

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

## Part I.

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## Introduction

As currently recognized, the genus *Haplochromis* Hilgendorf encompasses over 300 species, some doubtless nominal but the majority of apparent biological validity (see Fryer & Iles, 1972; Greenwood, 1974a). It is the most speciose African taxon in the family Cichlidae and, next to the genus *Sarotherodon* has the widest distribution in the continent, extending from Tunisia in the north to Namibia (South West Africa) in the south. It is, however, virtually absent from west Africa, being represented there by only one or two species from Nigeria.

Amongst its numbers, indeed contributing the greatest number of species, are the well-known *Haplochromis* flocks of Lakes Victoria and Malawi (Trewavas, 1935; Fryer & Iles, 1972; Greenwood, 1974a), together with the smaller and less studied flocks of Lakes Edward, George, Turkana (Rudolf), Albert and Kivu (see Regan, 1921a; Poll, 1932; Trewavas, 1933; Trewavas, 1938; Greenwood, 1973, 1974b).

It is amongst the species of these various lacustrine flocks that one encounters the great range of anatomical, dental and morphological differentiation usually associated with the genus. The fluviatile species appear to be less diversified, but even here there is more diversity than is realized at first.

With this wide range of anatomical and morphological variation it is not surprising that the present concept of the genus, both in morphological and in phyletic terms, is very ill-defined. Indeed, the concept of *Haplochromis* seems to be based entirely on some intuitive appreciation of 'overall similarity' amongst its constituent species. There has been, so far, no real attempt to test the validity of the implicit monophyly of these species. The recognizable and often noted intrageneric variability in *Haplochromis* has, until recently, not been seen as an analytical taxonomic tool because thinking amongst systematists working on cichlids has been dominated by a 'size of the morphological gap' approach to supraspecific classification.

A reappraisal of the situation with this variation seen in terms of derived (apomorph) and primitive (plesiomorph) character states has not been applied to the genus as a whole (but see Greenwood, 1974a, for the Lake Victoria species). It is this basically Hennigian approach (Hennig, 1966) that I have attempted to apply to the problem. Its use, I believe, does allow one to produce a more realistic classification of the species now lumped together in *Haplochromis*, or separated from that genus because of their showing an extreme manifestation of features already indicated in species still retained in *Haplochromis*.

The taxon *Haplochromis* was first introduced by Hilgendorf (1888), as a subgenus of *Chromis*, for his new species aptly named '*obliquidens*' (see Greenwood, 1956a). The fine, closely packed and multiseriate teeth of '*obliquidens*', with their protracted and obliquely truncate crowns (see Fig. 7B), provided the diagnostic features for Hilgendorf's subgenus.

No further species were added to *Haplochromis* until Boulenger (1906) elevated the taxon to generic rank and included in it six new species from Lake Victoria and the Victoria Nile. Boulenger gave no reasons for raising Hilgendorf's subgenus to a full genus, nor did he attempt to define *Haplochromis* so as to accommodate the new species, none of which had teeth like those of

*H. obliquidens*. A footnote to the paper (Boulenger, 1906 : 443) might be interpreted as a generic definition, but it is completely inadequate and rather confusing, merely noting that '... in addition to the character of the dentition, intermediate between *Paratilapia* and *Tilapia*, the fishes of this genus differ from the latter in usually having a considerable portion of the maxillary bone exposed when the mouth is fully closed'.

The following year Boulenger (1907 : 495) did provide a formal definition of *Haplochromis*, in which genus he then synonymized Pfeffer's (1893) genus *Ctenochromis* and Pellegrin's (1903) *Astatoreochromis* (now recognized as a distinct genus, see Greenwood, 1959a; Poll, 1974 and p. 285 below). This definition is, however, very vague and so worded that it is impossible to distinguish Boulenger's concept of *Haplochromis* from that of his redefined *Paratilapia* Bleeker.

The situation remained virtually unchanged, except for the addition of several more species, with the publication of the third volume in Boulenger's *Catalogue of African Freshwater Fishes* (1915) in which he again comments that some *Haplochromis* species '... vary to such an extent in their dentition that [they] might be referred to *Tilapia* and others to *Paratilapia*'.

Regan's (1920, 1922a) fundamental studies on the osteology of African Cichlidae, and his consequent revision of Boulenger's genera, resulted in many more species being included in *Haplochromis* (which then became the '... largest African genus', Regan, 1920 : 45). In his 1920 paper Regan also defined (in a footnote) several genera which, although apparently related to *Haplochromis*, differed from that genus in various dental features, both oral and pharyngeal.

Surprisingly, in the light of these other generic definitions, Regan was content to include in *Haplochromis* a majority of species whose dental characters were quite unlike those of the type species. In effect, Regan's redefinition of *Haplochromis* in these and subsequent papers (especially those of 1921a & b and 1922a & b) was only a slight improvement of that provided by Boulenger. *Haplochromis* remained a polymorphous assemblage of species showing a wide range of dental and other anatomical peculiarities, only united by having a particular kind of cranial apophysis for the upper pharyngeal bones. Since a similar apophysis occurs in other taxa defined by Regan, the monophyletic origin of *Haplochromis* was not established.

That Regan was aware of his system's shortcomings is shown by remarks in his papers on the cichlids of Lakes Malawi (1921b) and Victoria (1922b). For example, regarding the *Haplochromis* of Lake Victoria he wrote (Regan, 1922b : 158): 'The species of *Haplochromis* exhibit almost as great a diversity as in Nyassa, yet there are certain features which enable one to say almost at a glance to which lake a species belongs', and on page 160: 'From what has been said above as to the evolution and relationships of the Cichlidae of Victoria, it will be evident that I do not regard the classification here proposed as entirely satisfactory'.

Regarding the species of Lake Malawi, Regan (1921b : 686) has this to say: '... the absence of evident relationship to species found elsewhere leads to the conclusion that the Nyassa species are a natural group and may, perhaps, have evolved in the lake from a single ancestral form'. Regrettably, Regan does not elaborate on his remark about the absence of evident relationship to species found elsewhere, particularly since a year later he was to place the majority of Lake Victoria species in the same genus.

When revising the Lake Victoria species, Regan (1922b) divided the *Haplochromis* into five subgenera, *Neochromis* for *H. nigricans* and *H. nuchisquamulatus*, *Bayonia* for *H. xenodon* (now considered a synonym of *Macropheurodus*, see Greenwood, 1956b), *Haplochromis* for *H. obliquidens*, and *Ctenochromis* for the remaining 42 species. These latter were characterized by their having conical or bicuspid teeth separated by an interspace from the smaller inner teeth, the other subgenera having variously specialized crown forms to the teeth. Regan disregarded, or perhaps failed to appreciate the principal diagnostic feature which Pfeffer (1893) used to diagnose *Ctenochromis*, namely the very small scales on the thoracic region. Both Pfeffer and Regan overlooked other diagnostic features in *Ctenochromis pectoralis* (type species of the genus), none of which is found in any of the 42 Victoria species placed in Regan's *Ctenochromis* subdivision of that flock (see p. 287 below). Recent research (summarized in Greenwood, 1974a) also indicates that these 42 species, and about an equal number described since Regan's 1922 revision, can be subdivided into several distinct groups.

Similar arguments can be marshalled against Regan's (1922a : 253) statement that '... the species (of *Haplochromis*) not peculiar to the Great Lakes all belong to the subgenus *Ctenochromis*, Pfeffer . . .'; this aspect of the problem will be discussed later.

Since Regan's time, no real attempts have been made to subdivide the genus (which now contains almost double the number of species known to Regan). Some species have been separated off as mono- or oligotypic genera, but these actions have in no way simplified the problem either taxonomically or phylogenetically, and the genus has still not been shown to be a monophyletic unit.

Clearly, to test the phylogenetic integrity of such a large, ill-defined taxon will require much detailed and critical analysis. The present paper must be looked upon as a tentative first step in that direction. I shall limit my detailed analysis to those *Haplochromis* species which I have studied in some depth, *viz.* the species flock of Lake Victoria (which contains the type species, *H. obliquidens*) and those of Lakes Turkana, Albert, Edward and George, together with the few *Haplochromis* occurring in Lake Tanganyika, and the purely fluviatile species from Africa and the Middle East. Also included are the *Haplochromis*-like riverine genera *Orthochromis* Greenwood, *Serranochromis* Regan and *Rheohaplochromis* Thys van den Audenaerde, and the partly lacustrine *Astatoreochromis* Pellegrin. Unfortunately, I have been unable, through lack of firsthand knowledge, to include the Lake Malawi *Haplochromis* flock. However, I trust that the results of my analysis of these other *Haplochromis* species will enable workers on the Malawi fishes to review the species of that lake in a new light.

My review of anatomical, osteological and morphological features, including details of secondary sexual markings and coloration, has yielded one particularly significant (but not surprising) result; there is, apparently, not one derived feature shared only by the 190 species examined.

The commonly occurring tooth form, an unequally bicuspid tooth, is found in several other genera, as is the unicuspid and caniniform type. Even some of the specialized dental types seem to have evolved independently in other genera, these genera, and those in which bi- and unicuspid teeth also occur, each being recognizable on the basis of derived features not shared by *Haplochromis*.

The structure of the cranial apophysis for the upper pharyngeal bones (see Regan, 1920) is probably a derived feature (see Greenwood, 1978), but again it is a feature widely distributed amongst several genera whose close affinity with *Haplochromis* cannot be established. At best the pharyngeal apophysis can be used as an indicator of relationship at a more distant level than the 'generic' one (see Greenwood, 1978).

No derived features of the anatomy or the squamation are universally shared amongst all the species although, as with various other characters, distinct groups can be defined within *Haplochromis* on the basis of shared derived features.

The anal fin markings found in adult male *Haplochromis*, the so-called anal ocelli or egg-dummies (see Wickler, 1962a & b; Trewavas, 1973), have been considered a unique feature of the genus. Trewavas (1973 : 34) expressed the generally held view on these markings when she wrote '... within their endless diversity the species of *Haplochromis* have almost universally in common a feature of the colour-pattern, the well-known *ocellar spots* on the anal fin of the male' (italics mine). Certainly such ocellar markings are present in all the described species of *Haplochromis* from Lake Victoria, Edward, George and Kivu, and probably in those from Lake Turkana as well. But, true ocelli (i.e. a central coloured spot with a clear surround) are not found in the species of Lake Albert, in the majority of species occurring in the rivers, nor even in many of the Lake Malawi species (see figs in Axelrod & Burgess, 1977). Coloured markings do occur on the anal fins of these fishes (sometimes in both sexes), but are in the form of spots without a clear surround, often smaller than the true ocellar type, sometimes more numerous and covering the greater part of the fin, sometimes only as one or two spots, or, less commonly, similar in number (3-5) and linear arrangements to the true ocellar type.

Clearly, the presence of ocellar anal markings cannot be considered a character of *Haplochromis* as that genus is currently conceived, and the value of anal markings *per se* as an indicator of phyletic relationship must be reassessed.

Although a monophyletic origin for the 'genus' *Haplochromis* cannot be established, it is possible to recognize several seemingly monophyletic lineages (reconstructed on the basis of synapomorphic characters) amongst the species of Lake Victoria (Greenwood, 1974a and unpublished). None of the six major lineages recognized in that lake, however, could be interrelated on a sister-group basis (although sister-groups could be recognized within five of the lineages themselves). In other words, the synapomorphic features of each lineage are superimposed on a basic, plesiomorphic 'bauplan' shared by all\*.

A similar picture emerges when the fluviatile species, and those from Lakes Albert, Turkana and Tanganyika are examined closely. That is, one can postulate a number of lineages (some containing both fluviatile and lacustrine members), but none can be further interrelated on the basis of synapomorphic features.

With the possible exception of their occurrence in two species (one from Lake Victoria, the other from Lake George), none of the apomorph features used to delineate these lineages has been observed amongst the '*Haplochromis*' species of Lakes Victoria, Edward, George and Kivu.

Although no apomorph character has been found to unite all the species of Lakes Victoria, Edward, George and Kivu, and thus suggest their common ancestry, species from the different lakes can be grouped into common lineages each of presumed monophyletic origin. For that reason the '*Haplochromis*' of Lakes Edward, Kivu and George will be treated together with those of Victoria in a forthcoming paper (except for those species which are now referred to the redefined genus *Haplochromis*, see p. 280).

To summarize, the so-called *Haplochromis* species of Africa (excepting those of Lake Malawi which are not included in this review) can be split into a number of major lineages. Most of these lineages are characterized by derived features unique to its members.

The different lineages cannot be interrelated on a sister-group basis for want of ascertainable synapomorphic features which would permit the recognition of their sister-group status. I use the qualification 'most of these' because one of the groups cannot be defined on the basis of even a single shared apomorph character. This is the group in which must be placed the widespread *H. bloyeti* species complex of east Africa (see Greenwood, 1971, 1974a) and, probably, certain of the generalized endemic species of Lake Victoria, Edward and Kivu; it is recognized merely on the overall similarity (and plesiomorphy) of its constituent species.

Wherever breeding habits are known, members of the various lineages described in this paper are female mouth brooders, and all have a '*Haplochromis*'-type cranial apophysis for the upper pharyngeal bones (Greenwood, 1978), features shared with the '*Haplochromis*' and several seemingly related species in Lake Malawi (Trewavas, 1935; Greenwood, 1978). Oral brooding and its associated spawning behaviour, as compared with substrate spawning and brood-care, is a derived condition; the '*Haplochromis*'-type apophysis would also seem to be a derived feature. One may therefore hypothesize a shared common ancestry, at some point, both for the lineages described below and for those which eventually will be recognized amongst the Lake Malawi haplochromine species (i.e. those with a '*Haplochromis*'-type pharyngeal apophysis and, probably species with a '*Tropheus*'-type apophysis as well; see Greenwood, 1978).

For the moment, however, and until it is possible to interrelate dichotomously the various lineages on a sister-group basis, one is faced with a series of unresolved dichotomies (see, for example, the problem discussed on p. 313). In classifying this assemblage I have followed the convention suggested by Nelson (1972), namely that the taxa (i.e. the individual lineages) be given equal rank. At this stage in our knowledge of supraspecific relationships amongst African cichlids, generic rank would seem to be the most appropriate.

## Methods and materials

### Methods

In essence I have attempted to break up the 'genus' *Haplochromis* into a number of monophyletic

\* It has been assumed (on the basis of overall morphological similarity between the least specialized members of each lineage) that the endemic *Haplochromis* species of Lake Victoria are of monophyletic origin (Greenwood, 1974a). Since no apomorph feature unique to the Victoria species has yet been found, that hypothesis is without formal support.

lineages, the members of each lineage being related by their relative recency of common ancestry. Recency of common ancestry, in turn, is recognized by members of a lineage possessing derived (apomorph) characters which are not shared with other species.

Determining the primitive (plesiomorph) or derived status of characters in the Cichlidae is at present a very difficult task. No guidance is available from the entirely inadequate fossil record, and the family's nearest living relatives have yet to be recognized. Comparisons between different character states (outgroup comparison, see Hecht & Edwards, 1977) ideally should be carried out across the whole family. As there are well over 600 nominal species in Africa and America, few of which have been studied in the detail necessary for proper phyletic analysis, the level of outgroup comparisons employed in this paper is, perforce, a low one.

All comparisons have been restricted to African taxa, in particular to species and lineages within the group having a '*Haplochromis*'-type of pharyngeal apophysis. This decision was made on the assumption that all such taxa were derived from a common ancestor, albeit a distant one, and that the '*Haplochromis*'-type apophysis, relative to the '*Tilapia*'-type, is itself a derived character. The most detailed comparisons, of course, have been those made between species comprising the lineages discussed in this paper.

Outgroup comparisons have also been made with species having a '*Tilapia*'-type apophysis, in particular the lineages represented by the genera *Sarotherodon* and *Tilapia*.

When comparisons were made with *Haplochromis* from Lake Victoria, the Victorian lineages were those discussed in Greenwood (1974a). Since no such breakdown is available for the endemic *Haplochromis* of Lake Malawi or for the endemic genera with a '*Haplochromis*'-type apophysis in Lake Tanganyika, these various taxa were not involved in the analysis.

The particular characters and character transformations studied are those which, after a preliminary survey of the taxa involved\*, seemed to be most likely to yield information on their derived or primitive states within the material available and within the limits of the tests which could be applied to the conclusions reached.

As might be expected, the principal test was that of the distribution of a character state amongst the species compared. The state having the widest occurrence is assumed to be the most primitive one, that with the most circumscribed distribution the derived one (the so-called commonality principle of Schaeffer, Hecht & Eldredge, 1972).

The characters finally selected, and a few others that deserve comment, can now be discussed.

(i) *Squamation*. All *Haplochromis* have the scales on the chest region (the area anterior to a line through the pelvic and pectoral fin insertions, and ventral to a horizontal line through the ventral part of the pectoral fin insertion) smaller than those on the ventral and ventrolateral parts of the body. The common condition is that in which the size change between the scales of the two regions is a gradual one, see Fig. 1; even when, as in *H. squamulatus* of Lake Victoria, the chest scales are noticeably small, the size change is still gradual (see fig. 17 in Greenwood, 1967). The less frequent condition is that in which the size transition (usually along the line between pectoral and pelvic fin insertions, but sometimes a little further posteriorly) is abrupt; since in these fishes the chest scales are generally small and numerous, the chest squamation is noticeably distinct from that of the belly and ventral flank regions (Figs 2 & 3).

A totally scaled chest, irrespective of squamation pattern, is the usual condition; circumscribed, bilaterally symmetrical naked patches are uncommon and are confined to species showing an abrupt size transition in thoracic-abdominal scale sizes. A completely naked chest is the most uncommon condition and would seem to be the end point in the apomorphic morphocline: abrupt size change  $\rightarrow$  bilateral naked patches  $\rightarrow$  completely naked chest.

Although the ventral body scales extending posteriorly from the pelvic fin insertions to the anus are smaller than those on the lateral and ventrolateral aspects of the flanks, the size gradation between the two fields is generally gradual. However, in a few species the ventral (belly) scales are much reduced in size and thus are clearly demarcated from the flank scales above them. This

\* The *Haplochromis* species of Lakes Victoria, Albert, Turkana, Tanganyika, Edward, George and Kivu, of the African rivers and those of Syria and Israel, and the species of *Serranochromis*, *Rheohaplochromis*, *Orthochromis*, *Astatoreochromis*, *Macrolepodus*, *Platytaeniodus* and *Hoplotilapia*, a total of some 390 species.

condition is correlated with an equally marked and abrupt size reduction in the scales on the chest, so that the tiny abdominal scales appear as a posterior and ventrolateral extension of those on the chest (Fig. 3). Such an arrangement is also considered to be a derived condition.

Surprisingly, in a group of species where most morphological features appear as elements in a continuum of differentiation, the various scale patterns discussed above are very trenchantly separated from one another. The few intermediate specimens I have observed are clearly individual rather than populational or specific variants.

As with the chest, a completely scaled cheek is the common condition, the scales being arranged in three or four horizontal rows. Reduced squamation is encountered infrequently, but ranges from a narrow naked band (one or two rows deep) along the ventral margin, to an almost completely naked cheek with only the suborbital row, or part of that row, persisting.

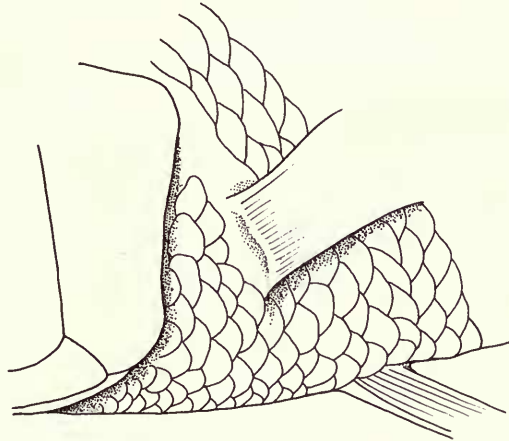


Fig. 1 Thoracic-abdominal scale transition in *Astatotilapia nubila*; left lateral view.

On the principle of commonality (Schaeffer *et al.*, 1972), strongly ctenoid body scales should be looked upon as the primitive condition, and an increase in the area of the body covered by cycloid or reduced ctenoid scales should be considered the derived one\*.

Some uncertainty about this conclusion could be raised by the situation in *Hemichromis*, also a '*Haplochromis*' group species (see Regan, 1922a). Here the scales are mostly cycloid with a few weakly ctenoid ones confined to the anterior part of the body; that is, a presumably derived condition. But *Hemichromis* species are substrate spawners and brood guards, a presumed primitive condition amongst African cichlids. Since certain other characters in *Hemichromis* are apparently derived ones (the unicuspid outer teeth, the number of inner tooth rows (one or none), and the form of the upper jaw), the cycloid scales may have evolved independently in the lineage. On the other hand, the presence of cycloid scales in '*Tilapia*' group species (see footnote), some of which are also substrate spawners and all of which have an apparently plesiomorph type of pharyngeal apophysis (see Greenwood, 1978), would appear to strengthen the argument for considering cycloid scales as primitive features. In the face of such contradictory observations it would seem advisable not to use this type of scale ornamentation in phyletic analysis.

All the *Haplochromis* and *Haplochromis* group species used in this review (see footnote p. 270) have less than the proximal two-thirds of the caudal fin covered by small scales; usually only the

\* Most taxa in the '*Tilapia*' group, as defined by apophyseal structure (see Greenwood, 1978), have cycloid scales, although some have a few weakly ctenoid scales on the anterior part of the body.

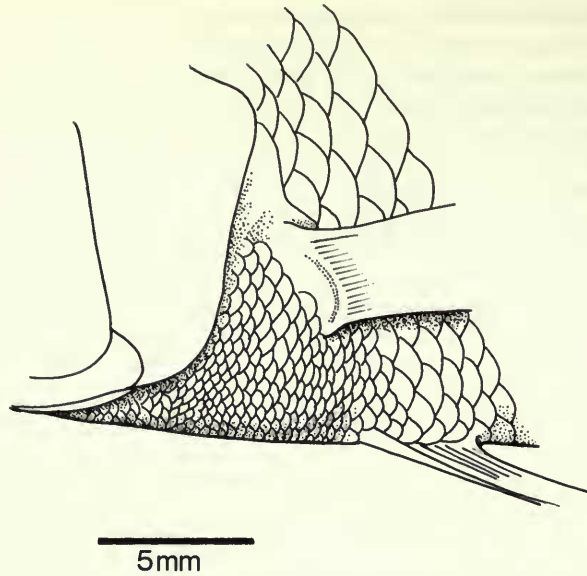


Fig. 2 Thoracic-abdominal scale transition in *Thoracochromis wingatii*; left lateral view.

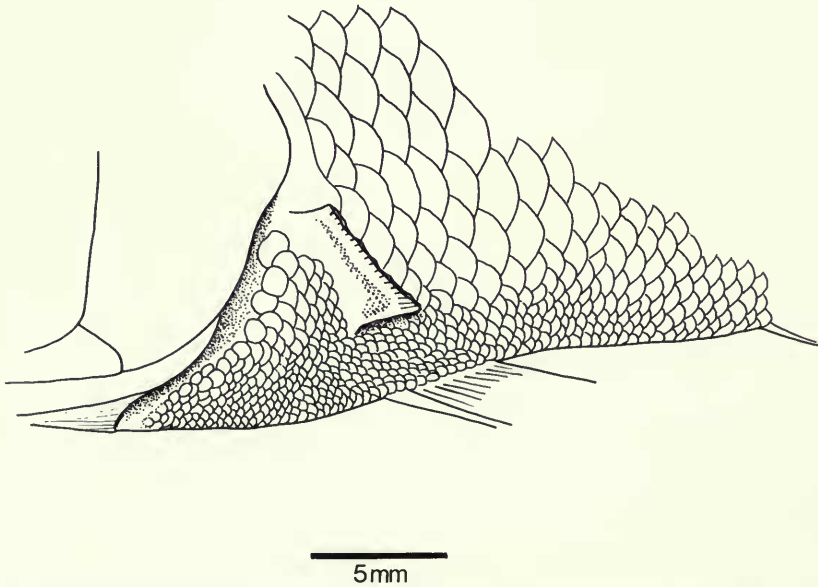


Fig. 3 Thoracic-abdominal scale transition in *Orthochromis polyacanthus*; left lateral view.

proximal half is covered. In contrast, all the endemic lacustrine species from Lake Malawi have the entire fin densely scaled (Trewavas, 1935). The partly scaled condition is assumed to be the plesiomorph one.

(ii) *Dentition*. Outer tooth row in both jaws. The most frequently occurring tooth form (Fig. 4) is that with an unequally bicuspid crown, moderately distinct neck and relatively stout body firmly attached to the underlying bone. Neither cusp is strongly compressed, their tips are acute or subacute and lie in or but slightly outside a vertical drawn through the corresponding outer margin of the tooth's body. Such teeth, apart from providing the definitive dental form in many



species, also precede the definitive tooth type in species having unicuspid teeth in adult fishes, and also, in at least some species, precede the definitive types when these are much modified versions of the basic bicuspid (e.g. in *H. obliquidens*). Unfortunately, ontogenetic data on tooth replacement are not available for many species, so the generality of the latter observation is unknown.

Because of its common occurrence and its primary position in the ontogenetic sequence of tooth replacement, the unequally bicuspid tooth is taken to be the plesiomorph dental type. Bicuspid teeth in which there is a differential growth of one cusp (usually the larger one) or equal development of both cusps are considered to be derived features, as are unicuspid teeth.

As mentioned above, most taxa having a definitive outer row dentition composed of unicuspid teeth also have an ontogenetically earlier one of bicuspid (usually persisting until an individual fish is between 80 and 100 mm standard length). Any shift forward in the time or body size at which the definitive unicuspid teeth appear can therefore be interpreted as being a derived condition.

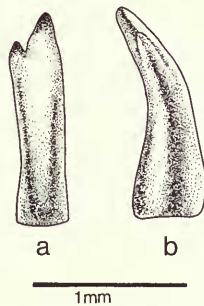


Fig. 4 Outer row jaw teeth (premaxillary) of *Astatotilapia flavijosephi*.  
A. Labial view. B. Lateral view (posterior aspect).

From one to six (rarely as many as twelve) enlarged and unicuspid teeth occur posteriorly on the premaxilla, even when the other teeth on that bone are bicuspid. The replacement of these unicuspid by teeth similar to those on the rest of the premaxilla must be considered a derived condition.

*Inner row teeth.* Here, on the grounds of common occurrence, small, tricuspid teeth must represent the primitive condition. As with the outer teeth, there can be an ontogenetic succession of teeth types, tricuspid or a mixture of tri- and bicuspid preceding unicuspid. Occasionally some or all inner rows are composed of highly modified bicuspid types resembling, albeit on a smaller scale, those of the outer row (e.g. *Haplochromis obliquidens* and *Macropodus bicolor*; see Greenwood, 1974a).

The presence of inner teeth other than tricuspid is a derived condition. Since most commonly there are from 2 to 3 rows of inner teeth, any increase or decrease in the number of rows must also indicate an apomorphic condition.

(iii) *The lower pharyngeal bone and its dentition.* The most commonly encountered form of lower pharyngeal bone has an approximately equilateral, triangular dentigerous surface, is not noticeably thickened or robust, and has its anterior blade-like portion neither noticeably elongate nor short (Fig. 5).

The teeth are arranged anteroposteriorly in about 30 to 50 rows, with those in the two median and in the posterior transverse row stouter than the others but, like them, retaining an unequally bicuspid crown in which the minor cusp is a near horizontal shoulder and the major one is weakly falciform and vertically aligned.

Apomorphic derivations from this basic type include changes in overall outline shape of the dentigerous area (Fig. 14), elongation of the anterior blade, increase or decrease in the number of tooth rows, an increase or, less commonly, a decrease in the number of rows of coarser teeth

(Figs 20 & 8), and changes in crown morphology of the teeth (generally a process of molarization associated with a general coarsening of tooth form; see Fig. 18B).

(iv) *Neurocranial morphology*. Modal neurocranial form (and thus the presumed plesiomorph condition) is best appreciated from a drawing (Fig. 6).

Salient features are the moderately high supraoccipital crest (*c.* three-quarters of the depth of the otic skull region measured from roof to ventral parasphenoidal face, but excluding the pharyngeal apophysis); the preorbital skull profile (from vomerine tip to the anterior point of the supraoccipital crest) rising at an angle of *c.*45°, its outline gently curved and its ethmovomerine region sloping forwards and downwards at a slight angle; the preotic part of the skull (measured from the vomerine tip to the anterior vertical wall of the prootic bone) comprising some 55–60% of the total length of the neurocranium, and the otic region of the skull not inflated. The pharyngeal apophysis is not enlarged, and the prootic does not contribute to the articular surface (Greenwood, 1978).

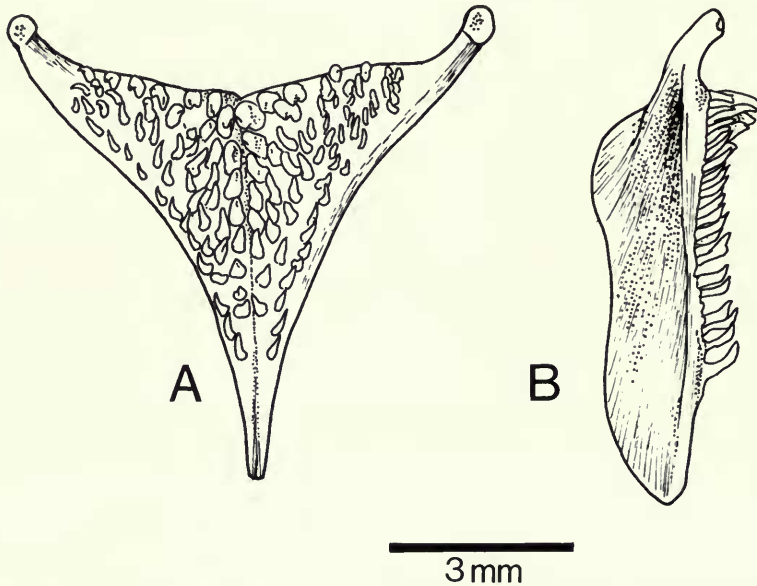


Fig. 5 Lower pharyngeal bone of *Astatotilapia bloyeti*. A. Occlusal view. B. Right lateral view (bone aligned vertically).

Derivative conditions include elongation of the preotic part of the skull (to about 70% of the neurocranial length) correlated with a flattening of the preorbital skull profile (Fig. 13); narrowing of the otic region, and in some variants a relative lowering of the supraoccipital crest; the retention of a basic skull form in the otic region but a marked increase in the slope of the ethmovomerine region (in some species almost to the vertical) and a correlated increase in the slope and curvature of the preorbital skull profile; the retention of basic otic and ethmovomerine regions but the elevation of the preorbital skull roof so that the neurocranium becomes higher and more angular in outline (see Greenwood, 1974*a*, for further analysis and figures).

Departure from the plesiomorph condition for the pharyngeal apophysis is always associated with an hypertrophy of the upper and lower pharyngeal bones and their dentition (see Greenwood, 1965*a*, 1974*a*, 1978).

(v) *Anal fin markings (egg-dummies) in male fishes*. Reference has already been made (p. 268) to the variety of these markings in *Haplochromis*. (See Wickler, 1962*a* & *b*, 1963 for a discussion of their importance in the breeding biology of these fishes).

Regrettably there is little information about these markings in live fishes, and what has been recorded is often insufficiently detailed to be of value. For instance, it is important to know if the

markings are merely coloured spots, whether each spot has a contrasting border, or whether it is truly an ocellus with a wide and translucent surround. The number and distribution of the markings are also important data. My own observations on live fishes from different parts of Africa, and on preserved material as well, all suggest that the anal markings (or their absence) may be of considerable value in helping to define lineages. But, because of a paucity of information for many species considered below it has proved impossible to use the character fully in this study.

It seems reasonable to assume that the egg-dummy markings (using that term in its widest sense and not just for true ocelli) were derived from coloured streaks and spots like those that are an almost universal feature on the dorsal fins of cichlids (see Wickler, 1962*a*). The first steps in the evolution of egg-dummies from a maculate colour pattern would involve a slight reduction in the number of spots and a consequent increase in the space between them, and the intensification or alteration of their colour so as to differentiate the anal spots from those in the dorsal fin. The end point in this process of differentiation seemingly would be reached with the development of ocellar spots.

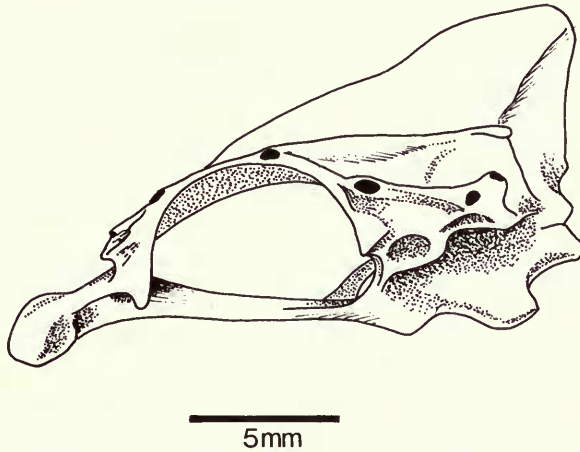


Fig. 6 Neurocranium of *Astatotilapia bloyeti*; left lateral view.

In species with true ocellar egg-dummies (e.g. the *Haplochromis* of Lake Victoria; see Greenwood, 1974*a*, especially plate I) the number of spots is reduced to modes of 3 or 4, the coloured centre of each spot is ovoid in outline, generally has a narrow black or dark border and is surrounded by a clear zone of fin membrane; other spots and markings on the fin are suppressed, although the greater part of the fin may have a coloured flush. The result is a most distinctive mark, with an illusion of three dimensionality, that is readily distinguished from any other fin or body markings.

There are, of course, other kinds of anal marking which, in their appearance, size and distribution on the fin, are intermediate between the supposed plesiomorph type (numerous, non-ocellate spots) and the presumed apomorph kind described in the last paragraph. Their possible phylogenetic importance will become apparent when more information is available not only on their appearance in live animals, but also on their functional role in mate recognition, courtship and spawning.

For the moment one can assume that the ocellar spots represent the apomorph condition and that the multiple spot type of anal marking is the plesiomorph one. Those *Haplochromis*-like species apparently without any spatially or chromatically differentiated anal markings (e.g. *Orthochromis malagaraziensis*; Greenwood, 1954) provide a particular problem because we know nothing of their reproductive behaviour. Thus the absence of 'egg-dummies' cannot necessarily be construed as representing a plesiomorph condition in these species.

(vi) *Vertebral numbers*. The modal range of total vertebral counts (excluding the fused  $PU_1 + U_1$  urostylar element) is 27–29 (comprising 12–14 abdominal and 15 or 16 caudal centra). On the grounds of its being the modal number, it is taken to be the plesiomorph condition.

Apomorphic deviations occur amongst the *Haplochromis* species of Lake Victoria where a few species show a higher modal count (30–32); these are all long-bodied piscivorous predators and the increase in the number of vertebrae occurs in the caudal section of the column. Parenthetically, it may be noted that Lake Malawi *Haplochromis* species with more than 32 vertebrae also show an increase in the number of caudal elements.

The most marked increase in vertebral numbers (apart from that in some Malawi species) is found in the genus *Serranochromis*. Here the modal counts are 33 and 34 (abdominal modes 16–17, caudal modes also 16 and 17), with an increase in the number of abdominal rather than the caudal elements as was the situation in the Victoria and Malawi *Haplochromis* species.

A similar increase in the number of abdominal vertebrae is also found in the seven Zambezi species of so-called *Haplochromis* revised by Bell-Cross (1975). In these species there is, however, a reduction in the number of caudal vertebrae as compared both with *Serranochromis* and with the plesiomorphic *Haplochromis* condition (14 and 15 in the Zambezi species, 16 and 17 in the others). In consequence, the modal total count (29–32) for the Zambezi fishes overlaps that of the plesiomorph *Haplochromis* type.

For want of falsifying evidence, the *Serranochromis* and 'Zambezi *Haplochromis*' conditions are both considered to be apomorphic ones.

In some *Haplochromis*-like genera, certain species have low counts for caudal vertebrae, but modal ones for the abdominal elements (see p. 290); probably these taxa, in the phyletic context of their particular lineages (and for this particular character), should be considered derived (i.e. autapomorphic).

(vii) *Caudal fin skeleton*. Vandewalle (1973) has provided a summary of the caudal fin skeleton in 108 cichlid species, mostly African. He shows that, overall, there is a remarkable constancy in this feature but that in some species individual hypural elements may fuse (especially hypural 1 with 2, and 3 with 4; the fifth hypural is always free except in one species (see p. 292) – Vandewalle finds no instance of fusion between all hypurals).

My own observations generally confirm those of Vandewalle, but strongly indicate that, with one possibly exceptional lineage (see p. 297), hypural fusion is an individual and not a specific or lineage trait. It is thus of very restricted value as an indicator of phyletic affinities, as is the organization of the whole caudal fin skeleton amongst the taxa examined.

(viii) *Number of dorsal and anal fin rays*. Amongst the *Haplochromis* species and related taxa reviewed (see footnote p. 270) the modal numbers of dorsal fin rays are 15 and 16, and of branched rays 9 and 10. Except for obvious individual variants, and two species of *Astatoreochromis*, all these taxa have 3 spinous rays in the anal fin and, modally, 8 or 9 branched rays.

If, on the principle of commonality, these numbers are taken to be the basic (i.e. plesiomorph) counts, then modal ray counts for either fin that are higher or lower should be considered derived features.

(ix) *Gill rakers*. There is a fairly narrow range of both gill raker numbers and shapes (counts and observations restricted to the outer row of gill rakers on the lower part of the first gill arch). In most species the rakers are relatively robust, simple structures (with sometimes the upper 2 or 3 of the series flattened and bi-, tri- or even polyfid), of moderate length and numbering from 7 to 12 (modal counts 8 and 9).

## Materials

All the BMNH material (spirit specimens, alizarin preparations, dry skeletons and radiographs) of all the taxa named in this paper has been examined, as have the Museum's collections of *Haplochromis* species from Lakes Victoria, Edward, George and Kivu, and selected specimens from the collection of Lake Malawi *Haplochromis* species and related genera.

In addition, the following specimens, borrowed from other institutions, have also been studied (and radiographed).

<i>Haplochromis albolabris</i>	(Holotype)	H1784
<i>Haplochromis angusticeps</i>		ANSP 54369-76
<i>Haplochromis bakongo</i>	(Paratypes)	RMAC 16945-947
<i>Haplochromis buysi</i>	(Holotype)	WH P1219
<i>Haplochromis darlingi</i>		AM/P2461
<i>Haplochromis fasciatus</i>		RMAC 48407-415
<i>Haplochromis giardi</i>	(Holotype)	MHN A2754
<i>Haplochromis luluae</i>	(Paratypes)	ANSP 51759-62
<i>Haplochromis oligacanthus</i>		RMAC 167930-931
<i>Haplochromis polli</i>	(Paratypes)	RMAC 99403-404
<i>Haplochromis stappersi</i>		RMAC uncatalogued
<i>Haplochromis thysi</i>	(Holotype)	RMAC 163991
<i>Haplochromis toddi</i>	(Holotype)	RMAC 1346
<i>Haplochromis torrenticola</i>		IRSN 1809-1960
<i>Chetia brevis</i>	(Holotype)	AM/P951
<i>Chetia brevis</i>	(Paratypes)	AM/P952
<i>Chetia brevis</i>		AM/P1425-6
<i>Chetia flaviventris</i>		AM/P1298
<i>Ctenochromis pectoralis</i>	(Lectotype)	ZMH402
<i>Ctenochromis pectoralis</i>	(Paratypes)	ZMH403

AM/P, Albany Museum; ANSP, Academy of Natural Sciences of Philadelphia; IRSN, Institut Royal des Sciences Naturelles de Belgique; H, Zoologisches Museum, Hamburg; MNH, Museum National d'Histoire Naturelle, Paris; RMAC, Musee Royal de l'Afrique Centrale, Tervuren; WH, Windhoek Museum; ZMH, Zoologisches Museum, Berlin.

### Classification

Applying the methodology and reasoning discussed above and in the Introduction, nine lineages, here given generic rank, may be recognized amongst the taxa studied. With the exception only of *Chetia*, each of these genera now contains species that were previously placed in *Haplochromis*.

Unless indicated otherwise, all the genera have a cranial apophysis for the upper pharyngeal bones formed from the parasphenoid and basioccipital (see '*Haplochromis*'-type apophysis in Greenwood, 1978) and a caudal fin scaled on its proximal half or less.

All vertebral counts quoted exclude the fused PU<sub>1</sub> and U<sub>1</sub> centra, and may thus be lower than those used by some other authors; abdominal vertebrae are identified as those bearing pleural ribs (including, of course, the first two vertebrae that have no ribs), and the caudal centra as those without ribs but, except occasionally the first (anterior) centrum, with a haemal arch.

Since the genus *Haplochromis* is now restricted to five species (see p. 280), difficulties arise when reference is made either to species formerly included in that genus, but which have not yet been assigned to other genera, or to the former concept of the genus *Haplochromis*. To avoid confusion, I have adopted the convention proposed and used by Patterson & Rosen (1977 : 163) for dealing with such situations. Namely, to prefix the species name with its former generic name cited between quotation marks, i.e. '*Haplochromis nigricans*' or '*H nigricans*'. When reference is made to the former concept of the genus the generic name alone, but in quotation marks, is used.

The Lake Victoria '*Haplochromis*' species will be reviewed in a paper now in preparation; until its publication these species can be referred to by using the old generic name in quotes. As a temporary expedient for general use until such times as the Lake Malawi '*Haplochromis*' are revised, a purely formal generic name for these species is proposed on p. 317.

Species mentioned in this paper are listed in the index on p. 321 under their former generic names (usually *Haplochromis*), with a reference first to the page on which they are listed in their new generic grouping, and secondly to the page on which that genus is described.

In the generic descriptions, presumed apomorph (i.e. derived) character states are italicized.

The generic revision which follows is arranged in two parts. After redefining the genus *Haplochromis* Hilgendorf, 1888, the first section will deal with '*Haplochromis*' species from Lakes Turkana, Albert, Tanganyika and Mweru, and with those from the Nile and Zaire river drainage systems, and the rivers of Kenya, Uganda and Tanzania.

The genera *Orthochromis* Greenwood, 1954, and *Astatoreochromis* Pellegrin, 1903, will also be considered in this section of the paper.

The second section (p. 299) will be concerned with the genera *Serranochromis* Regan 1920 and *Chetia* Trewavas, 1961, together with those '*Haplochromis*' species from the Zambesi, Limpopo and Angola river systems, which were thought to be related to *Serranochromis* and *Chetia* (see Trewavas, 1964).

## Section I

### *HAPLOCHROMIS* Hilgendorf, 1888

TYPE SPECIES: *Chromis* (*Haplochromis*) *obliquidens* Hilgendorf, 1888 (type specimens in the Humboldt Museum, Berlin).

#### *Description*

Body relatively deep (depth 35–40% of standard length).

*Squamation.* Scales on the body below the lateral line, and behind a line through the pectoral and pelvic fin insertions, are ctenoid; those above the upper lateral line and on the head and chest are cycloid.

The small scales on the chest grade imperceptibly in size with those on the ventrolateral and ventral aspects of the flanks (p. 270).

Cheek and chest fully scaled.

Lateral line with 29–34 scales (modal range 30–32); all but the last 3 or 4 scales of the upper lateral line are separated from the dorsal fin base by at least two scales of approximately equal size.

*Neurocranium.* The skull is of a generalized type (see p. 274; Fig. 6, and Greenwood, 1974a), its ethmovomerine region having only a slight downward slope, the dorsal surface of the vomer sloping in the same plane and at the same angle as the anterior part of the skull roof; the preotic part of the skull comprises some 55–60% of the total neurocranial length.

*Vertebral numbers:* 28–30 (modes 28 and 29), comprising 12–14 (mode 13) abdominal and 15 or 16 caudal elements.

*Dentition.* The outer teeth in both jaws are weakly bicuspid or unicuspid, *the crown of the tooth compressed and noticeably expanded relative to its slender, cylindrical neck and body* (Fig. 7). *The major cusp in bicuspid teeth is very much larger than the minor one, which is often little more than a slight, obliquely truncated basal point on the posterior margin of the anteriorly protracted and slightly incurved (i.e. buccally directed) major cusp. The compressed, anteriorly protracted and dorsoventrally expanded major cusp gives to the tooth, be it bi- or unicuspid, the appearance of having an obliquely truncated crown. The tip of this cusp lies outside the vertical formed by the anterior margin of the tooth's body.*

*All outer teeth, save in some species for a few posterior teeth on the premaxilla, are moveably attached to the underlying bone.*

In some species the posterior one to six teeth on the premaxilla are unicuspid or acutely bicuspid, and are stouter and larger than the others in that series; *these posterior teeth in other species of the genus closely resemble, in size and cusp morphology, their anterior congeners.*

Teeth forming the inner rows in both jaws mostly are small and tricuspid, but *in some species the anterior and anterolateral teeth in the outermost row may be identical with those of the outer row.* The inner teeth are arranged so as to form a tooth band that is wide anteriorly and antero-laterally, but narrow posterolaterally. This is effected by an *increase in the tooth rows from the primitive state of two or three to the derived condition of from 4 to 6.*

*Lower jaw* is relatively slender in lateral aspect and not noticeably deepened posteriorly; the length of its dentigerous surface is equal or about equal to the greatest depth of the dentary (as

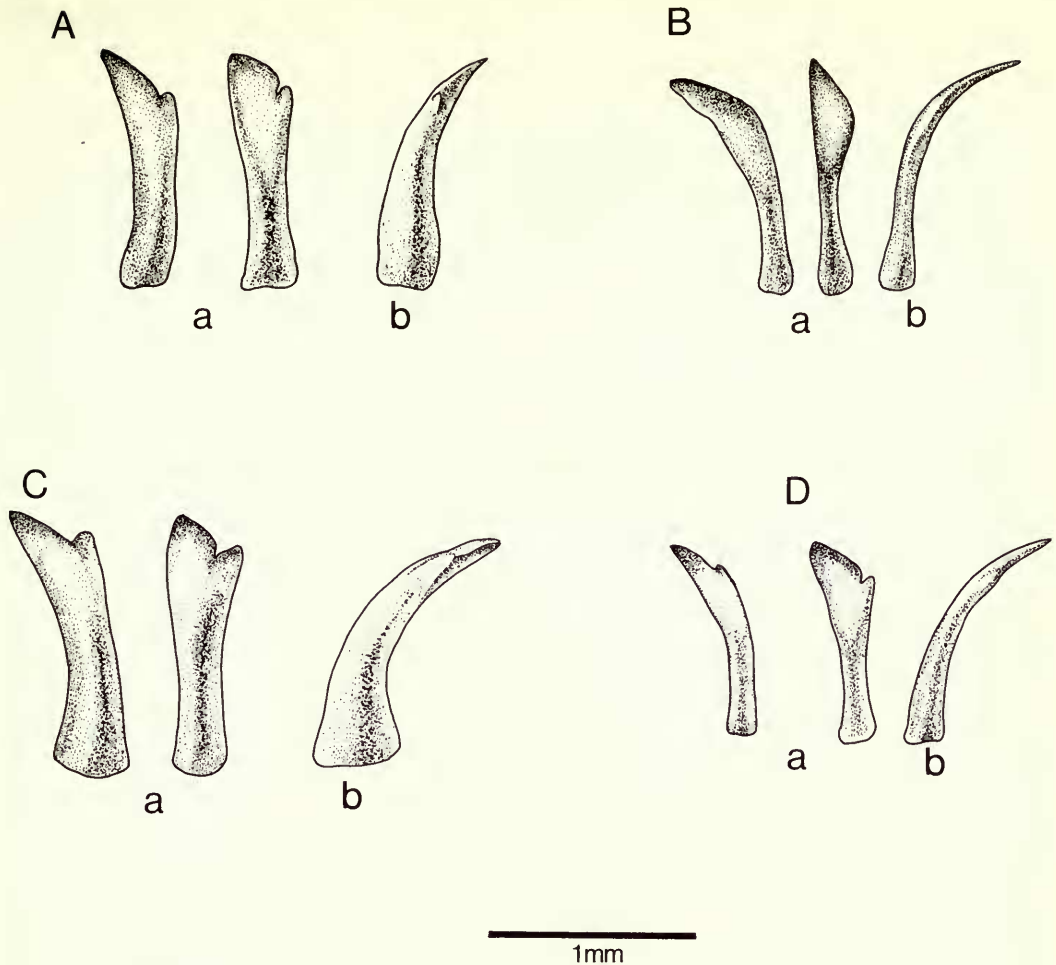


Fig. 7 Outer row jaw teeth (premaxillary) in various *Haplochromis* species; a. labial view, b. lateral (posterior) view. A. *H. annectidens*. B. *H. obliquidens*. C. *H. limax*. D. *H. astatodon*.

measured vertically from the posterior tip of its ascending coronoid process to the ventral margin of the bone).

*Lower pharyngeal bone and dentition.* The dentigerous surface of the bone is triangular and approximately equilateral in outline (Fig. 8). The teeth, except for those forming the posterior transverse row, are slender with the greater part of the cusp protracted and curved posteriorly so that most of the occlusal surface lies nearly parallel with the surface of the pharyngeal bone. (The absence of a distinctly coarser median series of teeth probably is a derived feature; see p. 273.)

*Dorsal fin* with 14–16 (modes 15 and 16) spinous and 8–10 (mode 9) branched rays.

*Anal fin* with 3 spinous and 7–10 (mode 9) rays.

*Caudal fin skeleton* without fusion between any of the hypural elements; none of the species reviewed here was examined by Vandewalle (1973).

*Caudal fin* truncate or subtruncate, the posterior margin straight or weakly emarginate.

*Pelvic fins* with the first branched ray the longest.

*Anal fin markings.* True ocellar egg dummys (see p. 274), usually 3 or 4 in a single row, are present in adult males. Some females may have a similar number of small, non-ocellate spots present in the same position on the fin.

*Gill rakers* are moderately slender, with 8–10 (mode 9), rarely 7, present on the outer row on the lower part of the first gill arch.

*Contained species*

*Haplochromis obliquidens* Hilgendorf, 1888 (Type species). Lake Victoria (see Greenwood, 1956a).

*Haplochromis lividus* Greenwood, 1956. Lake Victoria (see Greenwood, 1956a).

*Haplochromis annectidens* Trewavas, 1933. Lake Nabugabo (see Greenwood, 1965b).

*Haplochromis limax* Trewavas, 1933. Lakes Edward and George (see Greenwood, 1973).

*Haplochromis astatodon* (part) Regan, 1921. Lake Kivu. When reviewing this species I found that two distinct types of outer jaw dentition are represented amongst the 13 specimens and one skeleton on which Regan (1921a) based his original description of the species. That there are two types of teeth represented in this sample is implicit in Regan's comment that the dental morphology of *H. astatodon* is annectant between that of *H. obliquidens* and the simple bicuspid tooth found in many of Lake Victoria '*Haplochromis*' species.

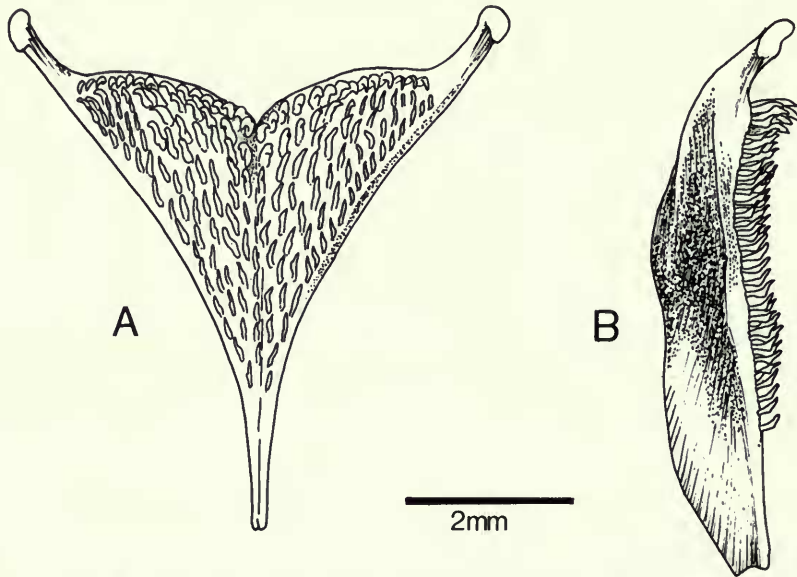


Fig. 8 Lower pharyngeal bone of *H. lividus*. A. Occlusal view. B. Right lateral view (bone aligned vertically).

Six of the syntypical specimens (BMNH reg. nos 1906.9.6:124–129) have outer teeth remarkably like those of *H. obliquidens*. That is, the crown is obliquely truncate and greatly produced (Fig. 7D), the neck and body fine, and the teeth are moveably implanted in the gum tissue. However, in these specimens a minute second cusp is present on many of the anterior and anterolateral teeth, a condition seen only amongst some of the posterior teeth in *H. obliquidens*. These particular specimens of *H. astatodon* also resemble *H. obliquidens* in having many teeth in the outermost of the multiseriate inner rows enlarged and often obliquely cuspidate; the inner teeth, like those in *H. obliquidens*, being small and tricuspid.

The pharyngeal dentition in those specimens is also like that in *H. obliquidens*, but the two species differ in certain morphometric features and thus would seem to represent distinct species.

The eight other syntypical specimens of *H. astatodon* (BMNH reg. nos 1906.9.6:130–132; 1977.5.2:1–4 (the material was originally under-registered, hence the lot registered in 1977)), and a skeleton (BMNH reg. no. 1906.9.6:133) have distinctly bicuspid teeth in which the major cusp, although somewhat obliquely truncate, is neither protracted nor expanded, nor is it markedly compressed; the minor cusp is not so greatly reduced as it is in the other syntypical specimens of *H. astatodon*, or in *H. limax*, *H. annectidens* and *H. obliquidens*.



The tooth form and dental arrangement in these aberrant syntypes does, however, approach closely that found in '*Haplochromis*' *nuchisquamulatus* of Lake Victoria and '*H.* *aeneocolor* of Lake George (see Greenwood, 1956a and 1973 for the species respectively).

Because of this marked difference in dental morphology I am restricting the name '*astatodon*' to the six syntypes (BMNH reg. nos 1906.9.6:124-129) with *H. obliquidens*-like teeth, and have selected specimen 1906.9.6:125 as the lectotype. The eight specimens with '*nuchisquamulatus*'-like teeth will be dealt with in a subsequent paper.

#### *Diagnosis and discussion*

The lineage here recognized as the genus *Haplochromis* is characterized by having obliquely truncate and protracted crowns to the outer jaw teeth, an increase in the number of rows of inner teeth in both jaws (some of these teeth also having obliquely truncate crowns), and all jaw teeth moveably articulated with the underlying bone. The species are also characterized by their fine lower pharyngeal teeth, and the presence of truly ocellar egg-dummies on the anal fin of adult males. In their gross morphology, and in most aspects of their osteology and anatomy (the greatly elongate intestine excepted), the species retain a generally unspecialized level of organization.

Dental features similar to those of *Haplochromis* do occur in other African Cichlidae, for example *Cyathochromis obliquidens* Trewavas (1935) of Lake Malawi, but are associated with characters which indicate that these other taxa do not share a recent common ancestry with *Haplochromis*. Since all the taxa are grazers on epilithic or epiphytic algae their dental similarities must be considered the results of convergent evolutionary trends.

Within the genus *Haplochromis*, *H. obliquidens* and *H. astatodon* have what appears to be the most specialized (i.e. derived) form of teeth, and *H. limax* the least specialized teeth (see Fig. 7C). The common ancestor could well have been a species with a '*limax*'-like dentition.

In a preliminary phyletic analysis of the Lake Victoria '*Haplochromis*' species flock (Greenwood, 1974a), '*H.* *nigricans* was considered to be the sister species of *H. lividus* and *H. obliquidens*, and '*H.* *nuchisquamulatus* the sister species of the other three species combined. My recent investigations now suggest, however, that '*H.* *nigricans* (together with species from Lakes Edward, George and Kivu) form a distinct monophyletic lineage which cannot be related to *Haplochromis* (as here defined) on the basis of shared derived characters. Neither, on those grounds, can '*H.* *nuchisquamulatus* be considered the sister group of *Haplochromis*. But, it cannot be denied that '*H.* *nuchisquamulatus* (and at least two other species, including the atypical *H. astatodon* noted above) do have a tooth morphology approaching that of *Haplochromis* (in particular *H. limax*). Tooth form in these species is what might be expected as an early stage of differentiation from the primitive bicuspid type in a morphocline leading to the '*obliquidens*' type. More research is needed before any possible relationship between the five *Haplochromis* species and the '*H.* *nuchisquamulatus* complex can be clarified.

#### *ASTATOTILAPIA* Pellegrin, 1903

TYPE SPECIES: *Labrus desfontainii* Lacépède, 1803 (type specimens, once in the Paris Museum but now apparently lost).

#### *Description*

Body relatively deep (35-40% of standard length).

*Squamation.* Over most of the body the scales are ctenoid, the ctenii generally strong and extending around the greater part of the scale's free margin; scales above the upper lateral line may be less strongly ctenoid than those below it, and in three species are partly or entirely cycloid. Scales on the nape and cheek are cycloid, as may be those on the chest, which is always completely scaled.

The chest scales show a gradual size transition with those on the ventral and ventrolateral aspects of the flanks (see Fig. 1); in some species the chest scales are not noticeably small, but in *A. flavijosephi*, *A. dolorosa* and *A. desfontainesi* these scales are distinctly smaller (and in *A. calliptera* somewhat smaller) than are the chest scales in other species of the genus.

The cheek is fully scaled, usually with 3 (less commonly 2 or 4) horizontal scale rows.

The lateral line has from 28 to 30 scales (31–33 in *A. desfontainesi*), all but the last 1 to 4 scales of the upper lateral line separated from the dorsal fin base by two or more scales of approximately equal size. *Astatotilapia swynnertoni* is exceptional in having the last 6–8 scales of the upper lateral line separated by less than two scales of equal size.

*Neurocranium.* The skull is of the generalized haplochromine type (see Greenwood, 1974a: 58–59, and p. 274 above). The preotic portion of the skull is not protracted (comprising some 55–60% of the neurocranial length), and the ethmovomerine region is short, sloping upwards at a slight angle. The dorsal skull roof may be straight or very slightly convex anterodorsal to the orbit. The supraoccipital crest is not reduced in length; its anterior border continues the line formed by the dorsal surface of the ethmovomerine region and the orbital part of the skull roof.

The ventral apophysis for the upper pharyngeal bones (see p. 274) is slightly enlarged in one species (*A. flavijosephi*). The otic region of the skull is relatively deep, and is not inflated.

*Vertebral numbers:* 27–30, rarely 26 (modes 28 and 29), comprising 12–14 (mode 13) abdominal and 14–16 (mode 15) caudal elements. The apophysis for the *retractor dorsalis* pharyngeal muscles is small, and situated on the third vertebra.

*Dentition.* In fishes less than 70 mm standard length unequally bicuspid teeth (Fig. 4) predominate in the outer row of both jaws. The crown in these teeth is not noticeably compressed, neither is it clearly demarcated from the neck of the tooth (cf. *Haplochromis*, p. 278). Except in two species, the cusps are acutely pointed and both lie within the verticals formed by the anterior and posterior margins of the tooth's body; in *A. calliptera* and *A. swynnertoni*, however, at least the major cusp is somewhat obliquely truncate. Unlike *Haplochromis*, the outer teeth in *Astatotilapia* are firmly attached to the bone.

Even in specimens less than 70 mm SL some weakly bicuspid teeth and some unicuspid teeth are found in both jaws. In larger specimens the unicuspid type predominates. The proportion of uni- to bicuspid teeth increases with the size of the individual; *A. dolorosa*, known only from the holotype, a fish 95 mm SL, has only unicuspid teeth.

All species, and specimens of all sizes, have the posterior 3–12 teeth in the premaxilla enlarged and unicuspid.

Teeth forming the inner rows are generally tricuspid and small; some weakly bicuspid or even unicuspid teeth may occur in these rows, particularly in larger fishes. There are 1–3 (usually 2) rows of teeth anteriorly and anterolaterally in both jaws, a single row posteriorly and posterolaterally.

*Lower jaw* is not foreshortened, nor is it noticeably deepened posteriorly.

*Lower pharyngeal bone and dentition.* The dentigerous surface is apparently equilateral in all species. Except in *A. flavijosephi*, all the teeth are compressed, slender and cuspidate, with only those teeth in the two median and the posterior transverse row somewhat coarser than the others. Cusp form is essentially similar to that in *Haplochromis* but the crown is not so markedly produced as in that genus (cf. p. 279 above). In *A. flavijosephi*, the teeth forming the median rows are enlarged, with molariform or submolariform crowns; some teeth in the lateral rows also are somewhat enlarged and have submolariform crowns. The lower pharyngeal bone, as compared with that in the other species, is stouter.

*Dorsal fin* with 14–16 (mode 15), rarely 13, spinous rays and 8–11 (modes 9 and 10) branched rays.

*Anal fin* with 3 spinous and 7–10 (modes 8 and 9) branched rays; specimens of *A. desfontainesi* with 4 spines have been recorded.

*Caudal fin skeleton.* *Astatotilapia burtoni* (7 specimens radiographed) and *A. nubila* (9 specimens) show no hypural fusion, but the other 7 species all yielded certain individuals with some degree of fusion in either the upper or the lower set of hypurals, or far less frequently, in both sets. It must be stressed, however, that these observations were made principally from radiographs and that these can be difficult to interpret with accuracy if the hypurals are closely apposed to one another. Vandewalle (1973) reports no fusion in the two specimens of *A. burtoni* he examined. (It is not possible to tell from his paper whether these were radiographed or dissected specimens.)

*Caudal fin* strongly subtruncate to rounded.

*Pelvic fin* with the first branched ray longest.

*Anal fin markings in male fishes.* True ocellar markings are present, usually 2–4 in number (but as many as 9 in large specimens of some species) arranged in one or less commonly in two rows, the number of rows positively correlated with the number of ocelli and the size of the specimen. The row or rows of ocelli run along a line situated approximately midway between the base and the distal margin of the fin. This linear arrangement (and that in *Haplochromis*) contrasts strongly with the near random arrangement of the anal spots in *Serranochromis* and *Chetia* (see pp. 302 and 308 respectively).

No information is available on the occurrence of anal spots (not ocelli, see p. 275) in the females of *Astatotilapia* species, except that 3 or 4 linearly arranged spots do occur in *A. nubila* from Lakes Victoria and George. Trewavas (1973), however, records seeing ripe female *A. nubila* and *A. bloyeti* with male-type ocelli on the anal fin, a phenomenon I never encountered when working with these species in the field.

Where breeding habits are known, *Astatotilapia* species are female mouthbrooders. Indeed, *A. burtoni* is the species on which Wickler (1962*b*) developed his dummy-egg theory to explain the function of anal ocelli in spawning.

*Gill rakers* of various shapes, from short and stout to moderately long and slender; 8 or 9, less commonly 7, in the outer row on the lower part of the first gill arch.

#### *Contained species*

*Astatotilapia desfontainesi* (Lacép.) 1803 (Type species)\*; as restricted by Regan (1922*a*) to specimens from Tunisia and Algeria.

*Astatotilapia flavijosephi* (Lortet), 1883. Israel and Syria. See Trewavas (1942) and Werner (1976) for redescription and biology.

*Astatotilapia bloyeti* (Sauv.), 1883. The type specimens are from Kandoa (Great Ruaha system), Tanzania. Regan (1922*a*) included three other species in the synonymy of *A. bloyeti*, viz. *Ctenochromis strigigena* Pfeffer, 1893, *Tilapia sparsidens* Hilgendorf, 1903 and *Paratilapia kilossana* Steindachner, 1916. For the purposes of this revision I have accepted Regan's synonymy, but much more research is needed into the alpha level taxonomy of fluviatile haplochromine cichlids in eastern and southern Africa before the species can be defined adequately. I have examined material from many localities in Kenya, Uganda and Tanzania, and also from Lake Chad and the Upper Niger. This material would seem to represent a taxon closely similar, if not identical, to *A. bloyeti*, at least on anatomical and morphometric characters. However, judging from colour notes made on certain specimens from Tanzania there are strong indications that at least some populations are distinguishable on the basis of male coloration.

An apparently undescribed species recently distributed by the aquarium trade under the name 'Nigerian mouthbrooder' or 'Nigerian *H. burtoni*' probably should be included in the *A. bloyeti* complex, as should an undescribed species from the Malagarasi river (personal observations).

Until the necessary revision of these 'species' and populations has been carried out, the different taxa involved can be referred to as the '*A. bloyeti* complex' (see Greenwood, 1971). Its distribution includes rivers, streams and certain lakes in Kenya, Uganda, Tanzania, Nigeria and, probably the Nile.

*Astatotilapia nubila* (Blgr.), 1906. Lakes Victoria, Kioga, Edward, George, Nabugabo, Kachira, Nakavali and Kijanebalola, and river systems in Uganda which are connected with these lakes (see Trewavas, 1933; Greenwood, 1965*b* and 1973). The species has been widely distributed in Uganda (and possibly Kenya and Tanzania as well) as a result of fishfarming and dam stocking activities; its natural distribution is that listed in the first sentence.

*Astatotilapia dolorosa* (Trewavas), 1933. Known only from the holotype, a specimen collected from the Chambura river which flows into the Kazinga channel connecting Lakes Edward and George.

\* The emended spelling of the trivial name, '*desfontainesi*', was first used by Boulenger (1899). Since Lacépède intended that the species be named for M. Desfontaines, Boulenger's emendation, although not explained, would seem to be justified.

*Astatotilapia burtoni* (Günther), 1893. Lake Tanganyika and rivers associated with that lake (see Poll, 1956). The specimens recorded from Lake Kivu by Boulenger (1915) were misidentifications (see Regan, 1921a).

*Astatotilapia stappersi* (Poll), 1943. Rivers associated with Lake Tanganyika, see Poll (1956).

*Astatotilapia swynnertoni* (Blgr.) 1907. Lower Buzi river, Mozambique.

*Astatotilapia calliptera* (Günther), 1893. Lakes Malawi and Chilwa; '... coastal rivers as far as the Save river, Mocambique' (Bell-Cross, 1976); Busi and lower Sabi-Lundi systems; Lower Zambezi and Pungwe systems.

Jubb (1967a) treats *A. swynnertoni* as a synonym of this species, but gives no reason for so doing. Judging from the material I have examined, I would consider the two species to be distinct.

*Incertae sedis*: *Chetia brevis* Jubb, 1968. The presence of 3 or 4 true ocellar markings on the anal fin would seem to exclude this species from the genus *Chetia* (see p. 307 below, and p. 274 above), as would the predominance of ctenoid over cycloid scales on the body, and the retention of bicuspid teeth as the predominant tooth form in specimens as large as 90 mm standard length (see p. 273).

The inclusion of *Chetia brevis* in *Astatotilapia* is, however, very tentative and may well be altered when the phylogeny and systematics of the 'Angolan *Haplochromis*' species are revised (see p. 312).

#### *Diagnosis and discussion*

The genus *Astatotilapia* is distinguished from the other fluviatile '*Haplochromis*' group species by the following combination of characters: male anal fin markings are true ocelli, large and usually numbering from 3 to 6, and are arranged in a single or, less frequently, a double row (the number of ocelli and hence the number of rows correlated positively with the size of the fish); scales on the chest region not sharply size-demarcated from those on the ventrolateral and ventral aspects of the body; chest and cheek fully scaled; most body scales are ctenoid, the ctenii on each scale not restricted to a narrow median arc on the scale's free margin but distributed along almost the entire free margin; most teeth in the outer row of both jaws are bicuspid, the cusps of unequal size, but the minor one never minute. The major cusp is acute or, rarely, somewhat obliquely truncate but not protracted (cf. Figs 4 and 7). A few stout unicuspid teeth occur posteriorly in the premaxilla of fishes at all sizes, and some may also be present anteriorly, in both jaws, of fishes > 80 mm SL; the inner teeth usually are tricuspid (occasionally some are weakly bicuspid or unicuspid) and are arranged in two rows anteriorly and anterolaterally; 27–30 (rarely 26) vertebrae, of which 12–14 (mode 13) are abdominal, and 14–16 (mode 15) are caudal elements; pelvic fin with the first branched ray the longest.

Apart from the ocellar anal fin markings, none of these characters can be considered derived, and the anal ocelli are an apomorphic feature shared with *Haplochromis* and most, if not all '*Haplochromis*' species from Lakes Victoria, Edward, George and Kivu, and some species from Lake Malawi as well. Thus, the possibility cannot be overruled that *Astatotilapia* is a non-monophyletic assemblage.

The absence of other synapomorphic features shared with the genera described in this paper at least indicates that no members of *Astatotilapia* are closely related to any one of those lineages (as was implied when, hitherto, most were placed in the genus *Haplochromis*).

The relationship of *Astatotilapia* to *Haplochromis* as now redefined is obscure. Both lineages share the apomorphic feature of anal ocelli, suggesting that both share a more recent common ancestry than either lineage does with any taxa not having this feature. Uncertainty also exists about the relationship between *Astatotilapia* and the anal ocelli-bearing lineages of Lakes Victoria, Edward, George and Kivu, and for that matter some of the anatomically generalized '*Haplochromis*' species of Lake Malawi.

Any member of the *Astatotilapia* line with acutely bicuspid teeth (except, because of its specialized pharyngeal mill, *A. flavijosephi*) could, on purely morphological grounds, be taken to represent the ancestral species for many lineages within the Victoria–Edward–Kivu species flock (see Greenwood, 1974a). It is, indeed, likely that a number of generalized but endemic species from that flock will have to be included in *Astatotilapia*, as may some from Lake Malawi.

Relationships within the *Astatotilapia* lineage cannot be indicated at present, partly because no intragroup synapomorphies are apparent and partly because the species are as yet poorly defined and understood (see p. 283).

*Astatotilapia*, like *Thoracochromis* (see p. 290) has a wide geographical distribution (one, indeed that extends beyond Africa into the Middle East). Both genera occur in north Africa, although *Astatotilapia* does not apparently occur in the Nile drainage (except in Lakes Victoria and Kioga); *Thoracochromis*, on the other hand, is widely distributed in the Nile system but is poorly represented, if at all, in Lake Victoria, and does not extend so far into southern Africa as does *Astatotilapia*.

In general, it could be said that *Astatotilapia* is a lineage of eastern and southern Africa, with outliers in the northeast (*A. flavijosephi*) and northwest (Algeria and Tunisia), and *Thoracochromis* a lineage of north, central and western Africa. Since the phyletic integrity of both lineages is uncertain (see above, and p. 294), and because large parts of the Zaire system are poorly known, this difference may be more artefactual than real.

#### *ASTATOREOCHROMIS* Pellegrin, 1903

TYPE SPECIES: *Astatoreochromis alluaudi* Pellegrin, 1903 (type specimens in the Paris Museum). For synonymy see Greenwood (1959a) and discussion below.

##### *Discussion*

Pellegrin (1903) distinguished *Astatoreochromis* (then monotypic) from similar '*Haplochromis*'-group species and genera principally on its having 5 or 6 anal and 18 or 19 dorsal fin spines. The type species is from Lake Victoria, but later, specimens were collected from Lakes Edward and George, the Victoria Nile and Lakes Kioga, Nakavali and Kachira (see Greenwood, 1959a).

Redescriptions based on this enhanced material added to the number of diagnostic features, at least with respect to the '*Haplochromis*' species of Lakes Edward and Victoria (Greenwood, 1959a). Amongst those features are the rounded caudal fin, the high number and multiserial arrangement (3 or 4 rows) of the anal ocelli in male fishes, the unusual coloration (golden overlain with olivaceous green, the median fins olive-yellow, flushed with maroon and margined with black), and the lack of sexual dimorphism in basic body and fin colours. This material also extended the known range of dorsal fin spine numbers (16–20) as well as those of the anal fin (4–6).

The species *Astatoreochromis alluaudi* is further characterized by its strongly hypertrophied crushing pharyngeal dentition and bones (with a correlated hypertrophy of the cranial apophysis for the upper pharyngeal bones; see Greenwood, 1959a and 1965a). A similar degree of pharyngeal hypertrophy does, of course, occur in at least five other species from Lakes Victoria, Edward and George (Greenwood, 1960 : 270–279; 1973 : 172–177; Greenwood & Barel, 1978 : 164–179), but these species differ from *A. alluaudi* in several features, all of which suggest that *A. alluaudi* represents a distinct phyletic lineage.

The principal diagnostic characters for *Astatoreochromis* are not easily assessed on a basis of their apo- or plesiomorphy. The enlarged pharyngeal mill clearly is a derived feature, but is one that has evolved independently in at least two '*Haplochromis*' lineages (see Greenwood, 1974a, and p. 279 above); it is thus of little value in assessing relationships at the level with which we are here concerned.

As yet too little is known about the evolution and phyletic distribution of anal ocelli (and other anal fin markings) to say whether the increased number and multiserial arrangement in *Astatoreochromis* is a derived feature. The basis for comparison here is with the fewer ocelli and their uni- or biserial arrangement in *Haplochromis*, *Astatotilapia* and the Lake Victoria '*Haplochromis*' species.

The absence of sexually dimorphic coloration in *Astatoreochromis* is a most unusual feature amongst '*Haplochromis*'-like taxa, but would seem, *a priori*, to be a primitive rather than a derived feature (although its correlation with the increased number of anal ocelli and thus, possibly its degree of relative importance in breeding behaviour, cannot be interpreted without appropriate ethological studies).

Only the increased number of anal and dorsal fin spines (but, it should be noted, not the total number of rays in these fins) would seem to be derived features.

In the absence of other and synapomorphic characters, however, it is impossible to use fin spines numbers to suggest any possible close phyletic affinities for *Astatoreochromis*. For example, the squamation pattern in the genus is of the supposedly plesiomorph type, and this would seem to rule out any possible relationship with the *Orthochromis* lineage (see p. 295) in which there is also a marked trend towards increased numbers of dorsal and anal fin spines. *Orthochromis*, it may be added, does not have anal ocelli or, apparently, any other anal fin markings in the males (the breeding habits of no *Orthochromis* species are recorded).

That *Astatoreochromis* may be related (possibly as the derived sister-group) to some of the 'Haplochromis' species with enlarged pharyngeal mills, cannot be completely discounted; but, equally there is little unequivocal evidence to support such an hypothesis (see above).

For the moment, then, *Astatoreochromis* is maintained as a distinct lineage because of its various distinctive features, taken in combination, and because its sister-group relationship to any other lineage cannot be hypothesised on the basis of uniquely shared derived characters.

Recently, Poll (1974) added a second species (*Haplochromis straeleni* Poll, 1944, from the Lukuga and Ruzizi rivers, Zaire) to the genus *Astatoreochromis*. This step was taken because some specimens of *straeleni* have 4 anal spines (i.e. 2 of the 7 specimens known), because of close similarities in overall coloration and in the pattern and number of anal ocelli, and because *straeleni* has a relatively enlarged lower pharyngeal bone with some molariform teeth (see fig. 1, Poll, 1974). The species also has, as compared with *Astatotilapia* and the Lake Victoria 'Haplochromis' species, more dorsal fin spines (17 or 18) but the same number of branched rays in that fin (8 or 9); in other words, the *Astatoreochromis* condition (see above). Furthermore, according to Poll's account, there is no sexually dimorphic coloration in '*H.* *straeleni*'.

There is another 'Haplochromis' species, '*H.* *vanderhorsti* Greenwood, 1954 (Malagarasi river, Tanzania) which closely resembles *straeleni* in all the characters under consideration, differing only in its slightly lower dorsal fin spine count (16 or 17), and in none of the 54 specimens examined having 4 anal fin spines; its lower pharyngeal bone and dentition are more massive than those of *straeleni* (i.e. like the condition in *A. alluaudi* of the same size). The resemblances between '*H.* *vanderhorsti*' and *A. alluaudi*, and those between '*H.* *straeleni*' and '*H.* *vanderhorsti*' have been noted already (Greenwood, 1954: 405-407; 1959a: 166-167), but were not analysed in terms of their apo- or plesiomorphy, and no conclusion was reached about the interrelationships of the species or their formal taxonomic status.

Apart from the increased number of dorsal fin spines (and the four-spined individuals of '*H.* *straeleni*'), the only other shared, and probably derived, characteristic common to the three species is the enlarged lower pharyngeal bone and its at least partly molariform teeth (again a trend character, least developed in *straeleni*, most developed in *Astatoreochromis alluaudi*, and one which is known to have evolved independently in several haplochromine lineages). But, taking into account the virtually identical, non-sexually dichromatic coloration of the three species (and the ubiquity of sexual dichromatism amongst fluviatile haplochromines) the most parsimonious solution would be to consider *alluaudi*, *straeleni* and *vanderhorsti* as being more closely related to one another than any one of them is to any other lineage.

On these grounds I would agree with Poll's (1974) inclusion of '*H.* *straeleni*' in *Astatoreochromis* and would now include '*H.* *vanderhorsti*' in that genus as well.

#### *Contained species*

*Astatoreochromis alluaudi* Pellegrin, 1903 (Type species). Lakes Victoria, Kioga, Edward, George, Nabugabo, Kachira, and Nakavali; rivers and streams associated with these lakes. The species has been widely distributed in Kenya, Uganda and Tanzania as a biological control agent against snails (McMahon, Highton & Marshall, 1977). For a full description of the species see Greenwood (1959a), and for evidence invalidating the two subspecies described in that paper see Greenwood (1965a).

*Astatoreochromis straeleni* (Poll), 1944. Lukuga and Ruzizi rivers, Lake Tanganyika drainage. See Poll (1974) for a redescription of the species.

*Astatoreochromis vanderhorsti* (Greenwood) 1954. Malagarasi river and swamps, Lake Tanganyika drainage.

*CTENOCHROMIS* Pfeffer, 1893

TYPE SPECIES: *Ctenochromis pectoralis* Pfeffer, 1893 (type specimens in Hamburg Museum and BMNH).

*Description*

Body relatively deep to relatively slender (depth 30–40% of standard length).

*Squamation*. Scales on the body below the upper lateral line are strongly to moderately ctenoid (weakly ctenoid in one species, *C. horii*), becoming cycloid over the posterior half of the body. Scales above the upper lateral line show the same range of ctenoidy or are all cycloid, the kind of scale being constant intraspecifically and positively correlated with those below the lateral line. Scales on the head and, when present, on the cheek, are cycloid.

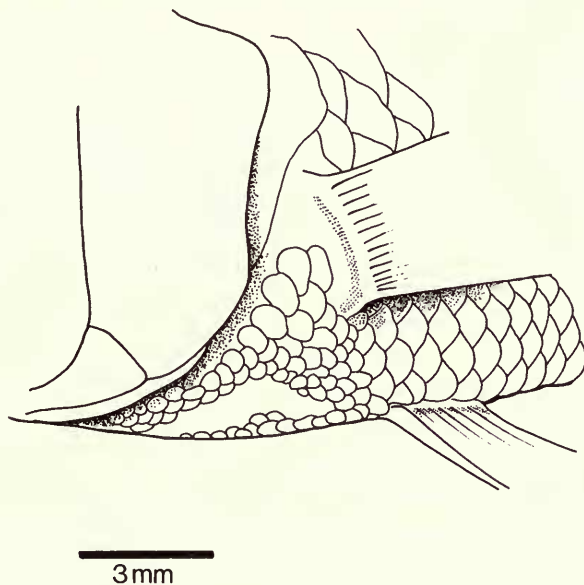


Fig. 9 Thoracic-abdominal scale transition in *Ctenochromis pectoralis*. Left lateral view.

The cheek always has a naked area along its ventral margin; in one species this area is less than a scale row in depth, in two others it is from 1 to 3 horizontal scale rows deep, and in a fourth virtually the whole cheek is naked, a few scales remaining immediately below and, or, behind the orbit.

Along or slightly behind a line joining the pectoral and pelvic fin bases there is an abrupt size transition between the very small scales on the chest and the much larger scales on the lateral and ventrolateral aspects of the body (Fig. 9).

The chest has a well circumscribed naked patch on each side of the body (Fig. 9), the two patches joined in some species by a ventral naked area. The size of the naked patch shows some interspecific variability, from a small and ventrolaterally situated area, to one covering most of the lateral and ventrolateral (but not the medial) aspects of the chest.

There are 27–33 scales in the lateral line series (modal numbers 30 and 31 for the two species from Tanzania, and 28–30 for the three Zaire river system species (see p. 290 below)); the last 8–12 (usually 8 or 9) pored scales in the upper lateral line are separated from the dorsal fin base by less than two scales of approximately equal size.

*Neurocranium*. The neurocranium is apparently of the generalized type (see Fig. 6), but in at least one species (*C. horii*; Fig. 10) its preotic region is more elongate (c. 68–70% of neurocranial length) and in others the preorbital region is slightly vaulted. Since little skeletal material is available these remarks are based mainly on radiographs and should be checked on actual skeletons.

*Vertebral numbers:* 25–29 (modal range 27–28), comprising 12 or 13 abdominal and 13–17 caudal elements (see p. 290 below).

*Dentition.* The outer teeth are unequally bicuspid, or, in two species, subequally bicuspid, are relatively stout and firmly attached to the underlying bone. Some posterior premaxillary teeth (as many as 16 on each side in *C. horii*) are unicuspid, caniniform and relatively larger than the preceding bicuspid. The crowns of the bicuspid teeth are not noticeably compressed, nor are they sharply demarcated from the shaft of the tooth; the cusps are acutely pointed.

The inner teeth are small and tricuspid, and arranged in 2 or 3 series anteriorly and antero-laterally, but a single series posteriorly.

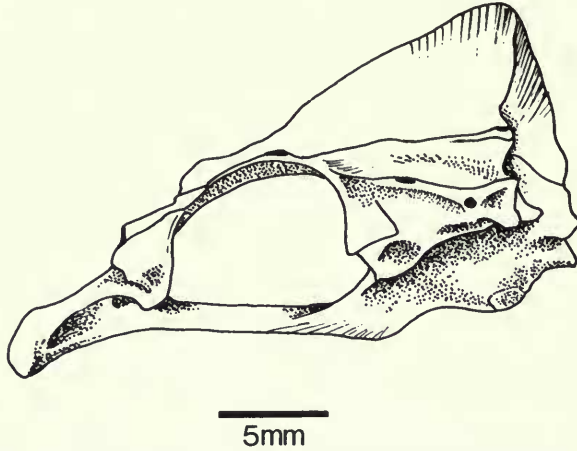


Fig. 10 Neurocranium of *Ctenochromis horii*; left lateral view.

*Lower jaw.* The dentary is relatively slender in lateral aspect, and not greatly deepened posteriorly.

*Lower pharyngeal bone and teeth.* The dentigerous surface is either triangular and subequilateral (slightly broader than long) in outline, or noticeably broader than long (c.  $1\frac{1}{2}$  times; Fig. 11). The teeth are cuspidate and compressed, those in the median and the posterior transverse row somewhat stouter than the others (the degree of stoutness, especially of teeth in the two median rows, shows a positive correlation with the fish's size).

*Dorsal fin* with 14–17 (modes 15 and 16) spinous and 8–10 (mode 9) branched rays. The holotype of *C. oligacanthus* (Regan) has only 12 spines, but all other specimens have 15.

*Caudal fin skeleton.* Because few dry skeletons or alizarin preparations are available, information on the caudal skeleton has been obtained mainly from radiographs. The difficulty of differentiating between fused and closely apposed hypural elements as seen in radiographs makes these observations of limited value.

*Ctenochromis pectoralis* (10 specimens radiographed) has all five hypurals free.

*C. horii.* Seven specimens (radiographed) have hypurals 1 and 2, and 3 and 4 fused, as does the dry skeleton examined. Two other specimens (radiographed) have hypurals 1 and 2 free, but 3 and 4 fused. Vandewalle (1973) found no fused hypurals in the two specimens he examined.

*C. polli* (2 specimens radiographed) has all hypurals free.

*C. oligacanthus.* Of the three specimens radiographed, one (the holotype) has all hypurals free, one has hypurals 1 and 2 free but 3 and 4 fused, and the third has hypurals 1 and 2, and 3 and 4 fused.

*Caudal fin* is markedly subtruncate, almost rounded in some species.

*Pelvic fin* with the first branched ray the longest.

*Anal fin markings in male fishes.* Where known (3 of the 5 species) from preserved and, or, living specimens, these are in the form of one or two (rarely three) brilliant white or yellow spots, without a dark margin and without a clear surround (cf. *Haplochromis* and *Astatotilapia*, p. 279 and



p. 283 respectively). The spot or spots may be on the anterior or the posterior part of the soft fin with, apparently, their position constant intraspecifically. For a colour picture of *C. polli* see Voss (1977 : 74).

*Gill rakers* short and stout in all species except *C. horii* where they are long and slender; there are 7–9 rakers in the outer row on the first gill arch, except in *C. horii* where there are 10–13.

*Contained species*

*Ctenochromis pectoralis* Pfeffer, 1893 (Type species). Known only from streams in south eastern Tanzania, near Korogwe.

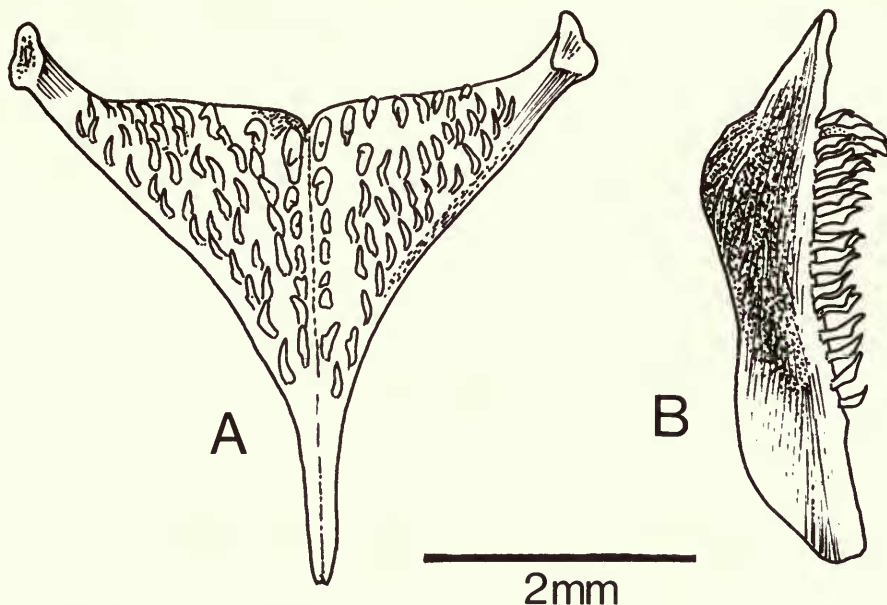


Fig. 11 Lower pharyngeal bone of *Ctenochromis polli*. A. Occlusal view. B. Right lateral view (bone aligned vertically).

*Ctenochromis horii* (Günther), 1893. Lake Tanganyika and the coastal reaches of associated rivers. See Poll (1956) for a detailed description and notes on biology.

*Ctenochromis polli* (Thys van den Audenaerde), 1964. Pool Molebo (Stanley Pool) and the lower Zaire river. For coloured plate see Voss (1977). For notes regarding specimens formerly identified as *H. fasciatus* see p. 293.

*Ctenochromis oligacanthus* (Regan) 1922. Ubangi river, an affluent of the Zaire river. The holotype and sole specimen available to Regan has only 12 dorsal fin spines and 9 branched rays; the two additional specimens I have examined have 15 spines and 9 branched rays.

*Ctenochromis luluae* (Fowler), 1931. Lulua river, Kasai drainage system, lower Zaire. I have examined four paratypes, and on the basis of that material would consider the species to be distinct from *C. polli* and *C. oligacanthus* (the other two *Ctenochromis* from the lower Zaire drainage), and from *C. pectoralis* and *C. horii*.

*Diagnosis and discussion*

Members of the genus *Ctenochromis* are characterized by the abrupt size transition between the very small chest scales and the larger scales on the ventrolateral aspects of the anterior flanks, by a naked area on either side of the chest, and by a failure of the cheek squamation to reach the ventral margin of the cheek. (In one species, *C. horii*, the entire suborbital region of the cheek is scaleless in some individuals and in others there is, at most, no more than a single scale row below and behind the orbit.) In three of the five species the anal fin markings of male fishes are in the form of one or two (rarely three), relatively small and simple, non-ocellate spots; no information is available on the other two species.

Virtually nothing is known about the biology of *Ctenochromis* species, which are, with the exception of *C. horii*, very poorly represented in study collections. Four of the five species are fluviatile and reach a small adult size (80 mm standard length); their feeding and breeding habits are unknown. The fifth species, *C. horii*, is essentially lacustrine, reaches a larger adult size (185 mm SL) and is at least partly piscivorous.

The geographical range of *Ctenochromis* extends from Tanzania in the east to the Zaire drainage (including Lake Tanganyika) in the west and lies between the latitudinal limits of c. 3° N and 8° S.

Various apomorph features shown by *Ctenochromis* suggest its relationships with two other genera; this problem will be discussed later (see p. 313).

Intrageneric relationships are difficult to determine, partly because the small size of some specimens limited the amount of anatomical information that could be obtained, partly because of the mosaic interspecific distribution of certain presumed apomorph characters, and partly because other characters form part of a morphocline continuum.

Both *C. pectoralis* (eastern Tanzania) and *C. horii* (Lake Tanganyika) have, relative to *C. polli* and *C. oligacanthus*, higher caudal vertebral counts (15–17, modes 16 and 17, cf. 13 and 14) and higher lateral line scale counts (29–33, modes 30 and 31, cf. 27–29, mode 28); these features should probably be considered plesiomorph ones (see p. 276). *Ctenochromis pectoralis* has relatively small naked patches on the chest (Fig. 9), and only the lower part of the cheek is scaleless. In comparison, *C. horii* has a large naked area on the chest and almost the entire cheek is without scales; the neurocranium in this species departs somewhat from the basic type found in *C. pectoralis* (see Fig. 10 and p. 287) in having larger preorbital and preotic proportions, and individuals reach a larger size than in *C. pectoralis*. On these grounds I would consider *C. horii* to be the derived sister species of *C. pectoralis*.

*Ctenochromis polli* (Stanley Pool and the lower Zaire river) and *C. oligacanthus* (Ubangi river, Zaire drainage) both have a reduced number of caudal vertebrae (13 or 14), fewer lateral line scales (27–29) and fewer branched anal fin rays (6 or 7 cf. 8 or 9 in *C. pectoralis*; *C. horii* with 7 (mode) or 8 anal rays occupies an intermediate position).

The third lower Zaire species, *Ctenochromis luluae* (Lulua river), however, also has an intermediate number of anal fin rays (7 or 8, mode 8), of lateral line scales (28–30) and of caudal vertebrae (15).

The outer jaw teeth in *C. polli*, *C. luluae* and *C. oligacanthus* are similar and differ from the basic, unequally bicuspid type found in *C. horii* and *C. pectoralis* in having the cusps subequal in size, with the tip of the smaller cusp directed away from the near vertical larger cusp. In both *C. polli* and *C. oligacanthus* the dentigerous surface of the lower pharyngeal bone is noticeably broader than long, whereas in *C. pectoralis* and *C. horii* its length and breadth are approximately equal (see Fig. 11); the bone in *C. luluae* has proportions that are intermediate between these two types. Finally, the naked area of the chest in *C. oligacanthus* is much larger than in *C. polli*, but a greater area of the cheek is scaled in the former species. Most of the cheek is scaled in *C. luluae*, and the naked chest area is intermediate between that of *C. polli* and *C. oligacanthus*.

On the basis of their dental morphology I would suggest that *C. polli*, *C. luluae* and *C. oligacanthus* together form the sister group to *C. pectoralis* and *C. horii*; *C. pectoralis* would seem to be the least derived taxon of the lineage.

As a postscript to this discussion it may be mentioned (with the reservations noted on p. 282) that hypural fusions in *Ctenochromis* species are relatively common, and certainly commoner than in *Haplochromis*, *Astatotilapia* and the 'Haplochromis' species of Lake Victoria (see p. 276 above, and Greenwood, 1974b : 159).

#### *THORACOCROMIS* gen. nov.

TYPE SPECIES: *Paratilapia wingatii* Boulenger, 1902 (see Greenwood, 1971 for a redescription of the species).

ETYMOLOGY. The name is derived from the latinized Greek word for a breastplate + *chromis*, a name when used in such a combination now associated with many genera of African Cichlidae;

it refers to the small and clearly size-demarcated scales on the thoracic region of species in this lineage.

### Description

Body form ranging from relatively deep to relatively slender (depth 30–40% of standard length).

**Squamation.** In the majority of species, the scales on the body above and below the upper lateral line, and behind a line through the pectoral and pelvic fin insertions, are ctenoid. A few species have cycloid scales above the upper lateral line, and weakly ctenoid scales below it. Scales on the cheek, head and chest are cycloid.

*The scales on the chest are small to very small and meet, with an abrupt change in size, the larger scales on the lateral and ventrolateral aspects of the flanks* (Fig. 2). Generally the line of this abrupt size change lies approximately between the insertions of the pectoral and pelvic fins, but may be a little behind or, less frequently, a little before that level. The chest is always completely scaled, although in two species the scales are so small and deeply embedded that the area appears to be naked.

The cheek is completely or almost completely scaled (in two species there is a very narrow, horizontal naked strip along the ventral margin, and in several other species there is a naked embayment at the anteroventral angle of the cheek squamation).

There are 29–32 (modal range 30–32) scales in the lateral line series; *about the last eight pore-bearing scales of the upper lateral line are separated from the dorsal fin base by not more than one large and one much smaller scale.*

**Neurocranium.** Most *Thoracochromis* species have a skull form that departs but slightly from the type found in *Ctenochromis* (see p. 287). That is, a generalized type (see p. 274) in which the preotic region of the neurocranium comprises some 65–70% of the total neurocranial length.

The most marked departure from this skull form is seen in two species, *Th. bullatus* (Lake Albert) which has a greatly inflated otic capsule and somewhat enlarged lateral line sensory canals, and *Th. macconneli* (Lake Turkana) where the sensory canals are hypertrophied and the braincase is shallower.

*Thoracochromis demeusii* (Zaire) deviates in a different way; here the supraoccipital crest is deepened, extends further anteriorly than in the other species and has a steeper slope to its anterior margin. These features may all be associated with the pronounced dermal hump developed in the nuchal region of this species.

**Vertebral numbers:** 26–31 (modes 28 and 29), comprising 12–14 (modes 12 and 13) abdominal and 13–17 (modes 14 and 17) caudal elements. With one exception (*Th. moeruensis*) the lower modal counts for caudal vertebrae are found in fluvial species from the Zaire river drainage system, the higher ones in species from Lakes Turkana, Albert, George and Mweru.

**Dentition.** Unequally bicuspid or unicuspid, caniniform outer teeth are the most frequently occurring types. The crown in bicuspids is not noticeably compressed, and the cusps are acutely pointed. Unicuspid teeth may be recurved or almost straight; where the material covers a sufficiently wide size range of specimens it shows that the unicuspid dentition is preceded by a bicuspid one. Fishes in all species with a bicuspid definitive dentition have a few (1–6) unicuspid posteriorly on the premaxilla, these teeth generally being larger than the anterior bicuspids.

In two species (*Th. fasciatus* and *Th. loati*) the outer teeth, although unequally bicuspid, have the major cusp obliquely truncate, somewhat protracted and relatively compressed; the minor cusp is much reduced and is also obliquely truncate. Thus there is a close resemblance between these teeth and those in *Haplochromis lividus* and *H. limax* (see Fig. 7C and p. 281 above; also Greenwood, 1971 : 360, fig. 5).

The inner teeth generally are tricuspid and in both jaws are arranged in 2 or 3 series anteriorly and laterally, but in a single series posteriorly. In those species with unicuspid outer teeth at least the outermost row of the inner series contains some unicuspid, a mixture of tri- and unicuspid, or it may be composed entirely of unicuspid.

**Lower jaw** relatively slender in lateral outline and not obviously deepened posteriorly.

**Lower pharyngeal bone and teeth.** With respect to the outline shape of the dentigerous area, two fairly distinct types of pharyngeal bone occur in this genus. One type (found in species of

the Zaire drainage, including *Th. moeruensis* but excluding *Th. demeusii*) has the surface clearly broader than long (Fig. 12). The second type (in species from Lakes Turkana, Albert and George) has its dentigerous surface only slightly broader than long, i.e. about  $1\frac{1}{2}$  times.

In all species the median tooth rows are noticeably coarser than their lateral congeners, and are even coarser than those in the posterior transverse row. Some species have stout and molariform or submolariform teeth in the median rows, and in three other species (*Th. albertianus*, *Th. mahagiensis* and *Th. pharyngalis*) teeth lateral to the median rows are also enlarged and submolariform to molariform, (see Trewavas, 1938 : 441 and 444; Poll, 1939 : 47; Greenwood, 1973 : 213). Associated with this enlargement of the dentition (especially in *Th. mahagiensis* and *Th. pharyngalis*) the lower pharyngeal bone is markedly thickened.

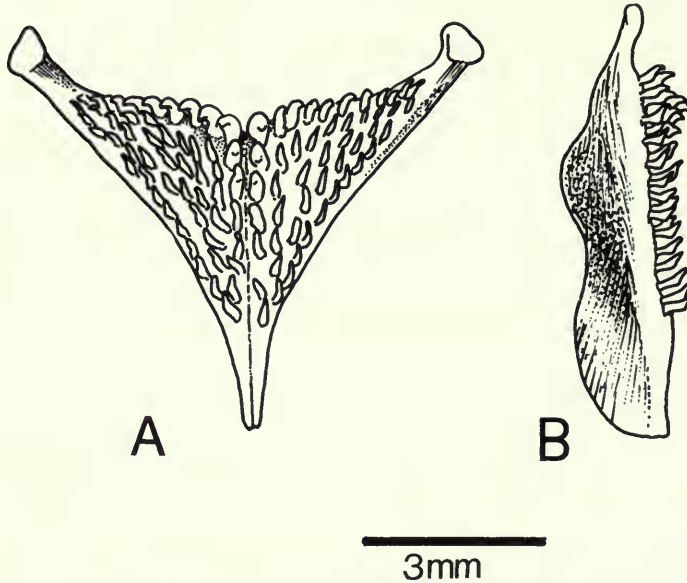


Fig. 12 Lower pharyngeal bone of *Thoracochromis bakongo*. A. Occlusal view. B. Right lateral view (bone aligned vertically).

Teeth other than the enlarged ones are compressed and cuspidate in all species.

*Dorsal fin* with 13–16 (modal range 14–16), rarely 17, spinous and 8–10 (modes 9 and 10), rarely 11, branched rays.

*Anal fin* with 3 spines and 6–10 (modal range 7–9) branched rays.

*Caudal fin skeleton*: the distribution of fused hypural elements amongst *Thoracochromis* species, as determined mainly from radiographs, is as follows:

(i) Lake Albert species, and those from the Nile and Lake George: no fusion in *Th. wingatii* (holotype), *Th. albertianus* (6 specimens), *Th. mahagiensis* (1), *Th. avium* (holotype), *Th. bullatus* (13), *Th. loati* (16) and *Th. petronius* (12); some specimens in most species have certain hypurals very closely apposed.

(ii) Lake Turkana. *Th. rudolfianus* has all hypurals free in 28 specimens examined, but hypurals 1 and 2 are closely apposed or perhaps fused in two others; *Th. turkanae* (4 specimens) has all hypurals free; in *Th. macconneli* 6 of the 26 specimens examined have all hypurals free, 4 have hypurals 1 and 2, and 4 and 5 fused, 11 have hypurals 1 and 2, and 3 and 4 fused, but hypural 5 free, and 5 have only hypurals 1 and 2 fused.

(iii) Lower Zaire drainage, and Lake Mweru. *Th. moeruensis* has hypurals 1 and 2, and 3 and 4 fused (6 specimens). *Th. demeusii* (holotype) has all free; *Th. fasciatis* (6 syntypes) has all free, as does *Th. bakongo* (3 specimens); *Th. stigmatogenys* has 2 specimens with hypurals 3 and 4 fused,

and 4 others with all hypurals free. Vandewalle (1973) reports no fusion in the two species he examined, namely, *Th. bakongo* and *Th. fasciatus*.

*Caudal fin* subtruncate to almost rounded, most species being in the latter category.

*Pelvic fin* with the first branched ray the longest.

*Anal fin markings.* Regrettably little information is available on this character, either from live or preserved specimens. True ocellar spots (3–8 in number) are present in *Th. petronius* (Lake George) and apparently in the three species from Lake Turkana, although the clear surround in these latter species is much narrower than in the ocelli of *Haplochromis* and *Astatotilapia*. The four species from Lake Albert and the Nile for which data are available (i.e. *Th. albertianus*, *Th. bullatus*, *Th. wingatii* and *Th. loati*) do not appear to have any clear area around the small, coloured or white spots, which are relatively large, well defined and number from 1 to 3. However, these observations were made on preserved material only and, since the whole fin is somewhat pigmented, a narrow hyaline surround could well be overlooked.

No information is available for the remaining species (Lake Mweru and the Zaire river drainage).

*Gill rakers* are of various shapes, with 6–12 (modal range 7–9) in the outer row on the first gill arch.

#### *Contained species*

*Thoracochromis wingatii* (Blgr.), 1902, type species; see Greenwood (1971) for a redescription and definition of the species. Upper Nile (Bahr-el-Jebel) and probably Lake Albert also.

*Thoracochromis loati* (Greenwood), 1971. Upper Nile (Bahr-el-Jebel) and Lake Albert.

*Thoracochromis rudolfianus* (Trewavas), 1933. Lake Turkana.

*Thoracochromis turkanae* (Greenwood), 1974. Lake Turkana.

*Thoracochromis macconneli* (Greenwood), 1974. Lake Turkana.

See Greenwood (1974b) for notes on the biology of the last three species, and for comments on their relationships.

*Thoracochromis albertianus* (Regan), 1929. Lake Albert.

*Thoracochromis mahagiensis* (David & Poll), 1937. Lake Albert (see also Greenwood, 1971 : 356).

*Thoracochromis avium* (Regan), 1929. Lake Albert. I follow Trewavas (1938) in considering *Haplochromis lanceolatus* David & Poll, 1937, a synonym of this species.

*Thoracochromis petronius* (Greenwood), 1973. Lake George, Uganda.

*Thoracochromis pharyngalis* (Poll), 1939. Lake Edward. See Greenwood (1973 : 213) for a discussion on the relationship of this species.

*Thoracochromis moeruensis* (Blgr.), 1899. Lake Mweru.

*Thoracochromis demeusii* (Blgr.), 1899. Lower Zaire river. See Thys van den Audenaerde (1964) for a redescription of the species and for other data; this author considers that the presumed type locality (Bangala country, Upper Congo) is in error.

*Thoracochromis bakongo* (Thys van den Audenaerde), 1964. Kasai drainage to the lower Zaire river.

*Thoracochromis fasciatus* (Perugia), 1892. Lower Zaire drainage at Vivi (5°38' S, 13°30' E; see Thys van den Audenaerde, 1964). At present I am restricting the concept of this species to the six syntypical specimens in the BMNH collections (reg. nos 1898.12.12:1–6). Certain other specimens in the BMNH collections identified as *fasciatus*, and at least part of the material on which Thys van den Audenaerde (1964) based his redescription of the species, are referable to one or possibly two other species. These, or this, species differ from the syntypes of *fasciatus* in dental characters and in having a graded rather than an abrupt size change between the chest and ventrolateral flank scales (i.e. they cannot be referred to the genus *Thoracochromis*; see p. 291 above).

Three further specimens in the BMNH collections (reg. nos 1899.9.6:2–4, ex Stanley Pool) which were included in *fasciatus* by Boulenger (1915 : 215–216) do, however, show an abrupt size change in the scales of this region. All 3 specimens are now in a very poor state of preservation but, judging from certain morphometric characters and also from their dental morphology, it seems that they should be identified as *Ctenochromis polli* (see p. 289).

Regan (1922a) tentatively included *Paratilapia toddi* Blgr., 1905 (Kasai river, Zaire drainage) in the synonymy of *fasciatus*. Regan's concept of *fasciatus* was essentially that of Boulenger (1915) since his study material included the misidentified specimens noted above. The only known specimen of *Paratilapia toddi*, the holotype, is considerably larger (127.0 mm SL) than any member of a known *Thoracochromis* species, and has the general facies and external cranial morphology of a *Serranochromis*-like fish (see Trewavas (1964) who, indeed, thought that *P. toddi* might be related to *Serranochromis*). However, the holotype of *P. toddi* does show an abrupt size transition between the scales of the chest and flanks, and it also has a low number of caudal vertebrae (13) and a low branched anal fin ray count (7), features shared with some species of *Thoracochromis* (see p. 291 above). On the other hand, there are several features of *P. toddi* that are not encountered in any member of that genus.

Until more specimens are available it would seem best to treat *P. toddi* as a taxon *incertae sedis*; it certainly cannot be considered a synonym of *Thoracochromis fasciatus*.

Thys van den Audenaerde (1964) considers Boulenger's (1899) *Chromis monteiri* (from Boma) to be a synonym of *fasciatus*. Regrettably the holotype (and unique) specimen of *C. monteiri* cannot now be found and so a comparison between it and the syntypes of *Th. fasciatus* could not be made. But, judging from Boulenger's original description and figure, it seems highly improbable that the specimens are from the same species. The possibility that *monteiri* holotype and some of the misidentified *fasciatus* material are conspecific cannot, however, be overlooked.

#### *Diagnosis and discussion*

Members of the genus *Thoracochromis* are characterized by the abrupt size transition between the small chest scales and the much larger scales on the ventrolateral and ventral aspects of the flanks. This is, apparently, the only derived character shared by all members of the lineage. Several other derived features are, however, found in member species. For example, the obliquely truncate tooth cusps in *Th. loati* and *Th. fasciatus*, the enlarged pharyngeal mills in *Th. mahagiensis*, *Th. albertianus* and *Th. pharyngalis*, the bullate otic region in *Th. bullatus*, the hypertrophied cephalic lateral line canals in *Th. macconneli* (and probably its near-dwarf males as well; see Greenwood, 1974b) and, finally, the short but broad lower pharyngeal bone in most species from the lower Zaire system. But, the restricted distribution of these apomorphic characters amongst the species obliges one to rank them either as autapomorphies or as low level synapomorphies suggesting possible intrageneric relationship (if, in the latter case, it can be shown that the characters have not evolved independently, an impossible task when there are no other features on which to establish intrageneric relationships).

Even the single synapomorphy used to define the lineage as a whole, the abrupt thoracic-flank scale size transition, is shared with *Ctenochromis* (p. 287) and *Orthochromis* (p. 296 below). The two latter lineages, however, have each their own derived features which can be interpreted as indicators of their monophyletic origin and thus their phyletic distinctiveness.

The possible interrelationships of *Thoracochromis*, *Ctenochromis* and *Orthochromis* are considered later (p. 313).

*Thoracochromis* has a wide but disjunct geographical distribution. In the north there are three species endemic to Lake Turkana, and two others in the Nile, both of which also occur with the three endemic species in Lake Albert. There is one species in Lake George, another in Lake Edward (with the possibility that the George species also occurs in Edward) and possibly a third in Lake Victoria.

Much further south (and a little to the west) there is one species in Lake Mweru, and a group of five species apparently confined to the lower Zaire drainage.

From an historical viewpoint (Greenwood, 1974b) the species of the Nile, Lake Turkana and Lake Albert could well be closely related and could also be related to the species from Lakes Edward and George. Indeed, *Th. mahagiensis* (Lake Albert) and *Th. pharyngalis* (Lake Edward) have three apparently derived characters in common, viz. hypertrophied pharyngeal mills, a low number of gill rakers (as compared with other species from Lake Albert) and a reduced cheek squamation; and again, *Th. bullatus* (Lake Albert) and *Th. macconneli* (Lake Turkana) both have

hypertrophied cranial lateral line systems, although in this instance, since both species live in deep waters, the resemblance could be the result of parallel evolution.

The lower Zaire species, with the exception of *Th. demeusii*, have distinctly broad and short lower pharyngeal bones (that of *Th. demeusii* is but slightly broader than long and resembles the bone found in all other *Thoracochromis* species). *Thoracochromis moeruensis*, a geographically isolated Zairean species from Lake Mweru, also has a short and broad lower pharyngeal bone, suggesting its possible relationship with the lower Zaire species group (perhaps, geographically speaking, through some past linkage via the Kasai drainage system).

More collecting in the Zaire river system, especially its middle reaches, and more information about the northern (i.e. Nile, Turkana, Albert) species is needed before any of these suggested intralinear groups can be developed further, and indeed before the phyletic integrity of the whole lineage can be tested adequately. Data on live coloration, anal fin markings and cranial osteology are particularly needed.

The absence, save for two or possibly three species of *Thoracochromis* from the Lake Victoria–Edward–George–Kivu cichlid flock (totalling some 200 species), is of particular zoogeographical interest, especially when it is recalled that in Lakes Turkana and Albert species of *Thoracochromis* are the only ‘*Haplochromis*’-group taxa represented. Likewise one may note the predominance of *Thoracochromis*, *Ctenochromis* and *Orthochromis* species in the Zaire river system.

#### **ORTHOCHROMIS** Greenwood, 1954

TYPE SPECIES: *Haplochromis malagaraziensis* David, 1937 (type specimens in the Musée Royal de l’Afrique Centrale, Tervuren).

##### *Synonymy*

*Rheohaplochromis* Thys van den Audenaerde, D. F. E. (1963), *Revue Zool. Bot. afr.* 68, 1–2: 145 (as a subgenus of *Haplochromis*); *idem* (1964), *Revue Zool. Bot. afr.* 70, 1–2: 169 (raised to generic rank). No type species by original designation.

When discussing the affinities of *Rheohaplochromis*, Thys van den Audenaerde (1964: 169) mentions my observations (*in litt.*) that the genus showed strong affinities with *Orthochromis*. Although agreeing with my remarks, Thys van den Audenaerde considered that ‘... l’écaille nuchale et ventrale vraiment minuscule des *Rheohaplochromis* (*polyacanthus* et *torrenticola*) nous semble un caractère suffisamment important pour maintenir ces espèces dans un genre séparé...’. I would argue that the suite of derived characters shared by these species and the two other species discussed below (including *O. malagaraziensis*) are a stronger argument in favour of their inclusion in a single lineage of presumed monophyletic origin (i.e. within the scope of this revision, a genus see p. 269 above).

Thys van den Audenaerde’s supplementary argument for placing the species *polyacanthus* and *torrenticola* together in a separate genus (because of their overlap in distribution as compared with the allopatric distribution of the other Zaire haplochromine species) might well be used to explain the presence of derived features shared only by *polyacanthus* and *torrenticola*, but it seems to have little bearing on the problem of determining their overall phyletic relationships.

In an earlier paper, Thys van den Audenaerde (1963) considered that the small ventral and nuchal scales, and the rounded pelvic fins, of *polyacanthus* and *torrenticola* could be ecophenotypic features associated with their rheophilic habits. In support of his contention he mentions similar features in *Steatocranus*, an unrelated taxon (see Greenwood, 1978). This argument of ecophenotypically evolved characters could also be used to explain the similar scale and fin characters in the two other species I would include in the same lineage as *polyacanthus* and *torrenticola*. But, to me, it would seem more parsimonious to conclude that, although the features possibly have selective advantage in a torrential habitat, their association in a number of species sharing other derived features is more likely to be indicative of common ancestry than of repeated parallel evolution. Since *Steatocranus* may well be a member of a much more distantly related branching within the African Cichlidae (see Greenwood, 1978), the similarity in scale and fin

organization in that instance would, I agree, be the result of convergence (and thus indicative of the characters having adaptive value in that type of habitat).

### *Description*

*Body elongate and slender (its depth 25–30% of standard length); dorsal head profile strongly decurved, eyes generally suprolateral in position, giving the fish a somewhat goby-like appearance.*

*Squamation.* Scales on the head and on the body above the upper lateral line are cycloid or weakly ctenoid, or cycloid over the anterior third of the upper body and ctenoid over the posterior two-thirds. Scales below the upper lateral line are ctenoid except on the chest and belly, where they are cycloid.

The chest is naked or scaled (if the latter there is sometimes a small naked area on one or both sides of the body); *the chest scales, when present, are very small, as are the scales on the ventral and ventrolateral body surface as far posteriorly as the anus* (Fig. 3).

*The small ventral body scales have an abrupt size transition with the moderately larger scales on the ventrolateral aspects of the flanks. When the entire chest is scaled, the small scales of that region extend posteriorly beyond a line joining the pectoral and pelvic fin insertions* (Fig. 3). *There is also a sharply defined size difference between the larger ventrolateral body scales and the small thoracic ones, the line of size demarcation curving gently in a posteroventral direction to merge with the demarcation line separating the belly and ventrolateral flank scales* (Fig. 3). *In effect, the corslet of small scales covering the chest trails backwards to the anus* (cf. *Ctenochromis* and *Thoracochromis* where the corslet is confined to an area anterior to the pelvic-pectoral fin insertions). Even when the major part of the chest is naked, there is a patch of small scales between and somewhat posterior to a line through the pelvic and pectoral fin insertions; as in the other species, these small scales are sharply demarcated from the larger ones on the flank.

The nuchal scales in two species (*O. polyacanthus* and *O. torrenticola*) are very small and deeply embedded.

There are 30–35 (modal range 30–32) scales in the lateral line, *all the pore-bearing scales of the upper lateral line being separated from the dorsal fin base by not more than one large and one small scale* (cf. *Ctenochromis* and *Thoracochromis* where only the last few scales of the upper lateral line are separated from the dorsal fin by less than two scales of equal size).

The cheek is naked or, if scaled, has a distinct naked area along its entire ventral border; in some individuals with otherwise naked cheeks, a few irregularly arranged scales may occur posterodorsally.

*Neurocranium.* The skull in *Orthochromis* differs from the generalized type *in having a relatively low and short supraoccipital crest, and in having the skull roof anterior to the supraoccipital crest gently rounded* (not concave or flat as is the generalized skull); *the entire neurocranium is relatively narrow, most noticeably in the interorbital region, and the preorbital skull profile slopes downwards at a steep angle.*

*Vertebral numbers:* 27–30 (modal range 28–30), comprising 12 or 13 (mode 13) abdominal and 14–17 (mode 17) caudal elements.

*Dentition.* The outer teeth in both jaws are either bicuspid (generally with the shaft of the tooth curved buccally) or slender unicuspid (in which case small fish have bicuspid teeth). Some slender unicuspid are present posteriorly in the premaxilla of all species.

Inner row teeth are small and tricuspid (with some unicuspid present when the teeth of the outer row are predominantly unicuspid), are arranged in 2 or 3 series anteriorly and laterally, and in a single row posteriorly.

*Lower jaw appears foreshortened in lateral view because its posterior region (angulo-articular bone and the coronoid process of the dentary) are deepened relative to the generalized condition seen, for example in *Astatotilapia*.*

*Lower pharyngeal bone and dentition.* The dentigerous surface of the lower pharyngeal bone is somewhat broader than it is long (c.  $1\frac{1}{2}$  times), but is not sufficiently broad to give the bone an overall short and broad appearance. The teeth are compressed and cuspidate, those of the two median rows showing some interspecific variation in form, from not as coarse or slightly coarser



than the lateral teeth, to being markedly coarser; teeth forming the posterior transverse row are coarse (but cuspidate) in all species.

*Dorsal fin* with 16–20 (modes 17 and 18) spinous and 9–11 (modes 9 and 10) branched rays.

*Anal fin* with 3 or, in one species, 4 spines, and 7–10 branched rays.

*Caudal fin skeleton.* The occurrence of fused hypural elements (as determined from radiographs, and in the case of *O. malagaraziensis* an alizarin preparation) is as follows: in *O. malagaraziensis* (7 specimens, including 1 paratype), *O. polyacanthus* (11) and *O. machadoi* (2), hypurals 1 and 2, and 3 and 4 are fused, but in *O. torrenticola* (2) none is fused although all are closely apposed to one another in each half of the skeleton. Vandewalle (1973) records no fusion in the specimen of *O. torrenticola* he examined.

*Caudal fin* is moderately to strongly subtruncate (almost rounded).

*Pelvic fin* with the second, or the second and third branched rays the longest, thus giving the fin a rounded rather than an acute distal margin.

*Anal fin markings in male fishes.* No discrete, egg-dummy-like markings have been described for any *Orthochromis* species, nor are any visible in the preserved material examined; certainly none was visible in the live specimens of *O. malagaraziensis* I examined (Greenwood, 1954). In some species the fin is without any form of maculate colour pattern so that if egg-dummies were present they should be visible. *Orthochromis torrenticola* does have a maculate anal fin (the spots arranged in oblique rows) and Thys van den Audenaerde (1963) reports that males have more densely spotted fins than do females.

Observations on live *O. malagaraziensis* suggest that sexually dimorphic coloration in that species may be confined to differences in the colour of the lips, anal fin, and branchiostegal membrane (Greenwood, 1954).

*Gill rakers* relatively slender but short, 6–9 (modes 7 and 8) in the outer row on the lower part of the first gill arch.

#### *Contained species*

*Orthochromis malagaraziensis* (David), 1937. Malagarasi river (Burundi and Tanzania); see Greenwood (1954) for a redescription of the species and notes on its biology.

*Orthochromis polyacanthus* (Blgr.), 1899. Lake Mweru, Upper Zaire river (Stanley Falls and Stanleyville, and certain affluent rivers (see Thys van den Audenaerde, 1963)). I have, for the moment, accepted Regan's (1922a) synonymy of Boulenger's (1902) *Tilapia stormsi* with this species; however, a review of material in the BMNH suggests that Regan's opinion may not be correct.

*Orthochromis torrenticola* (Thys van den Audenaerde), 1963. Lufira river (Upper Zaire river drainage).

*Orthochromis machadoi* (Poll), 1967. Cunene river, Angola.

#### *Diagnosis and discussion*

Members of the genus *Orthochromis* are characterized, principally, by the abrupt size change between the large scales on the ventrolateral aspects of the flanks and the small scales of the chest and belly, by the curved and posteroventrally directed line of size demarcation between these scales, and the union of this line with that separating the very small scales on the belly from the larger scales on the flanks, see Fig. 3. The very small belly scales, extending backwards to the anus, are another characteristic feature. Also characteristic (when taken in combination with those characters listed above) is the absence or extensive reduction of the cheek squamation, the posteriorly deepened lower jaw, the increased number of spinous rays in the dorsal fin (without a corresponding reduction in the number of branched rays, this comparison being based on the modal counts for branched rays in *Ctenochromis* and *Thoracochromis*), the elongate second or second and third branched rays in the pelvic fin and, apparently, the absence of egg-dummy-like markings on the anal fin of adult males.

Other diagnostic features are reviewed on pp. 295–296 above; the high frequency of hypural fusion, affecting both the upper and lower halves of the caudal fin skeleton, is particularly note-

worthy but requires confirmation from larger samples and the use of skeletal rather than radiographed material.

The absence of egg-dummy-like markings on the anal fin also requires confirmation from observations made on live specimens (their absence in *O. malagaraziensis*, however, seems certain; Greenwood (1954)). This is a most unusual feature amongst 'Haplochromis'-group species, and may imply that the courtship and breeding habits of *Orthochromis* species are also unusual for the group. Until something is known about these habits in *Orthochromis* it is impossible to determine whether the absence of egg-dummies is to be considered a primitive or a derived feature for the genus.

I am unable to demonstrate any clear-cut interspecific relationships within the *Orthochromis* lineage. *Orthochromis machadoi* (Cunene river) is probably the least derived member. It has a partly scaled cheek, the chest is either entirely scaled or, as in one specimen, it can have a small scaleless area unilaterally, the ventral (belly) body scales are relatively large and, finally, in its general facies the species has not fully achieved the elongate goby-like body form seen in the other species.

In his original description of *O. machadoi*, Poll (1967) argues that the species is closely related to *Pseudocrenilabrus philander* (Weber) an opinion I cannot accept (especially since Poll's views are, it seems, largely based on supposed similarities in coloration). Anatomically, and with regard to their squamation patterns, the taxa are quite distinct.

The preserved colours of *O. machadoi*, on the other hand, are like those of *O. malagaraziensis*. Both species have all the body scales (except on the chest and belly) narrowly outlined in black, giving the body an overall 'diamond-mesh' pattern; they also have a distinctive and vertically elongate dark blotch at the base of the caudal fin.

In *O. torrenticola* this diamond-mesh pattern is very faint but general over the body, whereas in *O. polyacanthus* it is restricted to a pair of narrow bands, one situated midlaterally, the other following the upper lateral line. *Orthochromis torrenticola* retains the caudal spot which is lost in *O. polyacanthus*. Both species have the body crossed by several closely spaced vertical bands. The apo- or plesiomorph states of these colour patterns cannot be determined.

*Orthochromis torrenticola* and *O. polyacanthus* have minute scales on the dorsal surface of the head and nuchal region (in *O. machadoi* and *O. malagaraziensis* these scales are only slightly smaller than those on the dorsal body surface), and the scales on the thoracic region are relatively smaller than in the other two species, especially *O. machadoi*. In other words, *O. torrenticola* and *O. polyacanthus* share derived features in their squamation.

If these various characters can be taken as indicators of relationship, then *O. machadoi* and *O. malagaraziensis* would be sister species, as would *O. torrenticola* and *O. polyacanthus*. But, one must set against these similarities the fact that the chest and cheek are naked (or largely naked) in *O. malagaraziensis* and *O. torrenticola*, and that both species have similar general facies (sharply decurved anterior head profile, elongate body and a suprolateral eye), all features which would appear to be derived rather than plesiomorph ones. The four anal spines in *O. torrenticola* must be considered an autapomorphic feature and as such cannot be used to assess relationships.

*Orthochromis*, *Ctenochromis* and *Thoracochromis* share one derived feature, the abrupt size transition between chest and body scales, and thus are presumed to be derived from a common ancestor also possessing this feature. However, no synapomorph character can be found to indicate which two of the three genera are more closely related to one another.

Since *Thoracochromis* has only one apomorph feature (chest-body scale size transition), a character shared by all three taxa, it can on that basis be considered to represent the least derived member of the group.

*Ctenochromis* and *Orthochromis* both exhibit, but do not share, a number of derived features which must, therefore, be considered autapomorphic for the lineage in which they occur (and define). If one were to consider 'trend' characters, for example a tendency to reduce cheek and chest squamation, then *Ctenochromis* and *Orthochromis* could be said to share some derived features not shared with *Thoracochromis*. But, I can find no trenchant synapomorphic character that would allow one to establish an unequivocal sister-group relationship between the two taxa. It is for this reason that I have given each lineage in this ultimately monophyletic assemblage the

status of a genus (see p. 269) rather than ranking *Orthochromis* and *Ctenochromis* as subgenera (i.e. implicit sister-groups) on the grounds of their having shared and presumed apomorph 'trend' characters.

## Section II

Although several of the species dealt with in this section have previously been referred to the genus *Haplochromis* (see Bell-Cross, 1975), at least one author (Trewavas, 1964) has suggested that these same species, together with the genera *Serranochromis* and *Chetia*, are more closely related to one another than to any of the species already accounted for. In part I would agree with Trewavas' groupings, but the available evidence does not allow one to substantiate, in their entirety, the relationships indicated in her phyletic diagram (Trewavas, 1964: fig. 1), nor is it possible to determine the relationships of these 'southern' taxa with the more northern '*Haplochromis*'-group genera considered in Section I.

### *SERRANOCHROMIS* Regan, 1920

TYPE SPECIES. *Chromys thumbergi* Castelnau, 1861 (neotype, designated by Trewavas (1964), in BMNH collections).

I have united several species (those previously placed in this genus by Trewavas (1964) and others placed in *Haplochromis* by Bell-Cross (1975)) into one lineage (=genus) because all share the following apparently derived features: (i) *A high number of abdominal vertebrae*, 16–18, rarely 15 or 19 (*modal numbers 16 and 17*). (ii) *A large number of gill rakers*, 9–15 (*modal range 10–13*) in the outer row on the lower part of the first gill arch. (iii) *A high number of branched fin rays in the dorsal fin*.

In addition, members of this lineage reach a large adult size, all have cycloid or a mixture of cycloid and weakly ctenoid scales (the ctenii confined to a small median sector on the scale's posterior margin) in which the cycloid kind predominate, and the anal fin markings (egg-dummies) in males are numerous, small and non-ocellate (in some species differing little in size, shape or colour from the spots on the soft part of the dorsal fin). It is not, however, possible to assess the primitive or derived states of these features which, therefore, are of no direct value in assessing phylogenetic affinities, (but see p. 274 regarding egg-dummies.)

Two sublineages, each based on shared derived features common to their constituent species, can be recognized within the genus *Serranochromis*, and these are given subgeneric rank.

### Subgenus *SERRANOCHROMIS* Regan, 1920

TYPE SPECIES. *Chromys thumbergi* Castelnau, 1861.

#### *Description*

The body form varies from deep to moderately slender (body depth 30–45% of standard length).

*Squamation*. The scales on the head, chest, cheek and above the upper lateral line are cycloid, those elsewhere on the body mostly cycloid. When ctenoid scales are present these are weakly ctenoid, with the ctenii confined to a short median sector on the free margin of the scale.

The scales on the chest (which may be relatively small) show a gentle size gradation with those on the lateral and ventrolateral aspects of the flanks; the chest is always fully scaled.

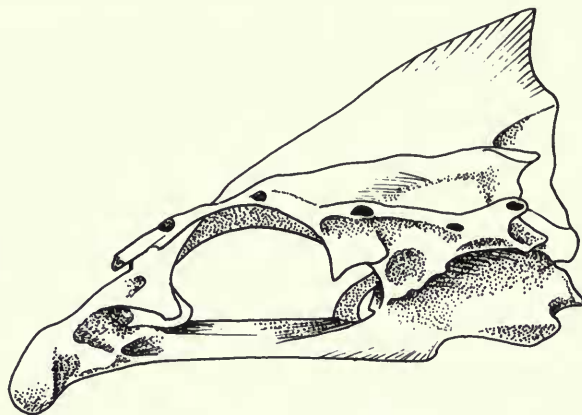
The cheek is fully scaled, with from 3 (*rare*) to 11 horizontal rows of scales (*usually 5–9 rows*).

There are 35–41, rarely 34 scales in the lateral line, all but the last 2 or 3 pore-bearing scales of the upper lateral line are separated from the dorsal fin origin by two scales of approximately the same size.

*Neurocranium*. The skull has a protracted preotic region (comprising some 65–70% of the total neurocranial length), especially noticeable in the ethmovomerine region which comprises c. 27–33% of the total neurocranial length. The ethmovomerine part of the skull is almost horizontally aligned, its dorsal surface sloping at a small angle (Fig. 13). The supraoccipital crest is variously developed, high in some species, relatively lower in others but never shallow relative to the total skull proportions.

*Vertebral numbers* and apophysis for the dorsal retractor muscles of the upper pharyngeal bones. There are 31–36 vertebrae, comprising 16–18, rarely 15 or 19 (modes 16 and 17) abdominal and 16–18, rarely 15 (modes 16 and 17) caudal elements. Such a high number of both caudal and abdominal vertebrae is rarely encountered amongst 'Haplochromis'-group cichlids, and is unique amongst the fluviatile taxa (see, also p. 313 below).

An apophysis for the origin of the dorsal retractor muscles of the upper pharyngeal bones is developed on the ventral face of either the 3rd or 4th abdominal vertebra; although the apophysis does occur on the 4th vertebra in other 'Haplochromis'-group taxa, it is usually confined to the 3rd centrum (see Trewavas, 1964 for comments on this feature).



10mm

Fig. 13 Neurocranium of *Serranochromis* (*Serranochromis*) *robustus*; left lateral view.

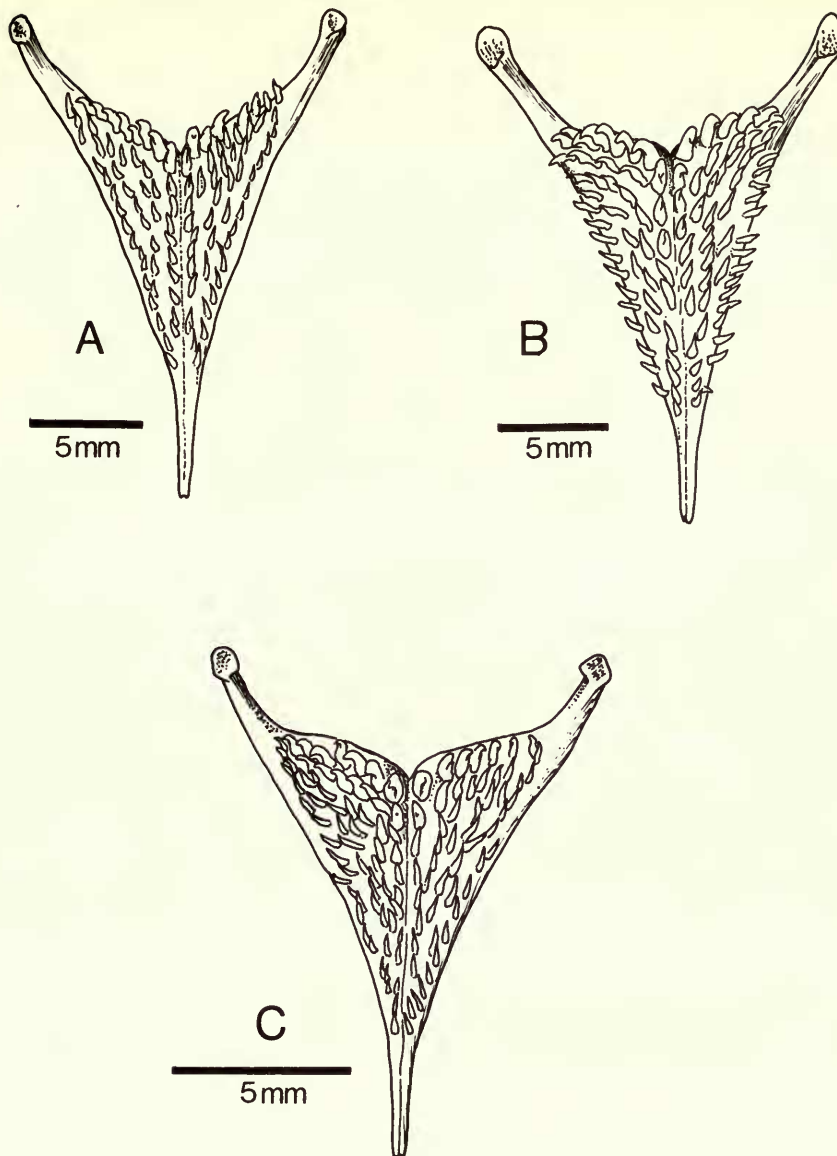
*Dentition.* The teeth in both the inner and the outer rows of the jaws are unicuspid, even in the smallest (29 mm SL) specimens examined. Other 'Haplochromis'-group species in which the adult dentition is a unicuspid one (and for which specimens less than 100 mm SL are available), have bicuspid outer teeth, and usually tri- or bicuspid inner teeth, in fishes less than 80–100 mm standard length.

The inner teeth are arranged in a single (rarely a double) row; when two rows are present, these are confined to the anteromedial part of the jaw, the series continuing posteriorly as a single row. In many species the inner teeth of the lower jaw are confined to a narrow, anteromedial arc. The majority of 'Haplochromis'-group taxa have a more extensive inner dental pattern, with the teeth arranged in at least 2 (and usually 3) rows over the anteromedial and anterolateral parts of the jaw bones.

*Lower pharyngeal bone and teeth.* With regard to its outline shape when viewed occlusally, two kinds of pharyngeal bone can be recognized (Fig. 14). In one, the commoner type, the bone is long and narrow, the dentigerous surface having the outline of an isosceles triangle (Fig. 14A & B). The second type (found in two species) is relatively broader and its dentigerous surface, although still slightly broader than long (c.  $1\frac{1}{3}$  times) is more nearly equilateral (Fig. 14C).

Irrespective of the bone's outline shape, the teeth (except those in the two median rows) are fine and either simply pointed or with a weakly developed shoulder anterior to the pointed cusp. The two median and the posterior transverse rows are made up of stouter teeth, those in the median rows are relatively the stouter and have the shoulder more clearly demarcated than it is in the outer teeth.

*Jaws.* The lower jaw is relatively slender in lateral view (Fig. 15B) and is not noticeably deepened posteriorly (angulo-articular region). The premaxillae have, in most species, long ascending pro-



**Fig. 14** Lower pharyngeal bones of various *Serranochromis* (*Serranochromis*) species, seen in occlusal view. A. *Serranochromis* (*S.*) *thumbergi*. B. *S. (S.) robustus*. C. *S. (S.) macrocephalus*.

*cesses* (Fig. 15A) which, in the entire fish, extend to the level of the midpoint of the dorsal orbital margin or even further dorsoposteriorly.

*Dorsal fin*: with 13–18 (modes 15 and 16) spinous, and 13–16 (usually 14–16) branched rays (a high branched ray count when compared with that in other fluviatile haplochromine taxa).

*Anal fin*: with 3 spines and 9–13 (modes 10 and 11) branched rays (again, a high branched ray count).

*Caudal fin skeleton*. No hypural fusion was noted in any of the radiographed material examined, i.e. *S. macrocephalus* (12 specimens), *S. spei* (1), *S. robustus* (14), *S. longimanus* (4), *S. angusticeps* (17), *S. stappersi* (1), *S. meridionalis* (1). No fusion was reported by Vandewalle (1973) in the *S. macrocephalus* (1) or *S. robustus* (1) he examined.

*Caudal fin*: subtruncate (slightly emarginate in one species) to weakly rounded.

*Pelvic fin*: with the first branched ray the longest.

*Anal fin markings in male fishes*. Most species have many small, generally circular spots without a clear surround and covering a large area of the soft anal fin, sometimes extending onto the spinous part as well. In their size and shape these spots are similar to those on the soft part of the dorsal fin and on the caudal fin. An exception to these generalizations is *S. spei* which has fewer and larger (but non-ocellate) spots covering the greater part of the soft fin.

From the little information available on live coloration it seems possible that the anal spots may differ slightly from the dorsal fin spots in colour and intensity, but this requires confirmation. (For coloured illustrations, see Jubb (1967a, pls 41–44) and Bell-Cross (1976: pls 26–28).

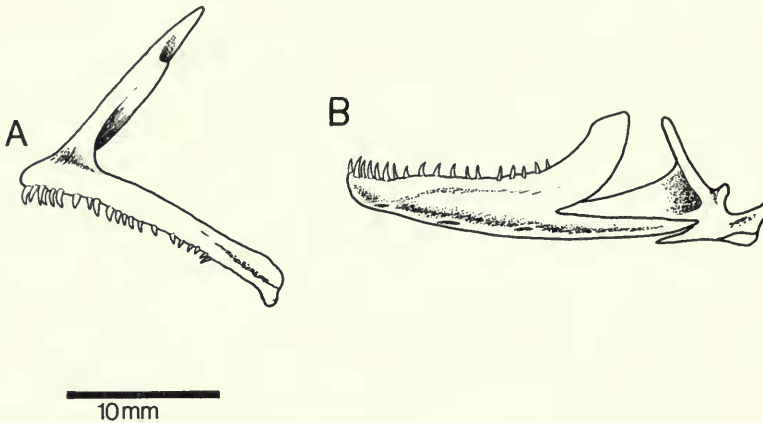


Fig. 15 Jaws of *Serranochromis (S.) robustus*; left lateral view.  
A. Premaxilla, B. Lower jaw.

Trewavas (1964) reports that similar spots are present on the anal fin of females, but are grey rather than red, yellow or orange as in males.

Where breeding habits are known, the species are female mouthbrooders.

*Gill rakers* are of various forms, from short and stout to moderately slender; there are 9–13 (modal range 10–12) rarely 8 rakers in the outer row on the lower part of the first gill arch.

#### *Contained species*

See Trewavas (1964) for detailed descriptions, figures, etc.

*Serranochromis (S.) robustus* (Günther), 1864. Lake Malawi, Upper Shire river; Mossamedes; Okavango; Upper Zambesi; Kafue river; Luangwa system (tributary of the Middle Zambesi); Bangweulu region; Luembe river, Kasai system (see Poll, 1967); possibly also in Lake Mweru and the Lualaba system.

*Serranochromis (S.) thumbergi* (Castelnau), 1861 (Type species). Mossamedes; Okavango river and Lake Ngami; rivers Kafue and Luansemfwa (Luangwa system); Bangweulu region; Upemba basin.

*Serranochromis (S.) macrocephalus* (Blgr.), 1899. Mossamedes; Okavango river; Lake Cameia (on an Angolan tributary of the Upper Zambesi); Upper Zambesi; Kafue river; Luansemfwa river, Luangwa system; Luapula river; Lake Mweru; Lulua river; Angolan Kasai.

*Serranochromis (S.) angusticeps* (Blgr.), 1861. Mossamedes; Okavango river and Lake Ngami region, Upper Zambesi; Kafue river; Bangweulu region; Luapula river; possibly Lake Mweru (see also Poll, 1967).

*Serranochromis (S.) longimanus* (Blgr.), 1911. Okavango river and the Upper Zambesi.

*Serranochromis (S.) stappersi* Trewavas, 1964. Lake Mweru and the lower Luapula river.

*Serranochromis (S.) spei* Trewavas, 1964. Lake Kafakumba (23°40' E, 9°40' S) on a tributary of the Kasai system; Lake Kabongo in the Lake Upemba depression.

*Serranochromis* (*S.*) *janus* Trewavas, 1964. Malagarasi swamps (Malagarasi river), Tanzania.

*Serranochromis* (*S.*) *meridionalis* Jubb, 1967. Incomati river system, Transvaal, South Africa (see Jubb, 1967b).

Dr Trewavas (1964) has discussed the possible affinities of these species (except *S. meridionalis*) at what should now be considered an intra-subgeneric level. Until more material is available for anatomical studies no further comment would be worthwhile. The relationships of the subgenus with its sister-group (*Sargochromis*), and of the genus as a whole, will be considered below (p. 306).

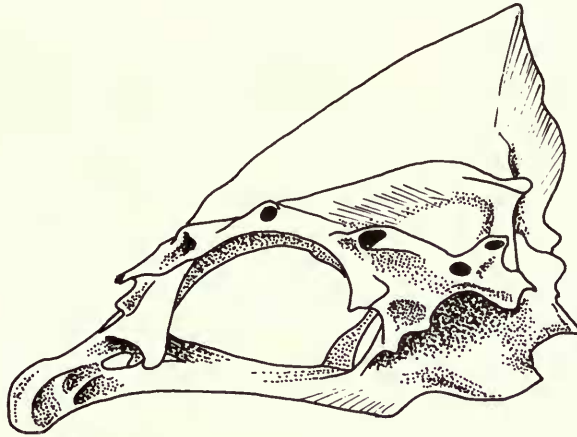


Fig. 16 Neurocranium of *Serranochromis* (*Sargochromis*) *codringtoni*; left lateral view.

#### Subgenus *SARGOCHROMIS* Regan, 1920.

TYPE SPECIES: *Paratilapia codringtoni* Blgr., 1908 (type specimen in the collections of the BMNH, see Bell-Cross, 1975).

#### Description

Body deep and stout (depth 35–50% of standard length).

*Sargochromis* differs from the nominate subgenus in the following characters:

*Squamation*. There are fewer lateral line scales (28–34, modes 30 and 31, cf. 35–41 rarely 34).

*Neurocranium*. Although basically of the same type as that in *Serranochromis*, most *Sargochromis* species have a somewhat shorter ethmoid region (but similar preotic skull proportions), a deeper otico-occipital region and, in some species, a more robust apophysis for the upper pharyngeal bones (Fig. 16). This latter character is positively correlated with the degree of enlargement of the pharyngeal bones and the extent to which their dentition is molarized (see Greenwood, 1965a and 1978). The more massive the pharyngeal bones the greater is the relative contribution of the basioccipital to the articular surface of the apophysis, and in those species with the largest bones the preotic also contributes to that surface.

*Vertebral numbers*. There are fewer caudal vertebrae (12–16, modal numbers 14 and 15), and hence a lower total count (28–32, mode 31). *The number of abdominal vertebrae, however, is high in both subgenera.*

*Jaws*. The dentary differs from that in *Serranochromis* in being relatively more foreshortened and thus deeper (Fig. 17). The premaxillary ascending processes do not extend beyond about the midpoint of the anterior orbital margin (beyond that point in most *Serranochromis*).

*Dentition*. Unlike small specimens of *Serranochromis*, small *Sargochromis* do have some bicuspid inner and outer teeth (at least some specimens < 10–15 cm, depending on the species,

have predominantly bicuspid outer teeth). The dental pattern is similar in both subgenera, save that *S. (Sargochromis) thysi* has 4 inner series in both jaws.

*Lower pharyngeal bone and teeth.* The bone shows some interspecific variation in outline shape (Fig. 18) but is always relatively broader than in *Serranochromis*, and thus the dentigerous surface more closely approximates to the equilateral. In only one species, *S. (Sargochromis) greenwoodi* (Fig. 18A), are there no markedly enlarged median teeth. Most of the other species have some enlarged, often submolariform, teeth in addition to those forming the two median rows. Generally these enlarged teeth are restricted to a central patch, several tooth rows wide, in the posterior (oesophageal) dentigerous field. Two species, *S. (Sargochromis) codringtoni* and *S. (Sa.) giardi*, have most of the pharyngeal dentition composed of coarse, molariform or submolariform teeth.

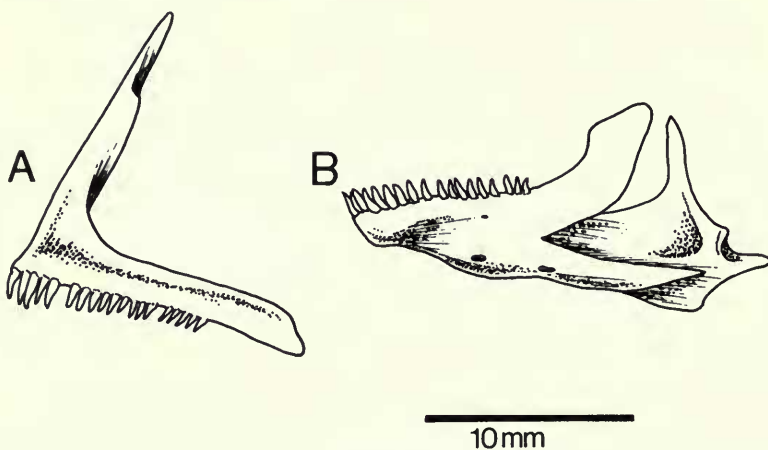


Fig. 17 Jaws of *Serranochromis (Sargochromis) codringtoni*; left lateral view. A. Premaxilla, B. Lower jaw.

Bell-Cross (1975 : fig. 1) described intrapopulational differences in the extent to which the pharyngeal dentition is enlarged.

Most *Sargochromis* species have the lower pharyngeal bone coarser than it is in the nominate subgenus, and markedly so when the pharyngeal dentition is hypertrophied.

*Dorsal fin* has a lower modal branched ray count (12 or 13 cf. 14–16 in *Serranochromis*) but there is an extensive overlap in the total ranges (11–16 cf. 13–16). There is also a broad overlap in spinous ray counts, although the higher numbers (17 and 18) recorded for the nominate subgenus have not been reported for *Sargochromis*.

*Anal fin markings* are essentially the same in both subgenera. For colour illustrations see Jubb (1967a : pls 40 and 45); Bell-Cross (1976 : pls 17 and 18).

*Caudal fin skeleton.* No hypural fusion was seen in the radiographs of *S. (Sa.) coulteri*, *S. (Sa.) greenwoodi*, and *S. (Sa.) codringtoni* (1 specimen each); in *S. carlottae* one specimen has hypurals 3 and 4 fused but two other fishes show no fusion. Of the two *S. (Sa.) mellandi* examined, one has hypurals 3 and 4 fused, but the other has none fused. Vandewalle (1973) records *S. (Sa.) mellandi* as having either no fusion (4 specimens) or hypurals 3 and 4 fused (2 specimens).

*Caudal fin* strongly subtruncate to virtually rounded.

*Gill rakers* are more numerous in *Sargochromis* (9–15, modal numbers 12 and 13).

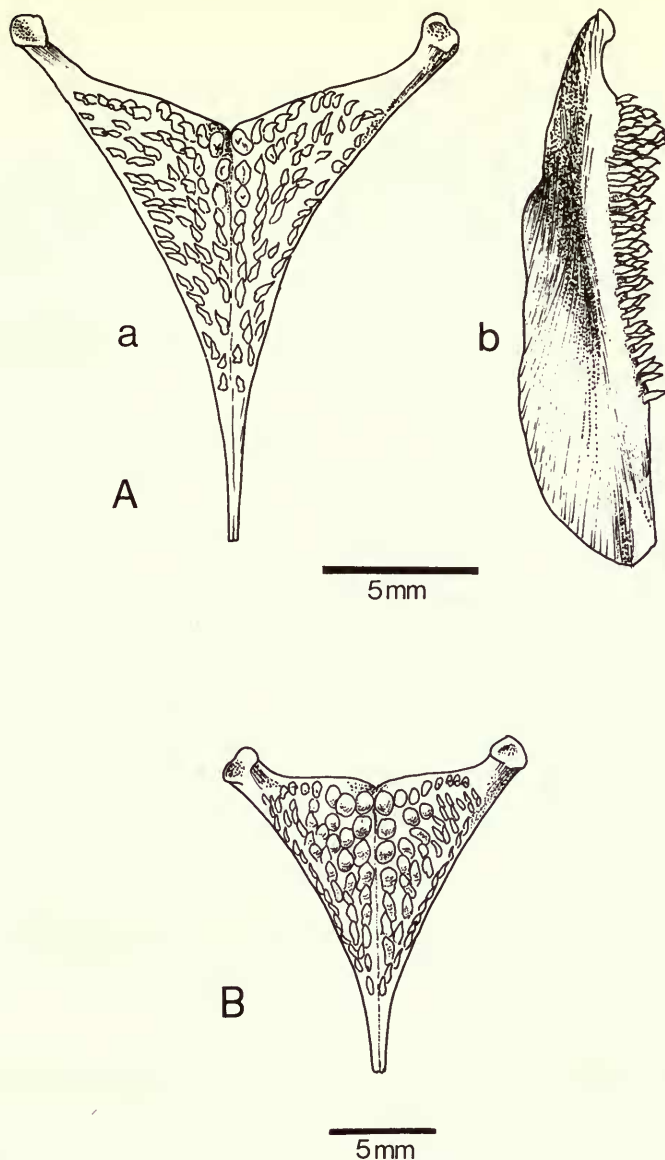
#### *Contained species*

For a systematic review and notes on the ecology and distribution of the first seven species listed below see Bell-Cross (1975).

*Serranochromis (Sa.) greenwoodi* (Bell-Cross), 1975. Upper Zambesi; Kafue system; Okavango system.

*Serranochromis (Sa.) coulteri* (Bell-Cross), 1975. Upper Cunene system.





**Fig. 18** Lower pharyngeal bone of : A. *Serranochromis (Sargochromis) greenwoodi* in a. Occlusal, and b. Right lateral view (bone aligned vertically). B. *S. (Sa.) codringtoni*; occlusal view.

*Serranochromis (Sa.) mortimeri* (Bell-Cross), 1975. Upper Zambesi; Kafue river (above the Lufwanyama-Kafue confluence); part of the Mulungishi river (a Middle Zambesi tributary).

*Serranochromis (Sa.) mellandi* (Blgr.), 1905. Chambesi river and Lake Bangweulu; the Luapula river and Lake Mweru; Lake Calundo, Angola (see Poll, 1967).

*Serranochromis (Sa.) carlottae* (Blgr.), 1905. Upper Zambesi; Okavango and Kafue systems.

*Serranochromis (Sa.) codringtoni* (Blgr.), 1905 (Type species of the subgenus). Upper and Middle Zambesi rivers (including the larger tributaries); Kafue and Okavango river systems.

*Serranochromis (Sa.) giardi* (Pellegrin), 1904. Middle and lower regions of the Upper Zambesi; the Okavango and the plateau section of the Kafue river; one record from the Cunene system.

*Serranochromis (Sa.) thysi* (Poll), 1967. Luembe river, Angola.

*Diagnosis and discussion*

Members of both subgenera comprising the genus *Serranochromis* are characterized by having a high modal number of abdominal vertebrae (16 or 17, rarely 15 or 19, modes 16–18) and thus a high total vertebral count (29–36), a high number of gill rakers in the outer row on the lower part of the first gill arch (10–15, rarely 9, modal range 10–13), a generally high number of branched dorsal fin rays (11–16, modal range 12–16), mostly cycloid scales on the body (if some ctenoid scales are present they are weakly so), a high number of lateral line scales (28–41) as compared with other fluvial 'Haplochromis'-group species and, at least in one subgenus, a greater number of scale rows on the cheek (5–9), in having a skull with a relatively protracted preotic region and relatively high supraoccipital crest, and in having numerous, small non-ocellate coloured spots on the anal fin of male fishes (these markings differing but slightly in size and colour from those on the dorsal fin).

Diagnostic features for the two subgenera are detailed on pp. 299–301 & 303–304, and in the key (p. 316). They involve, chiefly, the higher number of caudal vertebrae and branched dorsal fin rays in *Serranochromis* (*Serranochromis*) species, and the stouter lower pharyngeal bones and dentition in *Serranochromis* (*Sargochromis*) species.

Trewavas (1964) and Bell-Cross (1975) have considered intragroup relationships within the subgenera *Serranochromis* and *Sargochromis* respectively. A reconsideration of their conclusions is beyond the scope of this paper, although Trewavas' (1964: fig. 1 and p. 10) grouping of the *Serranochromis* (*Serranochromis*) species would seem, on the basis of the characters used, to be a sound hypothesis.

Trewavas (1964) also made an extensive analysis of the intergroup (i.e. intergeneric) relationships of what I am treating as the subgenus *Serranochromis* (treated by Trewavas as a genus). She brought into these considerations the 'genus' *Sargochromis* (*S. codringtoni* only) and three 'Haplochromis' species (*mellandi*, *frederici* and *carlottae*) which are now referred to *Sargochromis* (as a subgenus of *Serranochromis*). In discussing Trewavas' ideas, unless quoting directly, I shall use the terms 'Serranochromis', 'Haplochromis' and 'Sargochromis' to cover her concept of these taxa.

In Trewavas' view (1964: also fig. 1, p. 8) 'Serranochromis' is '... a gradal genus rather than a clade', of diphyletic origin from '... a small species-flock of Haplochromis' (i.e. the four *Haplochromis* of Angola, '*H. lucullae*', '*H. humilis*', '*H. acuticeps*' and '*H. angolensis*', plus '*H. darlingi*' of the Zambesi (see below, pp. 310–313).

'A cladal grouping,' Trewavas continues, 'would recognize *Chetia*, *S. robustus* and *S. thumbergi* on the one hand, and *H. welwitschii*, *S. macrocephalus* and the other species of *Serranochromis* on the other, but definitions would be almost impossible. . . . The broken line' (referring to fig. 1) 'at the Haplochromis–Sargochromis transition reflects the absence here too of a clear generic division'.

Because all 'Serranochromis' species share a high caudal vertebral count and other apparently derived features (see p. 299), I cannot accept Trewavas' concept of that taxon having a diphyletic origin, nor can I accept, without considerable qualification, the inclusion of *Chetia* (i.e. *C. flaviventris*) and '*H. welwitschii*' in one cladal grouping. Neither *Chetia* nor '*H. welwitschii*' has the high caudal vertebral count of 'Serranochromis' (i.e. the nominate subgenus recognized above) and, although these two species together with certain other endemic Angolan 'Haplochromis' and '*H. darlingi*' do share some features with *Serranochromis*, these are not of the kind that would suggest a close cladistic relationship.

The question of possible relationships between the Angolan species, '*H. darlingi*' and *Chetia flaviventris* will be considered on pp. 312–313.

Trewavas (1964: fig. 1, p. 9) recognizes the phyletic affinity between *Serranochromis* and *Sargochromis* (the latter now of course broadened to include the three 'Haplochromis' (see p. 305) species which she indicated as being more closely related to 'Sargochromis' than 'Serranochromis'). We would differ, however, in our interpretation of the relationship between *Sargochromis* and 'Haplochromis' *darlingi*. Trewavas (1964: 9) writes of 'The evolutionary line which leads from *H. darlingi* to *Sargochromis* . . .' But I can find only one derived character (the enlarged pharyngeal mill) that might link '*darlingi*' more closely with *Sargochromis* than with *Serranochromis*,

and none of the synapomorph characters shared by *Serranochromis* and *Sargochromis* alone. In the absence of these characters from '*H.* *darlingi*', and because an enlarged pharyngeal mill has apparently evolved independently in several haplochromine lineages, I consider that the affinities between this species and *Serranochromis* (including *Sargochromis*) are not as close as those implicit in Trewavas' proposed ancestor-descendant relationship.

In my view, *Serranochromis* and *Sargochromis* shared a recent common ancestry not shared with '*H.* *darlingi*' (the common ancestor for the former taxa could well have resembled *S.* (*Sa*) *greenwoodi* in its anatomical, morphological and meristic features; see description in Bell-Cross, 1975).

Any relationship between the genus *Serranochromis* and '*H.* *darlingi*' would be at a more distant level because these two taxa share fewer derived features than do *Serranochromis* and *Sargochromis*.

Finally, comment must be made on the superficially close resemblance between members of the subgenus *Serranochromis* (*Serranochromis*) and certain '*Haplochromis*' species of Lake Victoria (the *spekii-serranus* species complex, see Greenwood, 1967 : 109, and 1974a : 80 *et seq.*; also Trewavas, 1964 : 6). That the resemblance is the result of convergent evolutionary trends towards the production of an adaptive morphotype (piscivorous predator) and not one of close phyletic relationship seems evident from the several features in which the two taxa differ from one another. For example, the predominantly cycloid and weakly ctenoid scales of *Serranochromis* compared with the strongly ctenoid scales of the '*Haplochromis*' species, the few and fully ocellate egg-dummies of the latter as contrasted with the numerous, small and non-ocellate anal spots in *Serranochromis*, and the more numerous gill rakers, branched fin rays and, particularly, the high number of abdominal vertebrae in the latter taxon.

Certainly it would seem more parsimonious to suppose that *Serranochromis* and the Lake Victoria *Haplochromis* were derived from different lineages, rather than to suggest a common ancestry from some widespread lineage of fluviatile, piscivorous predators (an idea I had entertained previously when considering the phyletic history of the Lake Victoria species flock).

It would seem possible, too, that there is no close phyletic relationship between *Serranochromis* and certain '*Haplochromis*' species in Lake Malawi (see Trewavas, 1964 : 6), but more research is required on the Malwai species before this idea can be tested adequately.

#### *CHETIA* Trewavas, 1961.

TYPE SPECIES. *Chetia flaviventris* Trewavas, 1961 (Holotype and paratypes in the BMNH, 3 paratypes in the Transvaal Museum, Pretoria).

NOTE. The species *Chetia brevis* Jubb, 1968 is excluded from this genus because in adult males the anal fin markings are large, true ocelli and few in number (3 or 4). Also, unequally bicuspid outer jaw teeth are still present in specimens of a size (86–89 mm SL) when, in *Chetia flaviventris*, the outer row is comprised mainly of unicuspid and caniniform teeth; the few bicuspid teeth present in *C. flaviventris* of that size are different from those in *C. brevis* since the minor 'cusp' is a shoulder and not a point.

#### *Description*

The body form is moderately slender (depth of body 29–35% of standard length).

*Squamation.* The scales on the head, chest, cheek and body above the upper lateral line are cycloid, and cycloid scales predominate on the body below that level as well; a few weakly ctenoid scales may be present anteriorly on the body, the ctenii on these scales being confined to a short median arc on the scale's free margin. It seems possible that a higher proportion of ctenoid scales is present in smaller than in larger individuals; the largest specimen examined has only cycloid scales on all parts of the body and head (see also Trewavas, 1961).

The cheek is completely scaled (5 or 6 horizontal rows). The chest scales show a gentle size gradation with those on the belly and ventrolateral aspects of the flanks.

There are 34 or 35 scales in the lateral line series, with only the last one or two pore-bearing scales of the upper lateral line separated from the dorsal fin base by less than two scales of almost equal size.

*Neurocranium.* The skull has a moderately produced preotic region (c. 68–70% of total neurocranial length). The ethmovomerine region is not noticeably extended, and slopes at a slight angle. In its proportions and general shape, the neurocranium in *Chetia* approaches that in the subgenus *Serranochromis* (*Serranochromis*), but has a less elongate ethmovomerine region.

*Vertebral numbers* and apophysis for the dorsal retractor muscles of the upper pharyngeal bones. There are 30–32 (mode 31) vertebrae, comprising 14 or 15 (mode 15) abdominal and 15–17 (modes 16 and 17) caudal elements.

Trewavas (1961) reports an absence of any bony apophysis for the origin of the pharyngeal muscles; from the radiographs I have examined (i.e. of the holo- and 4 paratypes) the structure is visible in one specimen. Trewavas (1961) implies that the apophysis serves principally for the attachment of the swimbladder. That organ certainly is attached to the posterior face of the apophysis in all cichlids I have examined, but the greater surface area of the apophysis serves as a point of origin for the pharyngeal retractor muscles.

*Dentition.* Unicuspid teeth predominate (or are the only kind of teeth present) in specimens more than 30 mm standard length; the few bicuspid teeth present have a much reduced, shoulder-like minor cusp, and are mostly replaced by unicuspid teeth in specimens > 35 mm S.L. There is, however, a size correlated change in the kind of unicuspid teeth present. Fishes < 35 mm long have rather flattened, almost spear-shaped unicuspid teeth whereas in larger fishes the teeth are caniniform.

Unicuspid teeth also predominate in the inner rows of fishes at all sizes, although a few weakly bicuspid teeth are present in specimens less than 40 mm SL. There are one, or, less commonly, two rows of inner teeth anteriorly in both jaws, and a single series laterally.

*Lower and upper jaws.* The lower jaw has the appearance and proportions of that in *Serranochromis* (*Serranochromis*) species, but in the upper jaw the ascending premaxillary process does not reach to between the orbits as it does in many of the latter species; it reaches only to about the midpoint of the anterior orbital margin.

*Lower pharyngeal bone and teeth.* The bone is not thickened, has an almost equilateral denticulate surface, and its teeth are slender and weakly cuspidate (Fig. 19). Those teeth forming the two median rows and the posterior transverse row are slightly coarser than their congeners.

*Dorsal fin* with 14 or 15 spinous and 11 or 12 branched rays.

*Anal fin* with 3 spines and 9 or 10 branched rays.

*Caudal fin skeleton.* All the hypurals are free in the five specimens radiographed (the type series).

*Caudal fin* is subtruncate.

*Pelvic fin* has the first branched ray the longest.

*Anal fin markings in male fishes.* As in *Serranochromis* (see p. 302) there are numerous, small and non-ocellate spots covering a large area of the soft anal fin, the spots resembling in size and coloration those on the soft part of the dorsal fin.

According to Du Plessis & Groenewald (1953) the anal spots in *C. flaviventris* are more plentiful in males than in females, and the species is a female mouthbrooder.

*Gill rakers* are moderately short and slender, with 9 or 10 rakers in the outer row on the lower part of the first gill arch.

#### *Contained species*

*Chetia flaviventris* Trewavas, 1961 (Type species). Tributaries of the Limpopo and Incomati rivers, Transvaal, South Africa.

#### *Diagnosis and discussion*

The single species in this genus is distinguished from the other fluviatile '*Haplochromis*'-group species, except *Serranochromis*, by the nature of the anal fin markings in adult males, which are numerous, small and non-ocellate (and which barely differ from those in females). In addition, *Chetia* is distinguished from *Ctenochromis*, *Orthochromis* and *Thoracochromis* by the nature of

the scale pattern in the thoracic–abdominal region (a gradual as compared with an abrupt size change in the scales of the two body regions).

From *Serranochromis*, *Chetia* is distinguished mainly by having fewer (14 or 15) abdominal vertebrae (cf. 16–18, rarely 15, in *Serranochromis*) and by having bicuspid teeth in specimens of a larger size. In meristic characters, other than vertebral numbers, the two genera have a comparable overlap, but for each feature the modal values are distinct, those for *Serranochromis* being the higher.

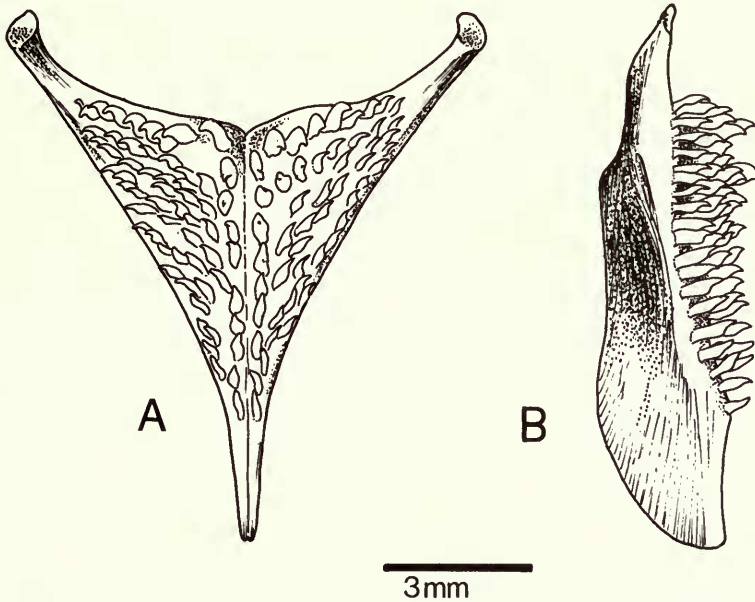


Fig. 19 Lower pharyngeal bone of *Chetia flaviventris*. A. Occlusal view. B. Right lateral view (bone aligned vertically).

I can detect no apomorph features which would suggest that *Chetia* might be related to any of the three lineages showing an abrupt size change in the thoracic–abdominal squamation, and nor can I find apomorph characters to associate it with *Haplochromis*, *Astatotilapia* or *Astatoreochromis*.

That *Chetia* and *Serranochromis* share a similar kind of anal fin marking does not necessarily imply a close relationship between them either, since it seems likely that this is a primitive (plesiomorph) feature for 'Haplochromis'-group species (see above, p. 275). I can detect no unequivocally synapomorphic features common to *Chetia* and *Serranochromis* and thus, despite their superficial similarities, cannot place the taxa in the same genus.

Likewise, the almost identical anal fin markings in *Chetia* and '*Haplochromis*' *darlingi* (see below, p. 310) cannot be taken to indicate a close relationship. It is for this reason, as well as their lack of uniquely shared apomorph features and the presence of autapomorph features in each species, that has led me to place *Chetia flaviventris* and '*H.*' *darlingi* in separate lineages, and thus to give the latter taxon generic rank (see p. 312).

Trewavas (1964 : 10) has remarked on the similarity between *Chetia* and certain *Serranochromis* species, a similarity which led her to consider *Chetia* an offshoot from a lineage that also contains *S.* (*Serranochromis*) *thumbergi* and *S.* (*S.*) *robustus*. That there are similarities between the three species is undeniable, but *Chetia* does not share with the two *Serranochromis* species (and with other species of the genus) the derived feature of a high number of abdominal vertebrae. It does, of course, share with all *Serranochromis* (*Serranochromis*) species the early ontogenetic appearance of unicuspid outer and inner jaw teeth (see p. 300), an apomorph feature which *Serranochromis* (*Sargochromis*) does not share with the nominate subgenus.

Thus at present, one cannot find a totality of shared apomorph features which would indicate a clear-cut sister group relationship for *Chetia*. For that reason I would consider that *Chetia* is best represented as a monotypic lineage (genus) of uncertain affinities. Intuitively one suspects that *Chetia* is related either to *Serranochromis* (especially the nominate subgenus of that taxon) or to '*Haplochromis*' *darlingi*. But, the evidence to propose formally one or other of these relationships is not available if the classification adopted is to reflect phyletic relationships.

Superficially, *Chetia* also resembles one of the Angolan '*Haplochromis*' species, '*H.*' *welwitschii* Blgr., a taxon known only from its now poorly preserved holotype. Until more and better documented material of the Angolan '*Haplochromis*' is available for study, any possible relationship between *Chetia flaviventris* and '*H.*' *welwitschii* cannot be investigated (see also p. 312 below).

### *PHARYNGOCHROMIS* gen. nov.

TYPE SPECIES. *Pelmatochromis darlingi* Blgr., 1911. (Holotype in the BMNH collections.)

SYNONYMY. See Regan (1922a).

#### *Description*

Body form moderately slender (body depth 30–33% of standard length).

*Squamation*. The body squamation type and pattern is like that in *Chetia* (see p. 307). The cheek is fully covered by 4 or 5 horizontal scale rows. There are 32–34 (modes 32 and 33), rarely 31, scales in the lateral line.

*Neurocranium*. The preotic portion of the skull is slightly less protracted than in *Chetia*, the brain case is a little higher and the slope of the dorsal skull profile a little steeper. In other words, the overall skull morphology is somewhat more like that in *Serranochromis* (*Sargochromis*) species than in *Chetia*, a resemblance that may be associated functionally with the enlarged pharyngeal bones and dentition present in both taxa.

*Vertebral numbers*: 29 or 30 (mode 29), comprising 13 or 14 (mode 14) abdominal and 15 or 16 (mode 15) caudal elements. An apophysis for the dorsal retractor pharyngeal muscles is present on the third centrum.

*Dentition*. There is a predominance of unicuspid, caniniform teeth in the outer row of both jaws in fishes over 60 mm standard length, but even in the largest specimens examined (90 mm SL) many unequally bicuspid teeth persist (and, occasionally, may be the predominant form). Unicuspids also predominate in the inner tooth rows, the other teeth being bi- or weakly bicuspid.

The inner rows of both jaws are arranged in two series anteromedially and a single row laterally and posteriorly.

*Jaws*. The lower jaw is somewhat shorter and deeper than in *Chetia*, but the premaxilla is similar in both genera.

*Lower pharyngeal bone and dentition*. The dentigerous surface is equilateral or almost so, and the bone itself is somewhat thickened medially (noticeably so when compared with that in *Chetia*). The two median tooth rows are composed of coarse, stout and molariform or submolariform teeth (Fig. 20), the latter retaining traces of a small, near-central point on the occlusal surface. The teeth in the row, or the two rows on either side of the median series, are markedly coarser than those in the lateral rows (which are also clearly cuspidate), and may have submolariform crowns.

*Dorsal fin* with 14 or 15 (mode 14), rarely 13, spines and 10–12 (mode 11) branched rays.

*Anal fin* with 3 spines and 7–8 branched rays.

*Caudal fin skeleton*. All hypurals are free in the 4 specimens (including the holotype) radiographed.

*Caudal fin*: strongly truncate to virtually rounded.

*Pelvic fin*: with the first branched ray the longest.

*Anal fin markings in male fishes*. As in *Chetia* and *Serranochromis*, there are numerous (up to 18, according to Bell-Cross, 1976), small orange spots on the soft part of the fin, and sometimes extending onto the membrane between the spines as well. *Pharyngochromis darlingi* is a female

mouthbrooder (Bell-Cross, 1976). For coloured illustrations see Jubb (1967a : pl. 46); Bell-Cross (1976 : pl. 16).

*Gill rakers* are short and stout, with 9 or 10 (less commonly 7 or 8) in the outer row on the lower part of the first gill arch.

*Contained species*

*Pharyngochromis darlingi* (Blgr.), 1911. Type species. Widely distributed in the Zambesi river system and southwards to the Limpopo.

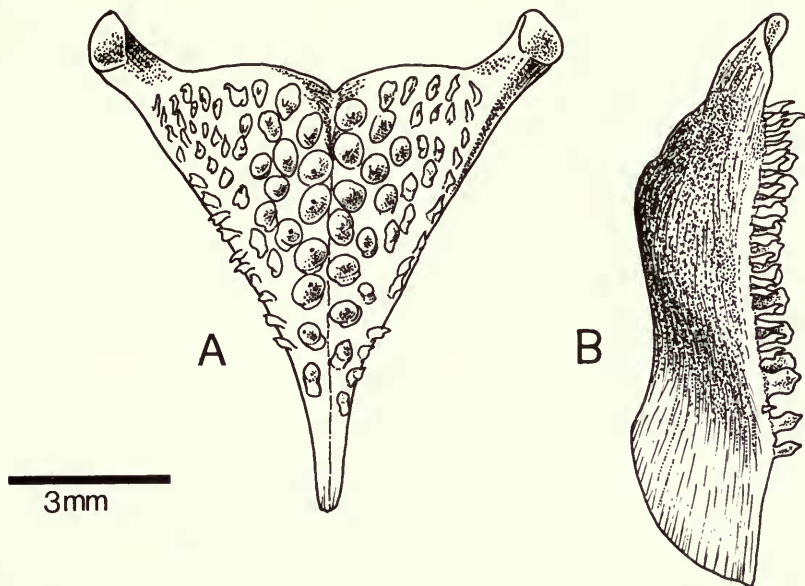


Fig. 20 Lower pharyngeal bone of *Pharyngochromis darlingi*. A. Occlusal view. B. Right lateral view (bone aligned vertically).

Poll (1967) recorded this species (as *Haplochromis darlingi*) from Lake Calundo (Zambesi drainage), Angola, and also redetermined, as *H. darlingi*, specimens from the Cubango river which Pellegrin (1936) had identified as *Haplochromis welwitschii*. However, judging from the nature of the anal fin markings in male specimens, I suspect that these specimens should not be referred to *P. darlingi*. Their identity should be more firmly established (possibly as a yet undescribed species) when a thorough revision of the Angolan '*Haplochromis*' species is carried out (see p. 312).

The same features distinguishing *Chetia* from the other fluviatile '*Haplochromis*'-group genera, including *Serranochromis*, also serve to distinguish *Pharyngochromis*.

From *Chetia* itself, *Pharyngochromis* is distinguished, chiefly, by its stouter lower pharyngeal bone and its partly molarized dentition, by having lower modal numbers of abdominal and caudal vertebrae, fewer lateral line scales, and by having a larger proportion of bicuspid teeth in the outer tooth row of both jaws in fishes more than 40 mm standard length.

My reason for not treating *Chetia flaviventris* and *Pharyngochromis darlingi* as members of the same genus is their lack of shared derived features (see above, p. 310). The same reasons led me to exclude *Pharyngochromis* from the *Sargochromis* division of the *Serranochromis* lineage.

Presumably it is the presence of enlarged pharyngeal teeth, as well as overall similarity in body form and oral dentition, that led Trewavas (1964 : fig. 1 and p. 9) to place *P. darlingi* at the base of a lineage leading to *Sargochromis* (then restricted to the type species, *S. codringtoni*). Derivatives from, and members of, this lineage also included a number of Zambesi '*Haplochromis*' species which I now place in *Sargochromis*.

Since the subgenera *Serranochromis* and *Sargochromis* share certain derived features (especially an increased number of abdominal vertebrae) not found in *Pharyngochromis* it would seem more parsimonious to consider that the two former taxa share a recent common ancestry and that any relationship they may have with *Pharyngochromis* is a more distant one.

The alternative classification implicit in Trewavas' (1964) phyletic diagram, that *Chetia* and *Serranochromis* (i.e. my subgenus *Serranochromis* (*Serranochromis*)) are sister-groups, and that *Sargochromis* (i.e. my subgenus *Serranochromis* (*Sargochromis*)) plus *Pharyngochromis* is the sister-group of *Chetia* and *Serranochromis* combined, is not supported by the distribution of derived characters amongst the taxa involved. Such an arrangement would also imply that the derived features shared by *Sargochromis* and *Serranochromis* were evolved independently. Admittedly in my scheme one specialized feature (the enlarged pharyngeal bones and dentition of *Pharyngochromis* and most *Sargochromis* species) would have to be evolved independently. But, evidence from haplochromine lineages in Lake Victoria (see Greenwood, 1974a) and from *Thoracochromis* (e.g. *Th. mahagiensis* and *Th. pharyngalis*) seems to indicate that the independent evolution of an enlarged pharyngeal mill is not uncommon amongst 'Haplochromis'-group cichlids.

To summarize: the relationships amongst those 'Haplochromis'-group taxa with non-ocellate and numerous anal fin spots (a group essentially of the Zambesi, Limpopo, and Angolan rivers) cannot clearly be recognized at present. Two lineages with a presumed recent common ancestry (*Serranochromis* and *Sargochromis*) are treated as sister-groups and given subgeneric rank; the other two lineages cannot be related unequivocally (on the basis of shared derived characters) with either the *Serranochromis*-*Sargochromis* lineages or with one another; each therefore is treated as a monotypic and monophyletic assemblage (on the basis of autapomorphic features) and given generic rank (*Chetia* and *Pharyngochromis*).

The further resolution of relationships amongst these taxa awaits more detailed studies of their contained species (and of the Angolan 'Haplochromis' species), and an understanding of the phyletic importance which can be attached to anal fin markings.

### The Angolan 'Haplochromis' species

Several references have been made to these little-known and poorly represented taxa. The last comprehensive revision of the Angolan *Haplochromis* was that of Regan (1922a) who recognized three species, *H. humilis* (Steindachner), 1866, *H. acuticeps* (Steindachner) 1866 and *H. multiocellatus* (Blgr.) 1913. For some reason not stated (but probably because Boulenger (1915) included both species in *Pelmatochromis*), Regan omitted Steindachner's (1865) *Hemichromis angolensis* and Boulenger's (1898) *Pelmatochromis welwitschii*. Both species, however, would have fallen into Regan's definition of *Haplochromis*.

All the specimens representing these species (and others synonymized therein by Regan, 1922a) are poorly preserved, mostly represented by a single individual (or at best 4 or 5 syntypes), and often without precise locality data; the type of *P. angolensis* is now lost (see Bell-Cross, 1975: 427).

In recent years Poll (1967) has added three species (*H. thysi*, *H. machadoi* and *H. schwetzi*; see pp. 305 and 297 above for the first two species respectively), Trewavas and Thys van den Audenaerde (1964) a fourth (*H. albolabris*) and Penrith (1970) a fifth (*H. buysi*).

My revision of this material indicates that probably several lineages are represented within it, and that Regan's (1922a) re-definition of *H. acuticeps* (Steindachner) embraces at least two species. Some of the Angolan species seem to show affinity with the genus *Astatotilapia*, others with *Chetia* and some may represent lineages yet unrecognized. But, until the species can be revised and reviewed on the basis of more extensive, better preserved and better documented collections I believe that it is inadvisable to place any species in the genera recognized in this paper. It is certainly impossible to demonstrate that the Angolan species are more closely related to one another than to any other lineage, although intuitively one recognizes, in at least some species, an 'Angolan facies' and feels that this overall appearance suggests relationships with the Zambesi-Limpopo genera.



Trewavas' (1964) phyletic diagram illustrating the possible relationships of '*Serranochromis*' and '*Sargochromis*' indicates that a number of Angolan '*Haplochromis*' species are related to '*Serranochromis*' (i.e. the subgenus *Serranochromis* (*Serranochromis*) as defined on p. 299). I can find no synapomorph characters to support this supposition. The very faint traces of anal fin markings left on the holotype of *H. welwitschii* suggest that they may be of the *Serranochromis*-*Chetia*-*Pharyngochromis* pattern but this is probably a plesiomorph feature. Where anal fin markings are detectable in the other species mentioned by Trewavas (1964), for example *H. lucullae*, they appear to be of the true ocellar type and thus a derived feature not represented in *Serranochromis*.

The number of vertebrae (especially the abdominal elements) in *H. welwitschii* and the other Angolan species is lower than that in *Serranochromis* (although within the range for *Chetia*) and again represents a plesiomorph condition.

Other characters and character states are equally lacking in shared apomorph features, or represent autapomorphies characterizing the Angolan taxa alone.

As a temporary expedient I can only suggest that the Angolan species be given no formal generic status and that they should be referred to under the informal epithet '*Haplochromis*', whose use in no way implies a close relationship with the species of *Haplochromis* (or, indeed, the majority of species previously referred to that genus).

### Summary and conclusions

I am well aware of the shortcomings in this preliminary attempt to clarify the phylogenetic relationships of '*Haplochromis*'-group cichlids, and in particular members of that manifestly polyphyletic 'genus' *Haplochromis*.

Two major difficulties were encountered, and although one has been overcome to a greater or lesser degree, the other still stands in the way of a fully phylogenetic classification. The first difficulty lies in determining morphocline polarity amongst the characters available for research of this kind (p. 270). Then, when plesiomorph and apomorph features are recognized, there is the problem caused by an apparent absence of synapomorphic features at the various levels of relationship necessary to construct a truly cladistic classification.

In other words, one can identify fairly readily what appear to be monophyletic lineages, but the difficulties arise when one attempts to interrelate the different lineages on a sister-group basis.

The problem is well exemplified by the genera *Ctenochromis*, *Thoracochromis* and *Orthochromis*. All three taxa share the presumably derived feature of an abrupt size-change between the scales on the thoracic and ventrolateral flank regions of the body (see p. 270), and thus are assumed to share, at some level, a common ancestry. Both *Orthochromis* and *Ctenochromis*, but not *Thoracochromis* exhibit derived features that are unique for each genus (i.e. autapomorphies) but there are no synapomorphic characters that would indicate which two of the three genera are more closely related to one another. Since *Thoracochromis* shows only one apomorph feature common to all its species it is, presumably, the least derived member of the trio.

Similar difficulties arise with *Haplochromis*, *Astatotilapia* and *Astatoreochromis*, taxa which appear to be interrelated (along with the components of the Victoria-Edward-Kivu species flock) only on the basis of their possessing true ocellar spots on the anal fin of male fishes (p. 274). *Haplochromis* and *Astatoreochromis* (and each of the major lineages in the Victoria flock) have clear-cut autapomorphic features; *Astatotilapia*, apparently, has none. Again one is left with an unresolved polychotomy, but in this case, because the lake flocks are involved, a far more complex one.

Finally, but in a rather different category, since no unifying synapomorphic characters have been detected, are the genera *Chetia*, *Pharyngochromis* and *Serranochromis*. Intuitively the taxa would seem to be interrelated (as they have been assumed to be by other workers, e.g. Trewavas, 1964), probably because of their similar overall morphology, coloration, and the repeated occurrence of enlarged pharyngeal mills amongst their constituent species; in addition, the species form a well-defined, Zambesian geographical group. Yet, I have failed to substantiate their presumed relationship because there are no apparently derived features common to all three

genera (see p. 312). Of course, my interpretation of one shared feature (the non-ocellate, and very numerous anal spots) as a primitive condition may be incorrect (see p. 275); only further research, especially comparative ethological research, can clarify that point.

Further research is also needed to test the phylogenetic homogeneity of the speciose lineage *Thoracochromis* (see above and p. 294). As yet no way has been found to test the possibility, indicated by certain morphological features, that there are three infragroups represented in the lineage, viz. one in Lake Turkana, another in the Nile and Lake Albert (including also the outlier species from Lake Edward and possibly Lake Victoria), and a third from the Zaire river system.

Despite these limitations I believe that the classification suggested here is a more efficient one than that existing at present (the term 'efficient' used *sensu* Patterson & Rosen (1977 : 158–159) to denote a classification from which a '... theory of relationships is recoverable... without loss of information'). Clearly its efficiency can be improved, but that must await the phyletic analysis of 'Haplochromis'-group species in the Great Lakes, especially those of Lakes Malawi and Victoria.

It has been generally assumed (see Regan 1921*b*; Trewavas, 1935; Fryer & Iles, 1972) that the Malawi 'Haplochromis'-group species were derived from an anatomically generalized fluviatile 'Haplochromis' (i.e. *Astatotilapia*) species. I now suspect, however, that the story is far more complex, that the Malawi flock is probably of polyphyletic origin and that lineages related to *Thoracochromis* as well as to *Astatotilapia* and even to *Serranochromis* and *Chetia* may have contributed to the flock. Possibly some of the ideas put forward in this paper may contribute to the elucidation of that problem.

Likewise the assumed monophyly of the Lake Victoria 'Haplochromis' species flock (Greenwood, 1974*a*) must be thrown into doubt, because no characters have been found to support this concept (see p. 269). As compared with Lake Malawi, however, it does seem more likely that fewer and phyletically more closely related lineages were involved, and that most are related to the *Astatotilapia* lineage.

Geographically, the different lineages dealt with in this paper have interesting patterns of distribution.

*Thoracochromis* is essentially a Nilotic–Zairean taxon (see p. 294). Unlike the others with Zairean representatives (see below), it is best represented in the lower reaches of that river, since only one species (*Th. moeruensis*) is recorded from the upper Zaire system (see p. 293).

The virtual absence of *Thoracochromis* from Lakes Victoria, Edward and Kivu is, on the basis of its overall distribution, rather surprising. Possibly this is attributable to the relatively recent association between these lakes and the Nile system (see Beadle, 1974 : 139–146; Greenwood, 1974*b* and 1976; Berry, 1976; Livingstone, 1976; Rzóska, 1976*a* & *b* : 2–29). Lake Turkana and, as far as can be told, Lake Albert as well, have only ever had major and direct interconnections with the Nile system; the geologically recent riverine connection between Lakes Albert and Victoria probably is made impassable to fishes by the presence of the Murchison Falls (now Kabalega Falls), and the connection between Lakes Edward and Albert via the Semliki river also seems to be impassable for most fishes (see discussions in Greenwood, 1959*b*, 1973 and 1976; also Rzóska, 1976*c* : 197–202).

*Astatotilapia*, apart from its outliers in North Africa (*A. desfontainesi*), Syria and Israel (*A. flavijosephi*) and possibly in Nigeria (see p. 283), is essentially a lineage of the eastern Rift Valley (except Lake Turkana) and the rivers of eastern Africa; it is represented in the Zaire drainage only by its species in Lake Tanganyika (see p. 284). The absence of *Astatotilapia* from Lake Turkana probably is to be explained through the history of that lake (see above). Far more puzzling is the occurrence of two *Astatotilapia* species north of the Sahara (Tunisia, Algeria, Syria and Israel), and the possibility of one or two other species in Nigeria. This disjunct distribution may, of course, be the result of incorrectly assessing the phyletic relationships of the outlier species. On currently available evidence, however, there is nothing to suggest how else these outlier species might be interrelated.

*Ctenochromis*, with one exceptional species (*C. pectoralis*) from southeastern Tanzania (Indian Ocean drainage), is totally Zairean (including Lake Tanganyika) in its distribution (see p. 289). *Orthochromis* too is an essentially Zairean lineage and, like *Ctenochromis*, is confined to the upper

parts of that system; it has a representative in the Malagarasi river system of Tanzania, but historically that river should be considered part of the upper Zaire drainage (Poll, 1956). The only outlier species, *Orthochromis machadoi*, occurs in the Cunene river, Angola, a river whose ichthyofaunal affinities are closer to those of the Zambesi than the Zaire (Poll, 1967).

*Serranochromis* is widely distributed (see p. 302), having representatives in the Zaire and Zambesi systems, as well as in the Limpopo and certain Angolan rivers (including the Cunene). Both its Zairean and Zambesi components are confined to the upper portions of their respective systems (cf. the distribution of *Thoracochromis*).

*Chetia* and *Pharyngochromis* have, geographically speaking, the most restricted distributions of all the fluviatile species considered in this paper (apart from *Astatoreochromis* which occurs only in parts of the Malagarasi and Lukuga rivers, in Lakes Edward and Victoria and in some physiographically related water bodies, see p. 286). *Chetia*, a monotypic genus, is confined to the Limpopo drainage system, and *Pharyngochromis*, also monotypic, to the Upper and Middle Zambesi, the Sabi-Lundi system and the Limpopo system.

The only truly lacustrine lineage discussed in this paper, *Haplochromis*, is confined to Lakes Victoria, Edward, George and Kivu. The significance of this distribution, and the possible relationships of the genus, will be discussed in a forthcoming revision of the lineages from those lakes.

### Key to the genera

*Notes* (i) When citing the range for meristic characters, values rarely encountered are given in square brackets and precede or follow, respectively, the most frequently recorded low and high values for that character.

(ii) Modal values (or modal ranges) are in bold type and enclosed in round brackets.

(iii) Gill raker counts are for the outer row of rakers on the lower part of the arch, and do not include the raker (if such is present) on the epi-ceratobranchial articulation.

(iv) For further notes, and definitions of the characters used see pp. 270-276.

### Key

A gradual change in size between the scales on the chest (i.e. ventral and ventrolateral body region anterior to the insertions of the pectoral and pelvic fin bases) and those on the ventral and ventrolateral aspects of the flanks and belly (see Fig. 1) . . . . . 1

An abrupt size change between the small scales on the chest and the larger scales on the ventrolateral and ventral aspects of the body, the size demarcation line usually running between the pectoral and pelvic bases (but sometimes a little before or behind that level; see Figs 2, 3 & 9) . . . . . 2 (p. 316)

1) (a) Anal fin in adult males with 3-9 (**3 or 4**) ocelli (coloured spots each with a clear or translucent area surrounding it) arranged in one or two lines and lying about midway between the base and the distal margin of that fin. (Most females and juvenile males with 3 or 4 non-ocellate spots in the same position, or fin without spots.) Scales below (and often those above) the upper lateral line ctenoid, the ctenii arranged along almost the entire free margin of the scale. Anal fin with 3 spines (individuals with 4 spines are so rare that this number can be considered as an individual abnormality). Dorsal fin rarely with more than 16 spines. Marked sexual dimorphism in adult coloration (males colorful, females drab) . . . . . A

(b) Anal fin in adult males with 6-20 ocelli arranged in 3-5 regular rows and thus occupying a large area on the soft part of the fin; females with a similar pattern if spots (non-ocellate) are present. Anal fin with 3-6 spines, dorsal fin with 16-20 (**17-19**) spines. Caudal fin rounded. Lower pharyngeal bone thickened (strongly so in two species), its dentition partially or completely molarized. No marked sexual dimorphism in coloration; body colour yellow-green, fins with a maroon flush. Other features as in 1(a) above *Astatoreochromis* (p. 285)

(c) Anal fin in both sexes with numerous (18-40) small spots, none with a clear or translucent surround, not arranged in regular rows but covering most of the area of the soft anal fin; similar spots on the soft dorsal and the caudal fins. Scales below the upper lateral line are cycloid or predominantly cycloid; when ctenoid scales are present the ctenii are weak and confined to a small median sector on the free margin of the scale. . . . . B

- A) (i) Jaw teeth in the outer row (and sometimes the inner rows as well) with obliquely cuspidate compressed crowns, the major cusp drawn out beyond the tooth's vertical axis (see Fig. 7), the minor cusp reduced or absent. 12–14 (13) abdominal and 15 or 16 caudal vertebrae (total 28–30; 28 and 29). Dorsal fin with 14–16 (15 and 16) spines and 8–10 (9) branched rays. Anal fin with 3 spines and 7–10 (9) branched rays. Lateral line with 29–34 (30–32) scales. Cheek with 3 [4] horizontal rows of scales. Caudal fin truncate or weakly subtruncate. Lower pharyngeal bone without any noticeably enlarged or coarse teeth in the two median rows. Gill rakers [7] 8–10 (9) . . . . . *Haplochromis* (p. 278)
- (ii) Jaw teeth in the outer row unequally bicuspid or unicuspid, the crown neither compressed nor obliquely truncate, its tip lying within the tooth's vertical axis (see Fig. 4). Outer teeth mostly bicuspid in fishes <70 mm SL; an admixture of bi- and unicuspid in larger fishes, with unicuspid predominating in specimens >100 mm SL. Inner teeth predominantly tricuspid, small. 12–14 (13) abdominal and 14–16 (15) caudal vertebrae (total 27–30; 28 and 29). Dorsal fin with 14–16 (15) spines and 8–11 (9 and 10) branched rays. Lateral line with 28–30 (in one species 31–34) scales, cheek with [2], 3, [4] horizontal rows of scales. Caudal fin rounded or slightly subtruncate. Lower pharyngeal bone with at least the two median rows composed of coarser (sometimes molariform) teeth. Gill rakers [7] 8 or 9 . . . . . *Astatotilapia* (p. 281)
- B) (i) Abdominal vertebrae 13 or 14 (14), caudal vertebrae 15 or 16 (15), total number of vertebrae 29 or 30 (29). Dorsal fin with 14 or 15 (14) spines and 10–12 (11) branched rays. Lateral line with 32–34 (32 and 33) scales, cheek with 4 or 5 horizontal rows. Outer row of jaw teeth composed of unequally bicuspid in fishes <60 mm SL, unicuspid present and becoming commoner in larger individuals. Lower pharyngeal bone thickened, at least the two median rows composed of enlarged and molariform teeth (see Fig. 20). Gill rakers [7 or 8] 9 or 10. Anal fin with up to 20 spots . . . . . *Pharyngochromis* (p. 310)
- (ii) Abdominal vertebrae 14 or 15, caudal 15–17 (16 and 17), total number of vertebrae 30–32 (31). Dorsal fin with 14 or 15 spines and 11 or 12 branched rays. Lateral line with 34 or 35 scales, cheek with 5 or 6 horizontal rows of scales. Outer row of jaw teeth mainly unicuspid in fishes >30 mm SL, some weakly bicuspid (the minor cusp a shoulder rather than a point) present in smaller individuals. Lower pharyngeal bone not thickened, without molariform or submolariform teeth (see Fig. 19). Gill rakers 9 or 10 . . . . . *Chetia* (p. 307)
- (iii) Abdominal vertebrae [15] 16–18 [19] (16 and 17), caudal vertebrae 12–16 (14 and 15), total number of vertebrae 28–32 (31). Dorsal fin with 13–16 (15 and 16) spines and 11–16 (12 and 13) branched rays. Lateral line with 28–34 (30 and 31) scales, cheek with 3–6 (3–5) horizontal rows of scales. Outer jaw teeth mostly unequally bicuspid in fishes <150 mm SL, predominantly unicuspid in larger individuals. Lower pharyngeal bone thickened in all but one species, and in all but that species with at least the two median tooth rows composed of enlarged and molariform teeth (see Fig. 18); the exceptional species has coarse and slightly enlarged, but cuspidate, teeth in the median rows (see Fig. 18A), Gill rakers 9–15 (12 and 13). Anal fin with up to 40 spots. . . . . *Serranochromis (Sargochromis)*; p. 303
- (iv) Abdominal vertebrae [15] 16–18 [19] (16 and 17), caudal vertebrae [15] 16–18 (16 and 17), total number of vertebrae 31–36. Dorsal fin with 13–18 (15 and 16) spines and 13–16 (14–16) branched rays. Lateral line with [34] 35–41 scales, cheek with 3–11 (5–9) horizontal rows of scales. Outer jaw teeth predominantly or entirely unicuspid in fishes >30 mm SL. Lower pharyngeal bone not thickened, either elongate and narrow (see Fig. 14A & B) or its dentigerous surface almost equilateral in outline (see Fig. 14C); no teeth molariform, even the median row teeth only slightly coarser than the others. Gill rakers [8] 9–13 (10–12). Anal fin with up to 40 spots . . . . . *Serranochromis (Serranochromis)*; p. 299
- 2) (a) Pelvic fin with the first branched ray the longest. Scales on ventral body surface behind pelvic fins not markedly reduced in size (see Fig. 9) . . . . . 2A
- (b) Pelvic fin with the second or third branched ray the longest. Scales on ventral body surface and on ventrolateral aspects of flanks small to minute (see Fig. 3). Cheek naked or, if scaled, with a definite naked area along its entire ventral (preopercular) margin. Chest

completely scaled, or partly scaled, or naked. Dorsal fin with 16–20 (17 and 18) spines and 9–11 (9 or 10) branched rays. Anal fin with 3 or 4 spines and 7–10 branched rays. Lateral line with 30–35 (30 and 31) scales. Head profile strongly decurved, eyes suprolateral in most species . . . . . *Orthochromis* (p. 295)

- 2A) (i) Chest with a naked patch or extensive naked area on each side of the body (see Fig. 9). At least the ventral part of the cheek scaleless (almost the entire cheek naked in one species). Anal fin with 3 spines and 6–9 (6–8) branched rays. Lateral line with 27–33 (28 and 30 or 31) scales . . . . . *Ctenochromis* (p. 287)
- (ii) Chest completely scaled. Cheek completely or almost completely scaled (i.e. one horizontal row absent ventrally). Dorsal fin with 13–16 [17] (14–16) spines and 8–10 [11] (9 and 10) branched rays. Anal fin with 3 spines and 6–10 (7–9) branched rays. Lateral line with 29–32 (30–32) scales . . . . . *Thoracochromis* (p. 290)

## Appendix 1

### A replacement 'generic' name for the Lake Malawi '*Haplochromis*' species

Since the genus *Haplochromis* is now restricted to five species, all members of the Lakes Victoria, Edward, George and Kivu species flock (p. 280), the Lake Malawi species formerly referred to *Haplochromis* are without a generic name. Because it is obvious that the '*Haplochromis*' of Lake Malawi are a polyphyletic group, any generic placement at the present time must be considered merely a formal nomenclatural action unrelated to the phyletic affinities of the species.

Two generic names would appear to be available for this purpose (see Trewavas, 1935), namely *Cyrtocara* Boulenger (1902) and *Champsochromis* Boulenger (1915). A third name, *Otopharynx*, Regan (1920), apparently is also available, but it is junior to the others and there are anatomical grounds for regarding its contained species as representing a lineage distinct from that to which many Malawi '*Haplochromis*' belong (Greenwood, 1978).

*Cyrtocara* (type species *C. moori*) has a pharyngeal apophysis of the typical '*Haplochromis*'-type (Trewavas, 1935) and its oral dentition is composed of slender unicuspid outer teeth and mixed uni- and tricuspid inner teeth.

Although at least some members of the type species have a moderately developed hump in the frontal region of the head, I can see no morphological grounds for not accepting *Cyrtocara* as a temporary formal name for the '*Haplochromis*' species of Lake Malawi. I thus propose that it be used in that capacity until the Malawi species are revised. This action by no means implies that I consider many of these species to have a true phyletic relationship with *Cyrtocara moori*.

## Appendix 2

### The taxonomic status of the genus *Limnotilapia* Regan, 1920

In a recent paper (Greenwood, 1978) I treated the genus *Limnotilapia* Regan (1920) as a synonym of *Simochromis* Boulenger, 1898, thus unintentionally anticipating the publication of a paper giving detailed reasons for this nomenclatural change. Since publication of the paper in which the two 'genera' are to be discussed is likely to be delayed further, the reasons for synonymizing *Limnotilapia* with *Simochromis* are dealt with below.

A comparison of Regan's (1920) description for *Limnotilapia* with his redescription of *Simochromis* reveals that the taxa apparently are differentiable only on the former having a rather small, terminal mouth, and the latter having the mouth subterminal and rather wide.

When the type species of the genera, *Limnotilapia dardennii* (Blgr.) and *Simochromis diagramma* (Günth.), are compared, these differences can be translated into more substantial osteological ones involving the morphology of the premaxilla and dentary.

Viewed from below (i.e. occlusally), the premaxillary outline in *L. dardennii* is gently curved and relatively narrow; in other words, it has an outline approximating to that of a Norman arch. The premaxillary outline in *S. diagramma*, by contrast, has a virtually straight and wide anterior margin, with the short posterior dentigerous arms meeting it almost at right angles; the outline

of the bone is thus more nearly that of a hollow square. The posterior dentigerous arms of the premaxilla in *S. diagramma* are slightly bullate, whereas in *L. dardennii* they are slender and compressed.

There are, of course, comparable interspecific differences in the occlusal outline of the dentary. In *Limnotilapia dardennii* the lateral arms of the dentary are protracted relative to the transversely directed anterior part of the bone, and the outline of the whole bone is similar to that of the premaxilla. In *Simochromis diagramma* the dentary, like the premaxilla, is foreshortened, with the short lateral dentigerous arms (about equal in length to the transverse part) meeting the slightly curved transverse portion at almost a right angle. The dentary in *S. diagramma* also differs from that of *L. dardennii* in having virtually no upward sweep to its coronoid portion; in *L. dardennii* this region slopes upward at a gentle but noticeable angle.

Seen in these terms, the osteological 'morphological gap' separating the taxa would appear to be a more substantial one than that expressed in Regan's (1920) key and generic synopsis. But, the 'gap' is bridged when one examines the premaxilla and dentary of *Limnotilapia loocki* Poll, 1949 (see Poll, 1956 : 62, fig. 10 for an expanded description of the species, and illustrations of the jaws and dentition).

The morphology of both these bones in *L. loocki* is virtually intermediate between those in *L. dardennii* and *S. diagramma*. Thus, it is impossible to differentiate the 'genera' on the osteological features characterizing the jaws of the type species. Furthermore, the external oral characters used by Regan (1920) also intergrade when growth-series of the type species are examined, and I have been unable to detect other characters that might serve to distinguish the taxa (it being understood that the 'genera' are being interpreted here, as they were by Regan, merely on the presence of a discrete morphological gap that is 'greater' than one which might be used to characterize species). There would, therefore, seem to be no grounds for treating *Limnotilapia* and *Simochromis* as distinct genera, the more so when one considers the various (and apparently synapomorphic) features that are shared by all but one of their included species.

*Limnotilapia loocki* (like *L. dardennii*, *Simochromis diagramma*, *S. babaulti* Pellegrin, *S. curvifrons* Poll and *S. marginatus* Poll) has, in both jaws, slender-shafted, recurved, outer teeth with markedly compressed and expanded, obliquely bicuspid crowns, a greatly reduced (or absent) interspace between the numerous inner and single outer tooth rows in both jaws, a densely toothed lower pharyngeal bone (the teeth fine and compressed) and a strongly decurved anterior profile to the neurocranium (where, in some species, the ethmovomerine region is almost vertically inclined). In all these species, too, the chest scales are small, deeply embedded and have an abrupt size demarcation with the larger scales on the anterior abdominal region of the body.

For the moment it is these apparently apomorphic features which should be used to define the genus *Simochromis* Blgr., 1898 (with which is now included, as a junior synonym, the genus *Limnotilapia* Regan, 1920).

The one species not included in the character analysis given above is *Limnotilapia trematocephala* (Blgr., 1901), a taxon known only from its holotype. I have not, of course, been able to examine all the relevant osteological features in this specimen, but its relatively sparsely toothed lower pharyngeal bone, the morphology of its outer row jaw teeth (which are without noticeably compressed, expanded and obliquely bicuspid crowns, and which are not strongly recurved), and its relatively large pectoral scales, all suggest that the species probably belongs to a different lineage and should not, therefore, be included in the genus *Simochromis*.

For the moment it is impossible to indicate the phyletic relationships of the genus *Simochromis*, either within or without the cichlid flocks of Lake Tanganyika. Much further research will be required before this can be achieved (and will also be needed before a generic placement of '*Limnotilapia*' *trematocephala* can be effected).

As was noted in my paper on the pharyngeal apophysis in African cichlids (Greenwood, 1978), *Simochromis dardennii* has a near-typical *Tilapia*-type of apophyseal structure. *Simochromis loocki*, on the other hand, has an apophysis of the modified *Tropheus*-type; the basioccipital is inflated and bullate, with its ventral tip almost reaching the level of the parasphenoidal facets but not contributing in any way to the articular surface provided by these facets. In its general organization, the apophysis in *S. loocki* is intermediate between the *Tilapia* and *Tropheus* types

(see Greenwood, 1978), but differs from the modal condition of both types in having the basioccipital noticeably inflated.

Since *S. dardennii* (with a *Tilapia*-type apophysis) has the least specialized premaxillary and dentary of any *Simochromis* species, and since *S. babaulti* and *S. diagramma* have the most derived jaws (the species having, respectively, *Tropheus* and near *Haplochromis* type apophyses; see Greenwood, 1978), it is tempting to conclude that in this lineage the *Tilapia*-type apophysis is the plesiomorph one. That *S. loocki* (whose jaw morphology is intermediate between that of *S. dardennii* and those of the other *Simochromis* species) has an apophysis intermediate between the *Tilapia* and *Tropheus* types, would also seem to support this hypothesis.

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<i>H. albertianus</i>	293	290	<i>H. greenwoodi</i>	304	303
<i>H. albolabris</i>	312	312	<i>H. horii</i>	289	287
<i>H. angolensis</i>	312	312	<i>H. humilis</i>	312	312
<i>H. annectidens</i>	280	278	<i>H. limax</i>	280	278
<i>H. astatodon</i>	280	278	<i>H. lividus</i>	280	278
<i>H. avium</i>	293	290	<i>H. loati</i>	293	290
<i>H. bakongo</i>	293	290	<i>H. luluae</i>	289	287
<i>H. bloyeti</i>	283	281	<i>H. macconneli</i>	293	290
<i>H. burtoni</i>	284	281	<i>H. machadoi</i>	297	295
<i>H. buysi</i>	312	312	<i>H. mahagiensis</i>	293	290
<i>H. callipterus</i>	284	281	<i>H. mellandi</i>	305	303
<i>H. carlottae</i>	305	303	<i>H. moeruensis</i>	293	290
<i>H. codringtoni</i>	305	303	<i>H. mortimeri</i>	305	303
<i>H. coulteri</i>	304	303	<i>H. multiocellatus</i>	312	312
<i>H. darlingi</i>	311	310	<i>H. nubilus</i>	283	281
<i>H. demeusii</i>	293	290	<i>H. obliquidens</i>	280	278

*H. oligacanthus* 289 287  
*H. pectoralis* 289 287  
*H. petronius* 293 290  
*H. pharyngalis* 293 290  
*H. polli* 289 287  
*H. polyacanthus* 297 295  
*H. rudolfianus* 293 290  
*H. stappersi* 284 281  
*H. straeleni* 286 285  
*H. swynnertoni* 284 281  
*H. thysi* 305 303  
*H. torrenticola* 297 295  
*H. turkanae* 293 290  
*H. vanderhorsti* 286 285  
*H. welwitschii* 312 312

*H. wingatii* 293 290  
*Orthochromis malagaraziensis* 297 295  
*Paratilapia toddi* 294 294  
*Rheohaplochromis torrenticola* 297 295  
*Sargochromis codringtoni* 305 303  
*S. mellandi* 305 303  
*Serranochromis angusticeps* 302 299  
*S. janus* 303 299  
*S. longimanus* 302 299  
*S. macrocephalus* 302 299  
*S. meridionalis* 303 299  
*S. robustus* 302 299  
*S. spei* 302 299  
*S. stappersi* 302 299  
*S. thumbergi* 302 299