolateral aspects of the flanks; also, in all, adult males have true ocelli on the anal fin (see Greenwood, 1979 : 270, 281-2 and 274-6 for figures and discussions of these characters).

The five species treated as *incertae sedis* (pp 88-90) are not included in the guide.

Finally it must be emphasized that the guide is based on adult or near adult specimens because some of the characters utilized may not have reached their definitive expression in smaller fishes. The term 'adult size' refers to the size range of specimens which are either sexually mature or nearly so.

For a description of the various measurements used, see pp 4-6.

- Anal fin with 4 or more spines **Astatoreochromis**
(see Greenwood, 1979 : 285)
- Anal fin with 3 spines **A**
- A** (i) Intestine at least 3-4 times standard length, and much coiled¹.
Fishes with a small adult size (80-105 mm SL). Usually the teeth fine, close-set and arranged in broad bands; in most taxa the inner series not separated from the outer row by a distinct gap **B**
- (ii) Intestine less than 2½ times standard length and with few coils.
A wide range of adult sizes. Many different kinds of teeth represented amongst the numerous taxa, but generally the teeth are robust. Some taxa have the teeth in broad bands, but in most the inner teeth are in 2 or 3 series, and distinct from the outer row **C**
- B** (i) Outer teeth with a protracted and compressed major cusp, giving the crown an obliquely truncated appearance; the tip of the major cusp clearly lies beyond the neck of the tooth **Haplochromis** (p. 53)
(see also, Greenwood, 1979 : 278-81)
- (ii) α . Outer teeth unequally or subequally bicuspid, when unequally cuspid the major cusp clearly larger but not protracted; inner teeth in broad bands (4-6 rows). Dorsal head profile sometimes strongly decurved (a)
- β . Outer teeth as above; inner teeth not in broad bands (1-3 rows); separated from the outer row by a distinct space. Outer teeth with the crown broader than the neck, close-spaced but not contiguous **Enterochromis** (p. 43)
- (a) (i) Outer teeth unequally bicuspid, the crown not much, if at all wider than the neck; very close-set (often contiguous). Inner teeth in broad bands (usually 4-6 rows, sometimes up to 8) anteriorly and anterolaterally in the jaws, not obviously separated from the outer row by a distinct gap. Dorsal head profile not strongly decurved, usually straight **Xystichromis** (p. 46)
- (ii) Outer teeth equally or almost equally bicuspid, close-set (usually contiguous); inner teeth in broad bands (usually 5 or 6 rows) anteriorly and anterolaterally, not separated from the outer row by a distinct gap. Dorsal head profile very strongly decurved. Mouth appears small **Neochromis** (p. 49)

¹ If it is impossible to examine the gut, three of the four genera included under B can be recognized by their close-set, compressed, outer jaw teeth, which are moveably implanted, and by the rather wide bands of close-set inner teeth (generally not separated from the outer row by a distinct space). The fourth genus (*Enterochromis*) is not separable on dental characters from *Astatotilapia* (cf. full descriptions for other diagnostic features, especially the relative size of the nostril and the nasal lateral line canal opening).

- C (i) Lower pharyngeal bone manifestly enlarged and stout, with more than the two median tooth rows composed of enlarged, molariform teeth **Labrochromis** (p. 37)
(see also **Gaurochromis (Mylacochromis)**(p. 36)
- (ii) Lower pharyngeal bone not manifestly enlarged and stout (it may be slightly thickened), the median tooth rows not composed of molariform teeth, although often with slightly larger or coarser teeth (but these never have molariform crowns) D
- D (i) Jaw teeth exposed, not buried in the oral mucosa, and of varied form in the different taxa. Mouth with varying degrees of protrusibility and distensibility but never very markedly distensible laterally and never with the anterior part of the lower jaw closing within the upper (Lower jaw may, however, be shorter than the upper). E
- (ii) Jaw teeth small, deeply embedded in the oral mucosa, usually with only the tips of the outer teeth visible; in some species the tips of these teeth curve outwards. Inner teeth often completely hidden. Mouth large and protrusile, markedly distensible laterally. In some species the lower jaw is boat-shaped (narrow anteriorly), and its anterior part closes within the upper jaw; in others the lower jaw is broadly rounded anteriorly and does not close within the upper **Lipochromis** (p. 26)
- E (i) Inner tooth rows in both jaws arranged anteriorly in 2 or 3 series (very exceptionally as many as 5 or 6), narrowing gradually to a single row posterolaterally; always separated from the outer row by a distinct gap F
- (ii) Inner tooth rows in both jaws arranged in bands of equal or almost equal width over the entire dentigerous surface of the jaws, not separated from the outer row by a distinct gap.
- (a) Inner tooth bands wide (5–10 rows), outer teeth neither enlarged nor stout (α)
- (b) Inner tooth bands narrow (2 or 3 rows), outer and some inner teeth enlarged and stout; crown of outer teeth with a minute minor cusp and a strongly recurved and inwardly directed major cusp (β)
- (α) (i) In both jaws the inner tooth bands (5–10 rows) are in the form of a broad-based U (outer and some inner rows in lower jaw usually continued onto the ascending process of dentary) Teeth unicuspid even in specimens < 70 mm SL. Lower jaw flat and shovel-like, its anterior margin rectangular **Hoplotilapia** (p. 72)
- (ii) Wide tooth bands (6–10 rows) in the upper jaw either in the shape of a broad-based U (*ie* in fishes < 100 mm SL) or, in larger fishes, also U-shaped but with the posterior part of each arm greatly expanded medially so as almost to touch in the midline. Tooth bands of the lower jaw in the shape of two pyriform patches, contiguous medially. Anterior region of lower jaw rounded and bullate **Platytaenioidus** (p. 75)
- (iii) Wide tooth bands (6–11 rows) in both jaws in the form of broad crescents which abruptly taper posteriorly, a single row (the outer) continuing for a short distance beyond the crescent. The bicuspid teeth in the outer row have the crown markedly expanded and much broader than the slender neck. Body slender (30–33% of SL), and elongate **Allochromis** (p. 57)
- (β) Outer row of jaw teeth (and usually the first inner row) composed of stout bicuspid teeth in which the minor cusp is greatly reduced and lies labially to the strong, elongate and buccally orientated major cusp; major cusp lying almost at right angles to the body of the tooth. Laterally on one or both sides the upper lip is reflected to expose the teeth, even when the jaws are closed **Macropleurodus** (p. 80)
- F (i) Outer row of jaw teeth simple bi- and/or unicuspid teeth (sometimes a few tricuspid teeth as well); all inner row teeth smaller than those of the outer rows, and tri- and unicuspid G
- (ii) Outer row jaw teeth with a long, markedly expanded and compressed, spatulate crown that is about half the length of the tooth (which is thus paddle-shaped in outline) and is strongly recurved (almost at right angles). In the lower jaw the outer row teeth extend onto the ascending arm of the dentary. Lower jaw shorter than the upper **Schubotzia** (p. 85)
- G (i) Dorsal profile of head sharply concave; dorsal surface of snout almost horizontal; lower jaw sloping obliquely upwards at a marked angle (50–70° to the horizontal); cephalic portions of the epaxial musculature prominent. Head and body relatively compressed. Maximum adult length 117 mm **Pyxichromis** (p. 24)
- (ii) Dorsal head profile and overall head shape otherwise than in G (i); when mouth is oblique, the snout profile always slopes downwards and forwards (*ie* never horizontal or almost horizontal). When the dorsal profile is concave, the concavity is a gentle one H
- H (i) Body form slender and elongate (body depth 23–30% of SL, modal range 27–29%). Posterior $\frac{1}{4}$ – $\frac{1}{3}$

of the premaxilla edentulous. A small maximum adult size (85–110 mm SL) *Yssichromis* (p. 22) also cf. *Prognathochromis* (p. 14)

Body form other than H (i); save for exceptional individuals, the body is deeper (30% (rarely)–47% of SL). Premaxilla fully toothed (edentulous posteriorly in some *Lipochromis* for which see back, D (ii)). Wide range of maximum adult sizes (from 50–230 mm SL).

- I (i) Outer jaw teeth in both jaws slender, with strongly recurved crowns; 26–56 (usually 40–44) teeth in the outer row of the premaxilla. Inner teeth, also strongly recurved, arranged in broad bands (3–9 rows) anteriorly and anterolaterally in the jaws, narrowing to a single or double row laterally; separated from outer teeth by a distinct space. Lips usually thickened but not lobate. Lower jaw length 22–38% of head length (modal range 34–35%); lower jaw usually shorter than the upper. Dorsal head profile straight and steeply sloping (gently sloping in one species), or strongly decurved *Ptyochromis* (p. 60)
- (ii) Outer jaw teeth strong but slender, moderately recurved; those situated anteriorly in the lower jaw inserted somewhat procumbently so as to form with the upper teeth a forceps-like bite. Rather few teeth in the outer premaxillary row (16–48, modal range 30–35). Inner teeth not arranged in broad bands. Lips thickened, lobate in one species. Dorsal head profile straight and sloping steeply *Paralabidochromis* (p. 67)
- (iii) Dental patterns and gross morphology of the teeth, taken in combination, not as in I (i) & (ii) above: the genera, *Gaurochromis*, *Harpagochromis*, *Prognathochromis*, *Astatotilapia* and *Psammochromis*.

These genera are defined, principally, on osteological features. For their identification reference must be made to the full descriptions. As a rough guide, the following comments may be useful.

Gaurochromis (p. 32), has short, fine, compressed and close-set outer teeth, and in all but one species, a narrow, elongate lower pharyngeal bone with fine teeth. The exceptional species has a moderately enlarged lower pharyngeal bone with some molariform teeth; it is easily confused with *Labrochromis* (see p. 37).

Harpagochromis (p. 10) species reach a large maximum adult size (>200 mm SL) and have large jaws; there is, however, a strong superficial resemblance to *Astatotilapia*, especially in small specimens.

Prognathochromis (p. 14) species also have large jaws, but are more streamlined and shallower-bodied than species of *Harpagochromis*; they have what is generally thought of as a 'typical' predatory facies. There is a wide range of maximum adult body sizes, some species exceeding 220 mm SL, while others reach only ca 100 mm SL.

Astatotilapia (p. 6) species have a very generalized anatomy, pharyngeal and oral dentition, and few outstanding features in their gross appearance. The maximum adult size range is between ca 70–100 mm SL.

Psammochromis (p. 53) species, in their gross appearance, are intermediate between the slender-bodied, streamlined, *Prognathochromis* and the deeper, stouter-bodied *Astatotilapia* species. The lips are thickened (lower lip lobate in one species), and in some species the lower pharyngeal bone is slightly hypertrophied (with some enlarged, submolariform teeth).

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Certain Victoria–Edward–Kivu species which are essentially fluviatile in habitat, but which do occur in the lakes, are dealt with in Greenwood (1979). They are listed here but marked with an asterisk, as are the lacustrine species dealt with in that paper.

Former binomen	Current generic placement	Page			
<i>Astatoreochromis alhauaudi</i> *	<i>Astatoreochromis</i>	. .	<i>H. gilberti</i>	<i>Prognathochromis</i>	20
<i>Astatotilapia nigrescens</i>	? <i>Prognathochromis</i>	20	<i>H. gowersi</i>	<i>Prognathochromis</i>	20
<i>Haplochromis acidens</i>	<i>Psammochromis</i>	56	<i>H. granti</i>	<i>Ptyochromis</i>	66
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<i>H. empodisma</i>	<i>Gaurochromis</i>	36	<i>H. obliquidens</i>	<i>Haplochromis</i>	53
<i>H. engyostoma</i>	<i>Astatotilapia</i>	8	<i>H. obtusidens</i>	<i>Gaurochromis</i>	36
<i>H. erythrocephalus</i>	<i>Enterochromis</i>	45	<i>H. oregonoma</i>	<i>Astatotilapia</i>	9
<i>H. estor</i>	<i>Prognathochromis</i>	19	<i>H. orthostoma</i>	<i>Pyxichromis</i>	26
<i>H. eutaenia</i>	<i>Prognathochromis</i>	22	<i>H. pachycephalus</i>	<i>Harpagochromis</i>	13
<i>H. flavipinnis</i>	<i>Prognathochromis</i>	20	<i>H. pallidus</i>	<i>Astatotilapia</i>	9
<i>H. fuscus</i>	<i>Neochromis</i>	52	<i>H. pappenheimi</i>	<i>Yssichromis</i>	24
<i>H. fusiformis</i>	<i>Yssichromis</i>	24	<i>H. paragiarti</i>	<i>Prognathochromis</i>	20
			<i>H. paraplagiostoma</i>	? <i>Harpagochromis</i>	14
			<i>H. paropis</i>	<i>Enterochromis</i>	45
			<i>H. parorthostoma</i>	<i>Pyxichromis</i>	26

A REVISION OF THE *HAPLOCHROMIS* GENERIC CONCEPT

<i>H. parvidens</i>	<i>Lipochromis</i>	31	<i>H. squamulatus</i>	<i>Harpagochromis</i>	
<i>H. paucidens</i>	<i>Paralabidochromis</i>	71		(see <i>H. pectoralis</i>)	13
<i>H. pectoralis</i>	<i>Harpagochromis</i>	31	<i>H. sulphureus</i>	<i>Prognathochromis</i>	21
<i>H. pellegrini</i>	<i>Prognathochromis</i>	20	<i>H. taurinus</i>	<i>Lipochromis</i>	30
<i>H. percoides</i>	<i>Prognathochromis</i>	20	<i>H. teegelaari</i>	<i>Labrochromis</i>	42
<i>H. pharyngomylus</i>	<i>Labrochromis</i>	42	<i>H. theliodon</i>	<i>Incertae sedis</i>	89
<i>H. phytophagus</i>	<i>Xystichromis</i>	48	<i>H. thuragnathus</i>	<i>Harpagochromis</i>	13
<i>H. piceatus</i>	<i>Astatotilapia</i>	9	<i>H. tridens</i>	<i>Prognathochromis</i>	21
<i>H. placodus</i>	<i>Labrochromis</i>	42	<i>H. tyrianthinus</i>	<i>Prognathochromis</i>	21
<i>H. plagiodon</i>	<i>Paralabidochromis</i>	71	<i>H. velifer</i>	<i>Astatotilapia</i>	9
<i>H. plagiostoma</i>	<i>Harpagochromis</i>	13	<i>H. venator</i>	<i>Prognathochromis</i>	20
<i>H. plutonius</i>	<i>Prognathochromis</i>	21	<i>H. vicarius</i>	<i>Astatotilapia</i>	
<i>H. prodromus</i>	<i>Ptyochromis</i>			(see <i>A. eduardi</i>)	8
	(see <i>P. annectens</i>)	66	<i>H. victorianus</i>	<i>Harpagochromis</i>	12
<i>H. prognathus</i>	<i>Prognathochromis</i>	20	<i>H. vittatus</i>	<i>Prognathochromis</i>	20
<i>H. pseudopellegrini</i>	<i>Prognathochromis</i>	20	<i>H. welcommei</i>	<i>Allochromis</i>	60
<i>H. ptistes</i>	<i>Labrochromis</i>	42	<i>H. wittei</i>	<i>Incertae sedis</i>	90
<i>H. riponianus</i>	<i>Psammochromis</i>	56	<i>H. worthingtoni</i>	? <i>Harpagochromis</i>	14
<i>H. sauvagei</i>	<i>Ptyochromis</i>	66	<i>H. xenognathus</i>	<i>Ptyochromis</i>	66
<i>H. saxicola</i>	<i>Psammochromis</i>	56	<i>H. xenostoma</i>	<i>Prognathochromis</i>	20
<i>H. schubotzi</i>	<i>Psammochromis</i>	56	<i>Hoplotilapia</i>	<i>Hoplotilapia</i>	75
<i>H. schubotziellus</i>	<i>Astatotilapia</i>	9	<i>retrodens</i>		
<i>H. schoutedeni</i>	<i>Incertae sedis</i>	90	<i>Macroleuroodus</i>	<i>Macroleuroodus</i>	84
<i>H. serranus</i>	<i>Harpagochromis</i>	12	<i>bicolor</i>		
<i>H. serridens</i>	<i>Neochromis</i>	52	<i>Paralabidochromis</i>	<i>Paralabidochromis</i>	71
<i>H. simpsoni</i>	<i>Gaurochromis</i>	36	<i>victoriae</i>		
<i>H. spekii</i>	<i>Harpagochromis</i>	13	<i>Platytaeniodus</i>	<i>Platytaeniodus</i>	79
<i>H. squamipinnis</i>	<i>Harpagochromis</i>	13	<i>degeni</i>		